Effect of phosphate application levels on soybean [*Glycine max* [L.] Merr.] seed yield, elements and storage protein composition.

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Summary

Various levels of P application were imposed to hydroponically grown soybean plants, and the concentrations of mineral elements and storage protein composition in the matured seeds were analyzed. Non-nodulating (cv T201) and nodulating (cv Enrei) soybean plant were cultivated with nitrate ($NaNO_3$) and fix-N as solo nitrogen source, respectively. Application of phosphate increased P and reduced N concentration in seeds both non-nodulating and nodulating soybean plants. This result indicated that seed mineral composition could be changed by phosphate application irrespective of nitrogen source.

Low level phosphate (5μM-P) application to the non-nodulating soybean plants increased β-conglycinin, a major storage protein in soybean seed, concentration in seed compared with normal level of P (25μM-P) irrespective of nitrate application level. In the nodulating soybean plants, the concentration of β-subunit of β-conglycinin was decreased by high level of P (50μM-P) application both all through plants growth and increasing P level after flowering.

In conclusion, P application on soybean plants changed mature seed mineral composition and protein composition irrespective of N nutrition.

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Key words : soybean, seed, mineral composition, storage protein, phosphate application,

Introduction

In higher plant, P is important mineral fertilizer same as N and K. When P was absorbed from soil, unlike nitrate and sulfate, phosphate is not reduced in plants but remains in its highest oxidized form. After uptake, at physiological pH, P is mainly as $H_2PO_4^-$ form and transferred mainly young organs rapidly, then combined into high energy or ester compounds. P absorption altered by environmental pH or anion and cation balance. On the other hand, after P uptake the distribution could be changed by plant nutrition statue and growth stage.

Previous report, when non-nodulating soybean plants cultivated under N deficient condition, mineral element compositions, especially P and N, of mature seeds was different from nodulating soybean plants. Furthermore, these N deficient plants lack one of the storage protein subunit, β-subunit of β-conglycinin. The soybean seed storage protein comprises mainly of β-conglycinin and glycinin. β-Conglycinin is composed of α'-, α-, and β-subunits, and glycinin is composed of acidic and basic subunits. These storage proteins are accumulated in protein bodies in the cotyledon cells throughout the seed developing stage. Further studies indicate N nutrition greatly influences soybean seed storage protein composition (Ohtake et al.1996, Krishnan et al. 2000).

The relationship N and P was not uncertainly. In soybean seed, phytate commonly forms one to several percent of seed dry weight and is a major store of P, commonly forming 50 to 80% of total seed P (Lott, 1984). Significant amounts of phytic acid are localized in the crystalline globoid inclusions within protein bodies (Prattley and Stanley 1982). We assume that there is a possible way to change N concentration by P application in seeds without decreasing seed yield. In this report, we investigated various level of phosphate application to hydroponically grown soybean plants on the seed mineral concentration and protein composition using non-nodulating and nodulating soybean.

Materials and methods

Experiment 1

Non-nodulating soybean plants (*Glycine max* [L.] Merr. cv. 'T201') were hydroponically cultivated in a green house (Ohtake et al. 1996) and low (25 μM) and medium (25 μM) phosphate treatments were imposed. The chemical composition of the culture solution except for P and N was as follows (mg l^{-1}): K_2SO_4 (109), KCl (7.854), $CaCl_2 \cdot 5H_2O$ (184),

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$MgSO_4 \cdot 7H_2O$ (123), H_3BO_3 (0.367), $CuSO_4 \cdot 5H_2O$ (0.032), $MnSO_4$ (0.189), $ZnSO_4 \cdot 7H_2O$ (0.144), $(NH_4)_6Mo_7O_{24}$ (0.004), $NiSO_4 \cdot 6H_2O$ (0.0035), $EDTANa_2$ (14.6), $FeSO_4 \cdot 7H_2O$ (14.9). Two levels of phosphate at 5 µM or 25µM were applied as sodium hydrogen phosphate (adjust pH6.0). Each phosphorus treatment, nitrate was supplied at 1mM, 2.5mM or 5mM until maturity.

