A quantitative analysis of the relationship between absorbed and applied phosphorous and their contribution to seed production in soybeans under various applied nitrogen conditions

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Abstract

Aims

This study aimed to model the relationship between assimilated (P_A) and applied (P_F) phosphorus under diverse nitrogen applications (N_F), and to determine the contribution of P to N assimilation (N_A) and seed production in soybeans [*Glycine max* (L.) Merr.], as this has not been done before.

Methods

Over three years, pot experiments were conducted using nodulated [Lee(+)] and non-nodulated isoline [Lee(-)] soybeans under multiple levels of basal-dressed P_F and top-dressed N_F from R2 to R7.

Results

P_A in each N_F was represented by a function of P_F as a straight line with a positive slope and an intercept (P_S , soil P) connecting with a ceiling line of constant height. The slope [SLOPE = $(P_A - P_S) / P_F$], which represented the efficiency of P_F usage for P_A , asymptotically increased with N_F . As a result, P_A was represented by a single function of $P_F \times \text{SLOPE}$, which consisted of slope = 1 and a ceiling across different N_F rates. Seed production each year was explained by N_A regardless of P_A for both nodulation types, although responses of seed yield to P_A in Lee(-) differed due to N_A . P_A asymptotically increased the maximum N_A and N fixation by nodulation which were approximated by the N quantitative model.

Conclusion

P_A can be represented as a function of P_F by excluding P retained in soils, which is influenced by N_F . Accordingly, P_A effects seed production via N_A behavior determined by fertilizer, soil and fixed N.

Introduction

Phosphorus is one of the essential nutrients that determine seed yield in soybeans [*Glycine max* (L.) Merr.] (White and Veneklaas 2012). For instance, high P levels are required for nitrogen fixation (N_{FIX}) as a dominant nitrogen source for the seed production (Schulze et al. 2006), because N_{FIX} consumes large amounts of energy, and energy-generating metabolism depends on the availability of P (Israel 1987; Theodorou and Plaxton 1993). In addition, P is considered to have important effects on the development of roots, in terms of their proliferation, the number and weight of nodules, and nodule activity, which determine N fixation capacity in legumes (Cassman et al. 1980; Chaudhary and Fujita 1998; Chaudhary et al. 2008; de Mooy and Pesek 1966; Konno et al. 1990; Matsunaga and Matsumoto 1984; Schulze et al. 2006; Singh et al. 2005). However, not all applied P from fertilizer is absorbed by plants, because parts of P are fixed in soil depending on the soil phosphate absorption coefficient, which is strongly influenced by soil types (Auxtero et al. 2008; Kitou et al. 2009; Rubaek and Sibbesen 1995; Stewart and Tiessen 1987). Furthermore, some of the P will be retained in the soil if root distribution is insufficient to extend into fertilized areas (Silberbush and Barber 1983). Basal-dressing P fertilizer that is added to the soil at sowing time will not move much from the positions to which it was applied, especially in soil with a high P fixation capacity (Sleight et al. 1984). Therefore, P absorption by plants is highly dependent on root contact with soil P, as well as P fixation by the soil phosphate absorption coefficient (Caassen and Barber 1976; Marschner 1995).

Root length, which is closely related to root contact with soil P, significantly increases with increasing N application in soybeans (Arima et al. 2000). Significant increases in root length due to N application, sometimes without changes in root weight, have been observed in many plant species (Sathiyavani et al. 2017). Therefore, it is possible that N application influences P absorption, depending on root length and distribution. Hence, P absorption from applied P should be analyzed with known N conditions, where the interaction effect between P and N fertilizers on these nutrient absorptions by plants was observed (Marschner 1995).

Meanwhile, N is fundamentally a major yield-limiting factor in soybeans (Sinclair and de Wit 1976), and N assimilation (N_A) explains the variation in yield of many soybean cultivars (Pazderink et al. 1997; Rotundo et al. 2014). However, N_A does not simply correlate with applied N (N_F), due to a tradeoff between N_{FIX} and N_F (Fujita and Tanaka 1982; Tanaka et al. 1980).

