

Contrasting Effects of Phosphorus and Potassium Deficiencies on Leaf Area Development in Maize

Luis María Arias Usandivaras, Flavio Hernán Gutiérrez-Boem, and Fernando Salvagiotti*

ABSTRACT

Management of P and K in agricultural systems is similar, since both move mainly by diffusion in soil. In maize (*Zea mays* L.), radiation capture is a consequence primarily of leaf area formation and senescence, but little is known about P and K interaction in determining both variables. The objective of this study was to assess the effects of P, K, and P × K interaction on (i) leaf appearance rate and final leaf number, (ii) individual leaf area, (iii) leaf senescence rate, and (iv) leaf area development in maize. Two field experiments were performed in the 2011–2012 and 2012–2013 growing seasons, under no water and N limitations. Treatments consisted of different levels of P and K fertilization. Differential effects of both nutrients occurred for leaf area formation and senescence. Phosphorus deficiencies decreased average leaf appearance rate by 10% and individual leaf area by 18%, whereas K deficiency reduction of individual leaf area was 14%. Final leaf number did not change under both P and K deficiency. Phosphorus deficiencies decreased leaf senescence rate by 2%, whereas K deficiencies accelerated this process by 12%. As the result of the counteracting processes of expansion and senescence, P deficiency effects on green leaf area index were larger at the beginning of the crop cycle and tended to attenuate after, whereas K deficiencies were more important in later stages. These results may help in modeling the effects of P and K shortage in maize.

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Abbreviations: FSLAI, senescence expressed as a fraction of total leaf area; GLAI, green leaf area index; ILA, individual leaf area; LAR, leaf appearance rate.

DEFICIENCIES of P and K are present in many agricultural regions of the world (Römheld and Kirkby, 2010; Obersteiner et al., 2013). Fertilizer management recommendations for timing and placement are similar for both nutrients because of their relative mobility in soil, as both move mainly by diffusion (Barber, 1995). Several studies have addressed agronomic aspects of maize response to P and K fertilization (Bordoli and Mallarino, 1998; Dobermann et al., 1998; Borges and Mallarino, 2000; Clover and Mallarino, 2013).

In maize (*Zea mays* L.), leaf expansion and leaf senescence determine radiation capture. Even when both processes have some degree of temporal overlap, expansion is more relevant before anthesis (Maddonni and Otegui, 1996), when maximum green leaf area index (GLAI) occurs. Leaf senescence shows slow progress up to flowering and a sharp increase afterward (Muchow and Carberry, 1989; Borrás et al., 2003; Antonietta et al., 2014). Studies in maize and sweet corn (*Z. mays* var. *rugosa*) under field conditions have shown that P deficiency decreased leaf appearance rate (LAR) and final individual leaf area (ILA) (Colomb et al., 2000; Plénet et al., 2000; Fletcher et al., 2008). In wheat (*Triticum aestivum* L.), P deficiency reduced leaf expansion without limiting assimilate supply (Rodríguez et al., 1998a) by decreasing

Published in Crop Sci. 58:1–11 (2018).
doi: 10.2135/cropsci2018.02.0092

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cell number (Assuero et al., 2004). Potassium deficiency has been studied to a lesser extent. Pettigrew (2008) showed that K shortage may decrease stomatal conductance and photosynthesis and also reduce water potential, turgor, and eventually cell expansion. In maize, Jordan-Meille and Pellerin (2004) showed delayed leaf appearance and reduced ILA under K shortage.

Total GLAI is the sum of ILA along the stem. The relationship between ILA and leaf position on the stem may be described by an exponential function (Dwyer and Stewart, 1986):

$$A_n = A_0 e^{-b(X_n - X_0)^2 + c(X_n - X_0)^3} \quad [1]$$

where A_n is the area of the leaf on the n th position, A_0 is the area of the largest leaf, X_0 is the position of the largest leaf in the main stem, X_n is the position of the leaf n in the main stem, b is the degree of breadth, and c is the degree of skewness. This function was used in experiments evaluating different genotypes (Keating and Wafula, 1992; Elings, 2000), planting dates (Muchow and Carberry, 1989), N fertilizer rates, plant densities, and row widths (Valentinuz and Tollenaar, 2006). Since P and K have low mobility in soil, the relative effects of P and K deficiencies are expected to be larger in early stages of maize growth than in later stages. Therefore, a decrease in ILA in the left portion of the curve is expected, increasing the skewness of the function (parameter c in Eq. [1]). The contrary effect (i.e., reduction in leaf area in the right portion of this curve) has been shown when increasing interplant competition in maize (Maddonna et al., 2001).