Experiment 2

A nodulating popular soybean (cv. 'Enrei') seeds inoculated with *Bradyrhizobium Japonicum* stain USDA110 were germinated and grown in vermiculite for a week and then subjected to hydroponically culture. The basal culture medium without N was the same as above, that contains medium level of 25 µM P (referral to as the 25 µM-P treatment). High P treatment was increased phosphate concentration at 50 µM (sodium hydrogen phosphate, adjust at pH6.0, referral to as the 50 µM-P treatment). During the pod filling stages, some of the soybean shoots were sprayed with a phosphate fertilizer solution (Koei Chemical Co., Japan, Nagoya) once a week until yellow leaves stage. This phosphate fertilizer contained 55 % (w/w) phosphate and 15% (w/w) magnesium. About 100 mL of 500 times diluted solution was sprayed for each plant (referral to as the 3.5 µM-P spray treatment). At flowering stage control 3 plants with 25 µM treatment were changed to the culture solution with 50 µM P (referral to as the 25 to 50 µM-P treatment) until maturity.

Chemical analysis

Soybean seeds with each treatment were counted, lyophilized, and weighted then ground into a fine powder. Fifty mg of sample powder was digested by Kjeldahl method. N and P concentration was measured by colorimetric methods (Ohyama et al. 1993). Another 50 mg of samples were digested with HNO_3 and $HClO_4$ (Mizukoshi et al. 1996) and Ca, Mg and K concentrations were measured using atomic absorption spectrometry (Hitachi Co., Japan, Z-8200). The SO_4^{2-} concentration of the second digested solution was measured using capillary electrophoresis (Waters Co., U.S.A., Quanta 4000E) (Sato et al. 1999). Protein extraction and SDS-PAGE analysis was conducted the same as described previously (Ohtake et al. 1996).

Result

Effect of low and medium P treatments on mineral elements and mature seed storage protein composition in non-nodulating soybean plant with three level of N

When the plants were supplied with 5µM-P with 2.5 mM or 5mM nitrate, the plants exhibited a slight phosphorus deficiency, and the seed yield was only half of the seeds with 25µM-P. In 1mM nitrate treatment plants, it appeared more seriously N deficient both 5- or and 25µM-P treatments. When 1mM nitrate was supplied, seed yield was not significantly different by low and medium P levels, only 12.6g and 12.0g with 5µM-P and 25µM-P treatments respectively (Table 1). In 1mM NO_3^- supply, N should be a limiting for plant growth and seed yield and P did not influence the yield, seed number and one seed weight. When 2.5mM or 5mM nitrate was supplied as N source, 25µM-P treatment dramatically increase seed yield. The promotive effect was due to the increase in seed number rather than one seed weight. In the case of 2.5mM or 5.0mM nitrate supply, P might be a limiting factor for seed yield and 5µM-P is not sufficient to support the vigorous growth by assimilating a large amount of N. The result that seed yield, seed number and one seed weight were nearly the same between 2.5 mM and 5mM nitrate conditions indicates that 2.5mM nitrate might be sufficient as N source under the experimental conditions.

The chemical compositions of the seeds with N, P treatments in Exp. 1 is shown in Table 2. The P concentration in the seeds with 5µM-P treatment was significantly lower than those in 25µM-P treatment irrespective of N concentration. Nitrogen concentration in the seeds treated with 1mM nitrate was significantly lower than 2.5 mM and 5.0 mM nitrate treated seeds.

The concentrations of Ca and K in the mature seed tended to be lower in 5µM-P than 25µM-P treatment (Table 2). Alternatively, N concentration of seed was significantly ($p<0.01$) high by the supply of 5µM-P compared with 25µM-P. The K, P Ca and Mg concentrations are similar irrespective of phosphate concentration, the concentration in the seed was tended to decrease with increase of nitrogen supply from 1mM to 2.5 mM. The S concentration was relatively constant among N, P treatments. Fig. 1A and 1B shows the

Table 1. Seed number, dry weight and yeild of T201 cultivated under various N and P conditions