P fertilizer is derived from phosphate rock, the cost of which has increased due to an increase in P fertilizer use (Cordell et al. 2009). There has been concern that phosphorus demand will outstrip supply within this century if no fundamental changes are made to the current trajectory (Cordell, 2021). To increase the efficiency of P fertilizer usage (assimilated P / supplied P) to save P fertilizer use, a quantitative analysis of the relationship between assimilated and applied P is essential. Quantitative relationships between absorbed P by plants and soil P relating with the soil phosphate absorption coefficient were indicated in soybean and alfalfa (Aguilar and van Diest 1981) and in rice (Tanikawa 2016). Furthermore, a macro model of the relationship between P absorption and root distribution or structure was proposed for corn plants (Caassen and Barber 1976), kidney bean and six crop species (Föhse et al. 1991). However, a quantitative model that formulates P absorption by plants from applied P and accounts for the effects of N application on the P absorption has not been put forward for soybeans. Therefore, our objectives for this study were to establish a model concept of the quantitative relationship between absorbed and applied P under various applied N conditions and to determine the contribution of absorbed P to N absorption and seed production in soybeans.

Materials And Methods

Plant experiments

Plant materials and P and N treatments

The soybean cultivar 'Lee' [Lee(+)] and a non-nodulated isolate of Lee [Lee(-)] were used in the following pot experiments. The pot experiments were conducted in 2016 and 2017 in Setagaya, Tokyo, Japan (35°64' N, 139°63' E, at 45.9 m asl), and in 2020 in Atsugi, Kanagawa, Japan (35°26' N, 139°20' E, at 25.7 m asl). Plants were grown in pots filled with 11 L of commercially available soil (disinfected and aggregated natural Andosol; Akadama, Hujimi Engei Co., Japan). This soil drains well, has a pH of 5.5 – 6.5, and contains minimal amounts of N and P. The soil originated from volcanic sediments and thus had a high phosphorus-retention capacity (phosphate absorption coefficient = 10.3 – 12.4 g P kg⁻¹). To determine the effect of applied P and N on their assimilation, this P- and N-poor soil was used. Before sowing, magnesium lime (10 g pot⁻¹) and KCl (1.15 g pot⁻¹) were mixed with one of four or five concentrations of P (0, 1.31, 4.37, or 6.55 g pot⁻¹ in 2016 and 2017, and 0, 0.44, 1.31, 4.37, or 6.55 g pot⁻¹ in 2020; as superphosphate). These P treatments, are hereafter referred to as P0, P1, P3, P10, and P15, respectively. Three seeds of each of the soybean isolines (Lee[+] or Lee[-]) were sown in each pot. The sowing date was 14 June in 2016 and 2017, and 23 June in 2020. Two plants were removed at the V2–3 stage (second to third node; Fehr and Caviness 1977), and the remaining plant was left to grow. The plants were sufficiently irrigated by hand spraying throughout the growing season. Liquid fertilizer was applied, providing 0.1 g of N per pot as (NH₄)₂SO₄, on 18 and 25 July and 1 August in 2016, on 18, 24, and 31 July in 2017, and on 21 and 27 July in 2020.

N treatments were applied between the full bloom (R2) and beginning maturity (R7) stages (Fehr and Caviness 1977) over 10 weeks during the seed-filling period: from 8 August to 11 October in 2016, from 7 August to 9 October in 2017, and from 4 August to 6 October in 2020. Plants were treated weekly with 0, 0.05, 0.20, or 0.80 g N pot⁻¹ in 2016 and 2017, and 0, 0.2, 0.4, 0.8, or 1.2 g N pot⁻¹ in 2020, in the form of (NH₄)₂SO₄. These N treatments are hereafter referred to as N0, N0.5, N2, N4, N8, and N12, respectively. Thus, this experiment consisted of 16 or 25 treatment combinations, incorporating four or five different P treatments and four or five different N treatments. The experimental design was completely randomized and there were three replications.

Sampling and measurements

Individual plants were sampled at the R8 (full maturity) stage (Fehr and Caviness 1977). The numbers of nodes, total pods, ripening pods, and seeds were counted for each plant. The stems, leaves, pod shells, and seeds were separated from each sample, dried at 80°C for 48 h, and then weighed. During the growing period, abscised organs were carefully gathered two or three times per week, dried at 80°C for 48 h, and then weighed. These weights were added to the dry sample weights to obtain a total dry weight for each organ type.