Medium		Seed Yeild		Seed number		Seed weight	
N Conc.	P conc.	(g $plant^{-1}$)		(numbers $plant^{-1}$)		(mg $seed^{-1}$)	
1.0mM	5µM	12.6	(1.7)	86.3	(4.9)	145.7	(15.5)
	25µM	12.1	(1.7)	86.0	(6.0)	140.3	(8.5)
2.5mM	5µM	18.7	(2.0)	105.0	(4.7)	177.7	(8.1)
	25µM	34.2*	(5.8)	200.0*	(14.8)	154.3*	(13.2)
5.0mM	5µM	15	(1.2)	83.3	(3.2)	179.7	(9.3)
	25µM	35.3*	(4.9)	204.7*	(14.5)	172.0	(12.3)

Values in parentheses indicate standard deviations of means (n=3).
Statistical significance of difference between 5mM-P and 25mM-P plants. *:$p<0.05$, **:$p<0.01$

relationship between element concentrations versus N (1A) or P (1B) concentration in the seeds. It is obvious that P and N show negative correlation. The K, Ca, Mg and S concentrations were relatively constant, but those tended to decrease slightly with N concentration although those tended to increase with P concentration.

The concentration of each storage protein subunit is shown in Table 3. By the low P (5mM) supply in the same N concentration, the concentration of β-conglycinin, especially b-subunit was significantly higher than those in 25mM-P treatment (P<0.01). In 5 mM-P treatment, there is a little differences irrespective of the nitrate concentrations.

Table 2. Chemical composition of T201 cultivated under various N and P conditions

Medium		Concentration (mg g^{-1})											
N Conc.	P conc.	N		K		P		Ca		Mg		S	
1.0mM	5μM	43.1	(0.2)	20.8	(0.3)	3.93	(0.15)	3.55	(0.21)	2.78	(0.11)	1.05	(0.17)
	25μM	41.1	(1.3)	22.2*	(0.3)	7.69**	(0.33)	4.23	(0.12)	2.78	(0.04)	0.89	(0.03)
2.5mM	5μM	66.9	(0.3)	18.9	(0.1)	2.38	(0.05)	2.99	(0.30)	2.40	(0.11)	0.8	(0.13)
	25μM	51.8**	(1.3)	19.8	(0.3)	4.12**	(0.08)	3.92	(0.05)	2.72	(0.01)	1.19*	(0.06)
5.0mM	5μM	65.3	(1.7)	19.0	(0.0)	2.58	(0.05)	3.35	(0.10)	2.56	(0.04)	0.87	(0.09)
	25μM	54.9*	(2.5)	19.1	(0.2)	3.32*	(0.15)	3.67	(0.12)	2.50	(0.15)	1.14**	(0.10)

Values in parentheses indicate standard deviations of means (n=3).
Statistical significance of difference between 5mM-P and 25mM-P plants. *:p<0.05, **:p<0.01

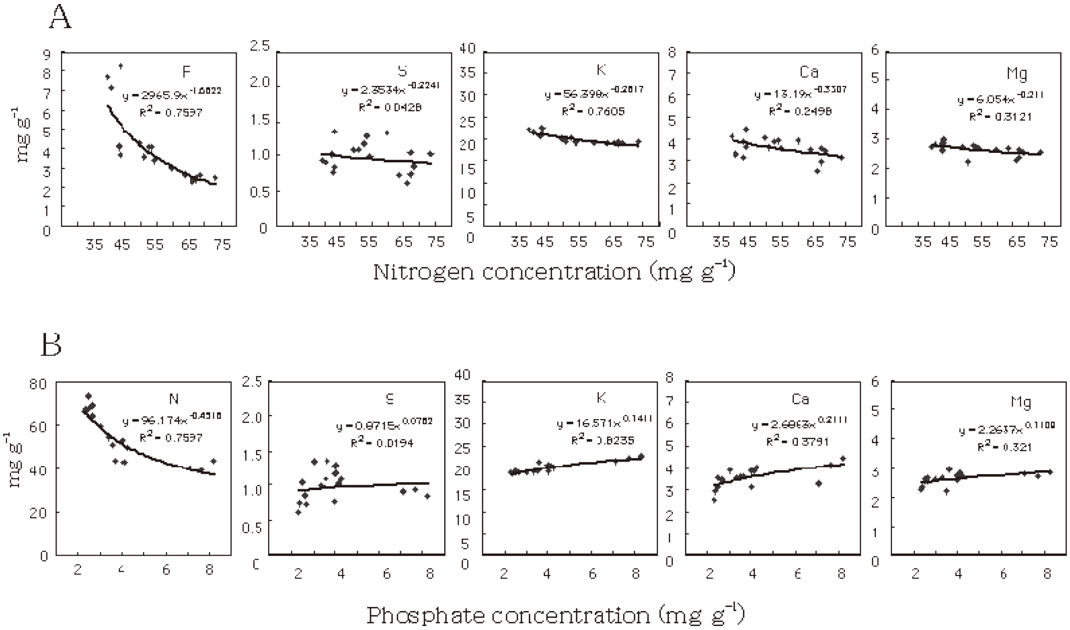

Fig 1. The soybean (cv T201) seed nitrogen (upper panel, A) or phosphate (lower panel, B) concentration compared with other dominant mineral concentrations. The seeds were obtained from non-nodulating soybean plants grown with supplying various N and P concentrations (see materials and methods Experiment 1).

Table 3. Subunit proportions of mature seeds of T201 cultivated under various N and P treatments.

Medium		β-Conglycinin						Glycinin			
N Conc.	P conc.	α'		α		β		Acidic		Basic	
1.0mM	5μM	9.3	(0.8)	12.9	(0.3)	11.3	(0.4)	32.2	(0.9)	34.6	(0.8)
	25μM	8.8	(1.1)	10.3**	(0.1)	7.7**	(0.3)	37.8*	(1.5)	36.7	(0.8)
2.5mM	5μM	11.5	(0.2)	15.4	(0.2)	17.0	(0.9)	29.1	(0.5)	27.0	(0.6)
	25μM	9.7	(0.5)	11.0*	(0.7)	9.8**	(0.6)	34.8**	(0.8)	34.8*	(1.3)
5.0mM	5μM	11.0	(0.1)	16.1	(0.8)	16.3	(0.3)	29.4	(0.4)	27.1	(1.1)
	25μM	9.9	(0.4)	11.4*	(0.2)	11.1*	(0.9)	34.8**	(0.3)	32.8*	(0.6)

Values in parentheses indicate standard deviations of means (n=3).
Statistical significance of difference between 5mM-P and 25mM-P plants. *:p<0.05, **:p<0,01

Effect of two levels of P treatments on mineral elements concentration and seed storage protein composition in mature seed of nodulating soybean plant

Compared with medium P (25μM-P) treatment, the seed number per plant was increased but seed weight was decreased with the high P (50μM-P) and the elevated phosphate concentration from flowering stage (25 to 50 μM-P). On the other hand, the seed number of the plant sprayed with 3.5mM-P on the leaf from pod filling stage (3.5 mM-P spray treatment) was similar to the control plant (Table4).

When a higher concentration of phosphate was added, the nitrogen concentration of the seed from nodulating variety became low (Table 5) in accordance with the result from non-nodulating soybean treated with low and medium P

Table 4. Subunit concentration of mature seeds of T201 cultivated under various N and P treatments.

Medium		β-Conglycinin						Glycinin			
NConc.	Pconc.	α'		α		β		Acidic		Basic	
1.0mM	5μM	24.9	(1.4)	34.2	(1.3)	30.3	(2.0)	86.6	(3.5)	93.2	(4.2)
	25μM	22.6	(5.4)	26.5**	(1.6)	18.5**	(2.4)	97.1	(7.6)	94.4	(8.6)
2.5mM	5μM	48.3	(1.1)	64.2	(1.2)	71.2	(6.5)	121.6	(4.0)	113.0	(4.0)
	25μM	31.2**	(1.9)	35.8*	(5.4)	31.7**	(4.0)	112.6	(8.5)	112.3	(3.7)
5.0mM	5μM	45.0	(2.5)	65.8	(3.6)	66.7	(3.0)	119.8	(5.3)	111.0	(11.9)
	25μM	34.0*	(4.6)	39.1**	(4.0)	38.4**	(7.7)	119.5	(7.9)	112.4	(5.3)