Each organ was milled and dissolved using a sulfuric acid-hydrogen peroxide digestion method (Matsunaga and Shiozaki 1989). The P and N content of each organ were then determined using the molybdenum blue method (Murphy and Riley 1962) and the distillation-titration method (Nelson and Sommers 1973), respectively.

Modelling and statistical analysis

Models of the relationship between assimilated P and applied P

Three cases of the relationship between P_A and P_F can be predicted (Fig. 1, left graph). Case 1 is that P_A continuously and linearly increases with P_F, where the slope = 1 (no phosphorus retention and no remaining P in soils) and all P_F is apparently absorbed by plants, and P_A at P_F = 0 represents available phosphate in the soil (P_S). Case 2 is that P_A increases linearly with P_F with a slope lower than 1 and an intercept of P_S.

when P_F is partially fixed by and/ or retained in the soil. Case 3 is that the increasing P_A in Case 2 has a ceiling; this relationship depends on Blackman's law (Thornley 1976), including observations of the relationship between N_A and N_F (Kakiuchi and Kobata 2017). In Cases 1 and 2 and the phase below the ceiling in Case 3, the slope [$\text{SLOPE} = (P_A - P_S) / P_F$] of the line representing the relationship between P_A and P_F with an intercept of P_S can be used to represent P_F use efficiency for P_A . The efficiency would decrease with increasing P fixation in soil or retained P in soil due to insufficient contact of roots with soil. Here, $P_F \times \text{SLOPE}$ represents the actual available P that is absorbed by plants.

Three cases of the relationship between P_A and P_F can be represented by two simple types of lines whereby P_F is changed to $P_F \times \text{SLOPE}$ (Fig. 1, middle graph). Furthermore, the relationship between P_A and $P_F \times \text{SLOPE}$ can be normalized to form a relative relationship between $x = (P_F \times \text{SLOPE}) / P_{A_{\max}}$ and $y = (P_A - P_S) / P_{A_{\max}}$, where $P_{A_{\max}}$ is the maximum P_A ; in Cases 1 and 2, $y = x$ limited by $y = 1$ and in Case 3, $y = x$ when $x \leq 1$ and $y = 1$ when $x > 1$ (Fig. 1, right graph).

Estimation of N_A and N_{FIX} using a quantitative N model

To estimate N_S , the maximum N_A , and N_{FIX} in soybeans, a quantitative N model indicating the relationship between N_A and N_F was used for each P application rate (Fig. 2, upper graph) (Kakiuchi and Kobata 2017). The relationship between N_F and N_A was incorporated into the model to estimate the maximum N_A ($N_{A_{\max}}$) and N_{FIX} . For Lee(-), N_A in the N0 treatment represented N_S , and N_A from the highest N treatment represented $N_{A_{\max}}$. However, N_A of the P0 treated Lee(-) plants was much lower than the other P_F treatments, as a result of extremely poor growth due to the negligible quantities of P in the used soil. Therefore, for Lee(-) plants, N_A of the N0 at P15 treatment represented N_S (Fig. 2, lower graph). From the fit lines in the model, the maximum N_{FIX} under nonfertilized conditions ($N_{\text{FIX}_{\max}}$), $N_{A_{\max}}$, N_S , and the rate ($s - 1$) of reduction of N_{FIX} due to increasing N_F were estimated. The goodness-of-fit of the observed data to the model was evaluated using the coefficient of determination (r^2).

Statistical analysis

Differences between treatments were considered significant if p values calculated by Tukey's test were < 0.05 . The least-squares method was used to fit curves, and the coefficients of determination (r^2) and their associated p values were calculated to assess the goodness-of-fit of the models. Multiple regression analysis was conducted to determine the contributions of N_A and P_A to seed production. The statistics software Excel Toukei 2012 (Social Survey Research Information, Tokyo, Japan) was used to conduct the statistical analysis.

Results

The relationship between P_A and P_F

P_A increased linearly with P_F from 0 to 2 – 3 g pot^{-1} and reached a ceiling when approximately over the values of P_F in all N_F treatments, for both nodulation types and all three experimental years, although the value of P_A at the ceiling differed depending on N_F (Fig. 3). Therefore, Case 3 in our predicted model most fitted the relationship between P_A and P_F (Fig. 1). When the SLOPE [$(P_A - P_S) / P_F$] was calculated from a phase of the linear relationship between P_A and P_F for the lower P_F values (< 2 g plant^{-1}), the SLOPE increased with N_F for both nodulation types across the three experimental years, although the maximum SLOPE differed among experimental years (Fig. 4).

The relationship between P_A and $P_F \times \text{SLOPE}$ was represented by a polygonal line with a slope of 1 and a ceiling for both nodulation types in the three experimental years, while the fitness in Lee(+) was higher than Lee(-) (Fig. 5). When P_A and $P_F \times \text{SLOPE}$ were normalized to $(P_A - P_S) / P_{A_{\max}}$ ($P_{A_{\max}} = P$ at the ceiling) and $(P_F \times \text{SLOPE}) / P_{A_{\max}}$, respectively (Fig. 1), all observations were appropriately described by the same line with higher fitness ($r^2 = 0.954$) (Fig. 6).

Contributions of P_A to seed production

Seed dry weight was asymptotically increased with increasing P_A , and the plateaus were similar for all Lee(+) treatments under different amounts of N_F across three years, but for Lee(-) treatments, the height of the curves in the seed weight significantly differed according to N_F , and the plateaus were higher with higher N_F (Fig. 7, upper panels). On the contrary, N_A consistently increased seed dry weight, irrespective of nodulation type [Lee(+) or Lee(-)] and differing P_F values in all years (Fig. 7, lower panels).

Multiple regression analyses of seed dry weight and two independent variables, N_A and P_A , for Lee(+) and Lee(-) plants across all three years showed that the contribution of P_A to seed dry weight in Lee(+) plants (68.0%) was much higher than in Lee(-) plants (23.4%) with high r^2

(Table 1). Conversely, in Lee(-) plants, the contribution of N_A (76.6%) was much higher than in Lee(+) plants (32.0%). Seed weight in Lee(+) plants was therefore highly dependent on P_A , while in Lee(-) plants, it depended on N_A .

Table 1
Multiple regression analysis and the contribution of nitrogen assimilation (NA) and phosphorus assimilation (PA) to seed yield in nodulated [Lee(+)] and non-nodulated [Lee(-)] soybeans from results in three-year experiments

Multiple regression equation		r^2	Contribution ratio (%)	
			N_A	P_A
Lee(+)	Yield = $2.67N_A + 65.2P_A + 6.03$	0.846	32.0	68.0
Lee(-)	Yield = $7.49N_A + 27.8P_A - 0.12$	0.937	76.6	23.4

The effect of P on N_{Amax} and N_{FIX}

The estimated values of N_S were very low for both Lee(+) and Lee(-) isolines (Table 2 and Fig. 2). The relationship between N_A and N_F was effectively explained by the model of nodulated isolines under various P_F rates with high r^2 [0.590 – 0.985 in Lee(+) and 0.947 – 0.998 in Lee(-)], except for P0 treatments [r^2 = 0.092 – 0.569 in Lee(+) and r^2 = 0.122 – 0.453 in Lee(-)] (Table 2).

Table 2

Parameter estimates (N_{FIXmax} , N_{Amax} , NS , and $s - 1$) and coefficient of fitness (r^2) from the quantitative N model based on results for the two isolines [Lee(+) and Lee(-)] in three years observations. N_{FIXmax} is maximum nitrogen fixation (NFIX), N_{Amax} is maximum nitrogen assimilation, NS is available soil nitrogen, and $s - 1$ is reduction of NFIX due to increasing NF. See Figure 2 for the model