Values in parentheses indicate standard deviations of means (n=3).
Statistical significance of difference between 5mM-P and 25mM-P plants. *:$p<0.05$, **:$p<0.01$
Each subunit concentration was cluculated nitrogen cocentration multiply by 6.25 (mg g^{-1})

Table 5. Seed number, dry weight and yeild of Enrei cultivated under various P conditions

Treatment	Seed Yeild (g plant^{-1})		Seed numbers (number plant^{-1})		Seed weight (mg seed^{-1})	
25mM-P	42.1	(4.5)	131.7	(16.1)	319.9	(6.0)
50mM-P	54.1*	(1.5)	175.0*	(7.1)	289.4*	(3.7)
25 to 50mM-P	44.2	(1.3)	178.3**	(2.9)	258.1**	(8.3)
3.5mM-P spray	41.8	(3.6)	148.3	(12.6)	281.8**	(9.3)

Values in parentheses indicate standard deviations of means (n=3).
Statistical significance of difference between 25mM-P and various P treatments. *:$p<0.05$, **:$p<0.01$

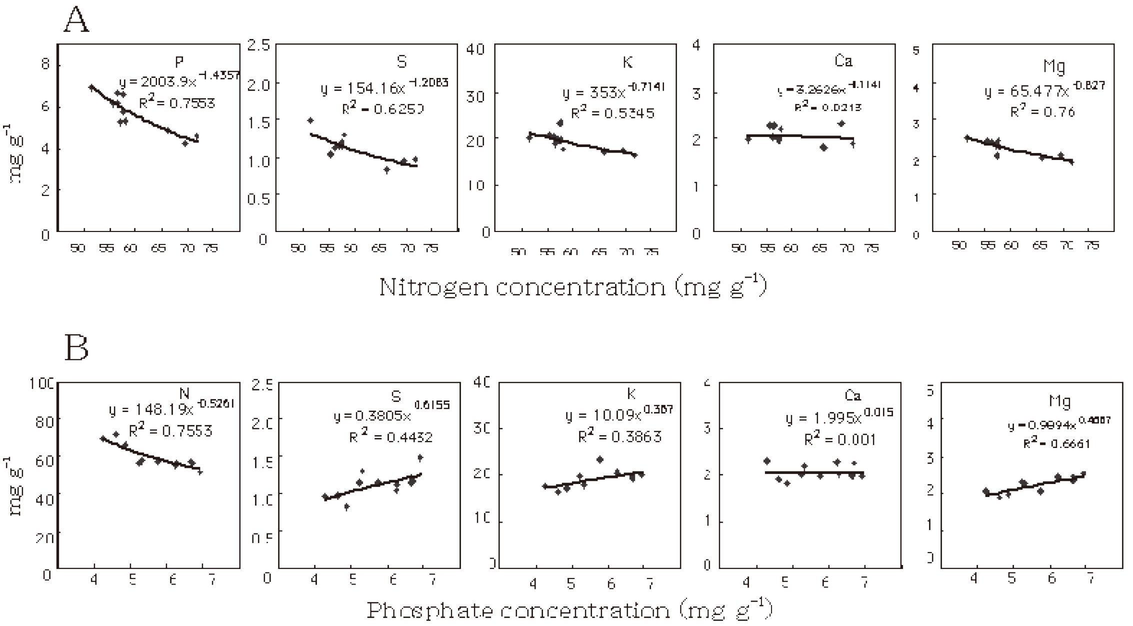

Fig 2. The soybean seed (cv Enrei) nitrogen (upper panel, A) or phosphate (lower panel, B) concentration compared with other dominant mineral concentrations. The seeds were obtained from nodulating commercial cultiver soybean plants grown with supplying various N and P concentrations (see materials and methods Experiment 2).