2016															
Lee(+)								Lee(-)							
	r^2	N_{FIXmax}		N_{Amax}		Ns		s-1			r^2	N_{Amax}		Ns	
g plant ⁻¹															
P0	0.092	0		0.49		0.23		-0.71			0.321	0.99		0.23	
P3	0.852	3.06		4.85		0.26		-0.58			0.993	5.83		0.26	
P10	0.977	4.30		6.70		0.26		-0.67			0.996	6.22		0.26	
P15	0.985	4.76		7.18		0.26		-0.69			0.998	6.85		0.26	
Average		3.03		4.80		0.26		-0.66				4.97		0.26	
CV		0.71 (0.22)		0.63 (0.20)		0.06 (0.00)		-0.09 (-0.09)				0.54 (0.08)		0.06 (0.00)	
2017															
P0	0.277	0		0.08		0.08					0.122	0.12		0.08	
P3	0.845	1.62		3.52		0.42		-0.44			0.997	4.96		0.42	
P10	0.928	3.68		6.25		0.42		-0.60			0.996	5.86		0.42	
P15	0.976	3.94		6.66		0.42		-0.63			0.997	6.53		0.42	
Average		2.31		4.13		0.33		-0.56				4.37		0.33	
CV		0.80 (0.41)		0.74 (0.31)		0.51 (0.00)		-0.18 (-0.18)				0.67 (0.14)		0.51 (0.00)	
2020															
P0	0.569	0		0.57		0.19					0.453	0.53		0.19	
P1	0.590	1.64		4.03		0.26		-0.49			0.947	4.70		0.26	
P3	0.943	2.62		5.35		0.26		-0.55			0.979	6.71		0.26	
P10	0.944	3.28		7.06		0.26		-0.51			0.980	5.38		0.26	
P15	0.875	3.96		8.46		0.26		-0.51			0.975	6.01		0.26	
Average		2.30		5.09		0.25		-0.52				4.67		0.25	
CV		0.67 (0.34)		0.60 (0.31)		0.12 (0.00)		-0.05 (-0.04)				0.52 (0.15)		0.12 (0.00)	

The estimated N_{Amax} and N_{FIXmax} of Lee(+) plants increased significantly and asymptotically with P_F (Fig. 8, upper panels), although these relationships differed between the three experimental years. However, the relative N_{Amax} and N_{FIXmax} (the ratio to the maximum value for each year) were able to be expressed with same line, regardless of year (Fig. 8, lower panels). N_{Amax} , defined as the highest N_A in each P_F treatment, similarly increased with P_A regardless of nodulation type and experimental year (Fig. 9, upper). N_{FIXmax} of Lee(+) plants increased with P_A regardless of experimental year (Fig. 9, lower). The variations of $s - 1$ (the change in the rate of reduction of N_{FIX} by N_F) were relatively small (coefficient of variation [CV] = 0.05 – 0.18) under different P_F rates (Table 2).

Discussion

Modelling the quantitative relationship between P_A and P_F

The relationship between P_A and P_F , regardless of nodulation type, was approximated by the Case 3 model, whereby P_A increased linearly with P_F , then reached a ceiling line (Fig. 1 and 3). The SLOPE increased linearly with N_F at low concentrations of applied N, and converged towards a constant rate under high concentrations of N_F (Fig. 4). This pattern suggested that an increase in the root mass as root length by N application (Arima et al. 2000), which promoted root contact with soil, resulted in an increase in P absorption. Soybean root weight was

around 17% of shoot weight (Ordóñez et al. 2020) and 19 – 29% with 10% of CV estimated in plants of the split root experiment under different nitrate nitrogen rate (Xia et al. 2017). From the result, when root weights were estimated by the observed shoot weight at the maximum for each treatment of N rate $\times$ 0.17 (root per shoot weight) as a case and the relationship between SLOPE and the root weight was plotted, SLOPE increased with an increase in root weight, while the relationship differed between nodulation types (Fig. 10). Hence, it was suggested that SLOPE changed by the root weight to contribute to contact with soil. The difference in the response of SLOPE to root weight between nodulation types was possible to result from that in root length, because an inverse relationship between nodule mass and total root length including different nodulation types was observed and hence root length in nodulated soybean might be shorter than that in non-nodulated soybean at same root weight (Cassman et al. 1980). After roots were distributed throughout the bulk pot soil due to adequate N supply, a ratio of absorbed to supplied P from fertilizer and soil P (SLOPE) converged towards a constant rate in each experimental year. The constant rate would reflect the phosphate absorption coefficient of the soil. The ceiling formed at higher N applications in the relationship between assimilated P and supplied P from fertilizer indicated that at most less than 30% of supplied P was available for the plants in both soybean nodulation types in the soil. Hence, it was suggested that N fertilizer alters P absorption via root development under limited N applications in soybeans, although root mass and length density were not directly observed in this experiment.