Table 6. Chemical composition of Enrei cultivated under various P conditions

	Concentration (mg g^{-1})											
	N		K		P		Ca		Mg		S	
25mM-P	69.1	(2.9)	16.3	(1.6)	4.57	(0.31)	2.00	(0.26)	1.97	(0.09)	0.92	(0.08)
50mM-P	56.4**	(1.0)	20.5*	(0.3)	6.24**	(0.03)	2.15	(0.18)	2.41**	(0.03)	1.08	(0.05)
25 to 50mM-P	55.1**	(1.2)	19.4	(0.5)	6.75**	(0.16)	2.07	(0.17)	2.44**	(0.08)	1.28*	(0.18)
3.5mM-P spray	57.4*	(0.5)	20.2	(2.8)	5.43*	(0.28)	2.05	(0.12)	2.21	(0.14)	1.19*	(0.09)

Values in parentheses indicate standard deviations of means (n=3).
Statistical significance of difference between 25mM-P and various P treatments. *:p<0.05, **:p<0.01

Table 7. Subunit relative proportion (%) of mature seeds of Enrei cultivated under various P treatments.

	β-Conglycinin						Glycinin			
	α'		α		β		Acidic		Basic	
25mM-P	5.4	(1.2)	11.8	(2.8)	20.5	(2.2)	30.3	(4.4)	35.1	(2.7)
50mM-P	5.4	(0.5)	12.3	(0.2)	15.8*	(1.7)	25.7*	(1.1)	40.8**	(1.0)
25 to 50mM-P	3.2*	(1.0)	7.8*	(1.1)	10.8**	(1.6)	28.1	(4.1)	50.0**	(4.0)
3.5mM-P spray	4.4	(0.5)	11.4	(1.5)	14.9*	(0.3)	21.9**	(1.2)	47.5**	(2.1)

Values in parentheses indicate standard deviations of means (n=3).
Statistical significance of difference between 25mM-P and various P treatments. *:p<0.05, **:p<0.01

Table 8. Subunit concentration (mg g^{-1}) of mature seeds of Enrei cultivated under various P treatments.

	β-Conglycinin						Glycinin			
	α'		α		β		Acidic		Basic	
25mM-P	22.3	(5.0)	48.1	(11.9)	90.9	(5.5)	130.8	(4.9)	140.0	(3.6)
50mM-P	18.9	(1.5)	43.3	(1.2)	55.9**	(7.0)	90.5**	(3.1)	143.8	(3.2)
25 to 50mM-P	9.3*	(2.6)	23.2*	(2.4)	32.0**	(6.3)	83.8*	(5.8)	148.0	(6.0)
3.5mM-P spray	15.1	(2.6)	39.4	(6.7)	51.2**	(2.7)	75.6**	(7.4)	163.3**	(2.4)

Values in parentheses indicate standard deviations of means (n=3).
Statistical significance of difference between 25mM-P and various P treatments. *:p<0.05, **:p<0.01
Each subunit concentration was cluculated nitrogen cocentration multiply by 6.25 (mg g^{-1})

levels in Exp. 1. This trend was most significant in the seed of 25 to 50μM-P treatment. Ca concentration was not increased with high P treatment, but Mg concentration increased. Fig. 2A and 2B shows the relationship between element concentrations versus N (2A) or P (2B) concentration in the seeds. It is obvious, same as non-nodulating T201 plants, that P and N shows negative correlation, although K, Ca, Mg and S concentrations were relatively constant.

β-Conglycinin, especially β-subunit concentration in seeds was decreased with all the 50 μM-P P treated plants compared with 25μM-P (table 6). The concentration of α'-, α- and β-subunits were decreased significantly (p<0.05) in the seed of the plant grown with a high concentration of P from a flowering stage (25 to 50 μM), and the same trends were observed in 50 μM-P and 3.5 μM-P splay treatments. While the concentration of basic subunit of glycinine increased but acidic subunit decreased with high P.

Discussion

It was reported that the accumulation of the soybean seed storage protein is influenced by seed nitrogen concentration (Ohtake et al. 1996, Paek et al. 1997, Krishnan et al. 2000) and the β-conglycinin, especially the β-subunit accumulation is positively corrected with the increase of seed nitrogen concentration (Ohtake et al. 1997). The amount of glycinin was relatively constant irrespective of total N concentration from 46.2mg to 86.1mg-N g^{-1} D.W, while β-conglycinin was low in N deficient seeds, and the amount was increased in paralleled with total N concentration in seeds. Especially β-subunit accumulation was completely depressed in severe N deficient seeds and most strongly responded to N supply (Ohtake et al. 1997). In this report, β-conglycinin, especially β-subunit, accumulation was also influenced by the level of phosphorus supply both in the non-nodulating (T201) and nodulating (Enrei) soybean plants (Table 3 and 6). The accumulation of the β-subunit could be decreased to half of the seed of Enrei with 25μM-P when phosphate level increased from flowering stage comparison with the control plants. Based on the results here, it is concluded that the effect of the phosphate supply affects in the seed protein composition, when the plants grown depending on nitrogen as nitrate or nitrogen fixation as N source. Although the detail of obscure lower P supply may primarily couse a decrease in seed number, followed by increase in seed N concentration and β-subunit concentration.

Thomas et al (1993) reported that nitrate uptake and amino acid accumulation in soybean plants was affected by deprivation of an external phosphorus supply. They showed phosphorus deprivation led to decreased rates of nitrate uptake and increased accumulation of absorbed nitrogen in the root. In this report, we showed that the N concentration of seeds was increased P deficiency and decreased high P application. Negative correlation was observed between P and N concentrations in seeds including nodulating and non-nodulating soybean plants.

The decrease in β-subunit in the higher P application may possibly due to the decrease in N concentration of seed caused by increasing seed number (Table 1 and 2, Table 5 and 6). High P supply might have beneficial effect on keeping the flowers and pods from falling off. It was reported that the decrease of the phosphate supply influenced on the concentration in other inorganic ions in xylem and phloem sap of castor bean (Jeschke et al. 1997). Although, in their report, the sulfate ion concentration in the xylem sap decreases in low phosphate treatment, the sulfate concentration increased in the phloem sap. The increase of the sulfate in the plant by supply phosphate might be caused the decrease of β-subunit accumulation.

Sulfur concentration of seed was slightly increased by higher concentrations of phosphate supply (Table 2 and 6). β-subunit accumulation is known to be depressed by adding L-methionine in *in vitro* culture system of immature cotyledon and also that the accumulation is controlled by the additional fertilizer of sulfate in the field. Gayler and Sykes (1985) reported that sulfur deficiency caused a decrease in the level of glycinin, and an elevation in the level of β-conglycinin. Conversely a high level of S-supply caused an increase in the accumulation of glycinin in the soybean seeds (Sexton at al. 1998a, b, Imsande and Schmidt 1998).

Furthermore, Takahashi et al. introduced N fertilization method. Using slow release N fertilizer (LP-120) at deep place of field, the soybean yield was increased and quality was steady. In combination with S and N fertilization method, together with the P fertilization will be more efficiency technique for soybean cultivation especially in the point of yield and quality.

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ダイズの種子収量、元素集積、貯蔵タンパク組成に対するリン供給量の影響

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要　約

ダイズをさまざまなリン濃度で水耕栽培し、種子の各種元素濃度および貯蔵タンパク質組成を比較した。根粒非着生系統ダイズ（品種 T201）と栽培ダイズ（品種エンレイ）をそれぞれ、硝酸あるいは窒素固定のみを唯一の窒素限として栽培した。両植物とも、植物体に対するリン供給量の増加は、種子におけるリン濃度を増加させ、窒素濃度を減少させた。この結果は、種子に貯蔵される元素濃度は、窒素の供給形態に関わらず、リン供給により変化することを示している。

根粒非着生系統ダイズに対する低濃度のリンの供給（5µM-P）は、対照区（25µM-P）と比較して、窒素の供給量によらず、種子貯蔵タンパク質のβ-コングリシニン含量を増加させた。栽培系統ダイズのエンレイでは、β-コングリシニンのβサブユニット濃度は、生育全期間あるいは開花期から高濃度のリンの供給（50µM-P）により減少した。

これらの結果から、ダイズにおける種子の元素集積および貯蔵タンパク組成は窒素の供給形態に関わらず、リンの供給量により変えることができることが示された。

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