Applied P in the pots was mixed uniformly into soils and root distribution was limited. However, applied P in the field is mainly located in cultivated soil layers, which change based on cultivation procedures. The shape of the regression of SLOPE below the ceiling and N_F at which the ceiling is reached (Fig. 4) would change depending on P distributions in the soil. Therefore, in the field a factor of P distribution in the soil should be considered in the model. However, in higher P soils in cultivated soil layers, such as the fields in Japan which have had P fertilizer applied conventionally over long periods of time, the relationship between assimilated and applied P would be indicated only by a constant ceiling line representing soil P without SLOPE in a model even if under diverse applied P conditions (Kakiuchi and Kamiji 2015).

Contributions of P_A to N_A and seed production

Absorbed P from soils (P_A) increased the seed dry weight of both nodulation types, although the increase was dependent on N_F for the non-nodulated isoline (Fig. 7). This suggested that for the non-nodulated isoline, N, rather than P, is a limiting factor for seed production. The higher contribution of N_A to the seed yield in Lee(-) was also indicated by a multiple regression analysis (Table 1). Contrary to the effect of P_A on yield, N_A was closely related to seed production under a wide range of P_F values in both nodulated and non-nodulated isolines (Fig. 7). The close relationship between seed yield and N_A can be followed by the fact that, in soybeans, assimilated N is mainly distributed to the seeds, so seed yield directly reflects the quantity of N assimilation (Jin et al. 2011; Kakiuchi and Kobata 2017; Salvagiotti et al. 2008; Zhao et al. 2014). In Lee(+) plants, N_A is secured by the nodules, and seed dry weight can increase immediately following an increase in P_A , but in Lee(-) plants, N_A is limited only by applied and soil N, so the response of seed weight to P_A is restricted by $N_A \cdot N_{Amax}$ of both isolines and N_{FIXmax} of Lee(+) plants increased with P_A , regardless of experimental year (Fig. 9). Hence, the limitation of N assimilation, seems to depend on P supply. However, as a result, assimilated P seemed to indirectly contribute to seed production via the effects of P on N_A which consisted of absorbed and fixed N.

Conclusion

Absorbed P by soybean plants can be indicated by a function of applied P by excluding P retained in soils significantly influenced by N_F . Furthermore, assimilated P effects seed production via N_A behavior, consisting of N absorption from fertilizer, soil, and fixed N. We believe that our model concept for P assimilation will contribute to the development of sub-models for saving fertilizer use and planning in soybeans.

Abbreviations

N_A , nitrogen assimilation; N_{Amax} , maximum nitrogen assimilation; N_F , applied fertilizer nitrogen; N_{FIX} , fixed nitrogen; N_{FIXmax} , maximum fixed nitrogen; N_S , available soil nitrogen; P_A , phosphorus assimilation; P_{Amax} , maximum phosphorus assimilation; P_F , applied phosphorus by fertilizer; P_S , available phosphorus in soil.

Declarations

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Figures

Figure 1

Models of the relationships between assimilated (P_A) and applied phosphorus (P_F) (left panel), between P_A and $P_F \times \text{SLOPE}$, where $\text{SLOPE} = (P_A - P_S) / P_F$ and P_S is soil P; SLOPE represents P_F use efficiency for P_A (middle panel), and a normalized relationship that y-axis and x-axis in the relationship of middle panel are normalized del by $(P_A - P_S) / P_{A_{\max}}$ and by $(P_F \times \text{SLOPE}) / P_{A_{\max}}$, respectively, where $P_{A_{\max}}$ is the height of the ceiling (right panel). Three predicted cases (Cases 1, 2, and 3) of the relationship are shown

Figure 2

The nitrogen quantitative model for the relationship between the nitrogen assimilation (N_A) or fixation (N_{FIX}) and the quantity of nitrogen applied as fertilizer (N_F) for nodulated [Lee(+)] (upper left) and non-nodulated [Lee(-)] soybeans (upper right) (Kakiuchi and Kobata 2017) and data fitted to the model for the Lee(+) (lower left) and Lee(-) (lower right) isolines in three years experiments. Each observed data point represents the mean of three replicates. N_S indicates amount of available soil nitrogen, N_{Amax} indicates maximum nitrogen assimilation by plants, and N_{FIXmax} indicates maximum nitrogen fixation. When $N_F > (N_{Amax} - N_S)$, then $N_A = N_{Amax}$ and when $N_F < (N_{Amax} - N_S)$, then $N_A = sN_F + (N_S + N_{FIX})$, where $N_{FIX} = N_A - (N_F + N_S)$ and $N_{FIX} = (s - 1)N_F + N_{FIXmax}$

Figure 3

Relationships between assimilated P (P_A) and the quantity of P applied as fertilizer (P_F) in Lee(+) and Lee(-) isolines, according to the model (Case 3) (Fig. 1, left). Each data point represents the mean of three replicates

Figure 4

The ratio of assimilated P (P_A) to applied P (P_F) plus soil P (P_S) [SLOPE = $(P_A - P_S) / P_F$] and applied N (N_F) in Lee(+) and Lee(-) isolines. SLOPE was derived from data in Fig. 3 when observed data was fitted to Case 3 in Fig. 1 (middle)

Figure 5

Relationships between assimilated phosphorus (P_A) and available P derived from applied P ($P_F \times \text{SLOPE}$) in Lee(+) and Lee(-) isolines, according to the model (Case 3) (Fig. 1, middle). Each data point represents the mean of three replicates

Figure 6

A normalized model of the relationships between the quantity of P applied as fertilizer (P_F) and assimilated (P_A) in Lee(+) and Lee(-) isolines (Fig. 1, left). Each data point represents the mean of three replicates

Figure 7

Relationships between seed dry weight and assimilated phosphorus (P_A) (upper) or nitrogen (N_A) (lower) in Lee(+) and Lee(-) isolines. Each data point represents the mean of three replicates. The coefficients in the equation $y = a[1 - b \exp(-cx)]$ and the coefficient of determination (r^2) for Lee(-) presented in the middle graphs are as follows, in the format (a, b, c , and r^2): for 2016, N0 (0.01, 251, 5.3, and 0.776); N0.5 (5.6, 1.1, 77, and 0.658); N2.0 (20, 0.98, 14, and 0.999); N8.0 (45, 1.2, 16, and 0.966); for 2017, N0 (3.8, 1.4, 261, and 0.945); N0.5 (11, 0.99, 17, and 0.996); N2.0 (28, 1.0, 15, and 0.997); N8.0 (78, 1.0, 3.7, and 0.999); for 2020, N0 (4.6, 0.8, 48, and 0.827); N2.0 (28, 1.1, 17, and 0.994); N4.0 (47.5, 1.0, 12, and 0.996); N8.0 (57, 1.0, 8.3, and 0.990); N12.0 (60, 1.1, 9.3, and 0.958)

Figure 8

Relationships between maximum nitrogen assimilation (N_{Amax}) or fixation (N_{FIXmax}) (upper), and the N_{Amax} or N_{FIXmax} values as ratios of the maximum for each year in Lee(+) (lower) and the quantity of phosphorus applied as fertilizer (P_F). Each data point represents the mean of three replicates. Coefficients in the equation $y = a[1 - b \exp(-cx)]$ are indicated in the form (a, b, c , and r^2) and are presented in the graphs

Figure 9

The relationship between maximum nitrogen assimilation (N_{Amax}) (upper) or maximum nitrogen fixation (N_{FIXmax}) (lower) and assimilated phosphorus (P_A). Each data point represents the mean of three replicates

Figure 10

SLOPE represented P_F use efficiency for P_A (Fig. 1) and estimated root weight under different applied N (N_F) in Lee(+) and Lee(-). The root weight was estimated from shoot weight at the maximum in each N_F rate $\times$ 0.17 (Ordóñez et al. 2020)