Leaf senescence in maize is slow before silking, but after this period, this process significantly increases. Borrás et al. (2003) observed that the moment when senescence is triggered (i.e., increase in leaf rate senescence) was not modified by source/sink ratio manipulations, row spacing, or plant density. Nitrogen and assimilate availability are important for maintaining a functional leaf area during the period in which leaf senescence is increasing in maize (Tollenaar and Daynard, 1982; Uhart and Andrade, 1995; Rajcan and Tollenaar, 1999a, 1999b). The role of P and K deficiency on leaf senescence has had less attention in literature. Some studies in maize showed a reduction (Colomb et al., 2000), whereas others found no effect in leaf senescence due to P deficiency (Plénet et al., 2000; Fletcher et al., 2008). Other studies in maize subjected to K deficiency had negligible effects on senescence during early stages of development (Jordan-Meille and Pellerin, 2004).

Under field conditions, crop growth is usually limited by more than one nutrient simultaneously. In cases where crop growth is influenced by an interaction among nutrient deficiencies, results of studies with a single nutrient may have limited usefulness in estimating responses to multiple deficiencies.

The objective of this study was to assess the effects of P and K deficiencies and their interaction on leaf area development in maize. Since P and K have similar dynamics in soil, the main hypothesis of this work was that both deficiencies would show similar effects, by decreasing leaf area formation during early stages of crop growth without major effects on leaf senescence.

MATERIALS AND METHODS

Experimental Conditions and Treatments

Two field experiments were conducted at the INTA Mercedes Research Station (Mercedes, Corrientes, Argentina) (29°11' S, 58°2' W). Experiment 1 was sown on 12 Sept. 2011, and Exp. 2 was sown on 30 Aug. 2012. Treatments consisted of a combination of P and K fertilizer rates. Three levels of fertilizer P (0 [P0], 40 [P1], and 60 [P2] kg P ha⁻¹) and three levels of fertilizer K (0 [K0], 45 [K1], and 75 [K2] kg K ha⁻¹) were used. The lowest and highest fertilizer rate of both nutrients were combined in a two-by-two factorial arrangement of treatments (P0K0, P0K2, P2K0, and P2K2), whereas the intermediate level of P and K (P1 and K1) were applied only with the highest level of the other nutrient (P1K2 and P2K1). These six treatments were arranged in a randomized complete block design with four replicates. Potassium (KCl, 60% K₂O), and P (triple superphosphate, 46% P₂O₅) fertilizers were broadcast after the last tillage, a week before planting. A single N fertilizer rate (200 kg N ha⁻¹) was applied as urea, with one-half at sowing and one-half at the V6 stage (Ritchie and Hanway, 1982) to prevent N deficiency (Salvagiotti et al., 2011). Both experiments were irrigated to avoid water deficits using a sprinkler (Exp. 1) or drip (Exp. 2) irrigation for maintaining soil water content near field capacity throughout the crop cycle. A single-cross hybrid, DK747VT3P (Monsanto Argentina), was sown in both experiments. Both experiments were mechanically sown following tillage (two passes with a disc harrow and one pass with a spike tooth harrow). The previous crop in both experiments was a degraded gramineous-based pasture. Each plot was eight (Exp. 1) or six (Exp. 2) rows wide, spaced 70 cm apart, and 15 m long. Plant population at harvest was 6.8 and 7.3 plants m⁻² in Exp. 1 and 2, respectively. The soil series was Puesto Colonia silt clay (fine-clay, Typical Argiudoll) with a 0.5 to 1% slope. The silt clay soil extended to the depth of 1 m with moderate drainage (Escobar et al., 1996). Chemical analysis of the upper 20 cm of soil showed Bray I P (Bray and Kurtz, 1945) of 5.5 and 5.0 mg kg⁻¹, exchangeable K (ammonium acetate) of 51 and 47 mg kg⁻¹, and a pH (water, 1:2.5) of 5.5 and 5.8 in Exp. 1 and 2, respectively. In both experiments, weeds were controlled by applying glyphosate [N-(phosphonomethyl) glycine, 3 L ha⁻¹] and atrazine [6-chloro-N-ethyl-N'-(1-methylethyl)-1,3,5-triazine-2,4-diamine, 3 L ha⁻¹] prior to planting and glyphosate (3 L ha⁻¹) in postemergence. In Exp. 1, cypermethrin {[cyano-(3-phenoxyphenyl)methyl]3-(2,2-dichloroethenyl)-2,2-dimethylcyclopropane-1-carboxylate} was applied (0.3 L ha⁻¹) when the crop reached V5 stage to control *Spodoptera frugiperda* Smith. In both Exp. 1 and 2, azoxystrobin (100 g ha⁻¹) and cyproconazole [2-(4-chlorophenyl)-3-cyclopropyl-1-(1H-1,2,4-triazol-1-yl)butan-2-ol, 40 g ha⁻¹] were applied when the crop reached V10 stage to avoid foliar diseases.

Plant Measurements and Calculations

Leaf Appearance and Senescence

When crops reached two to three expanded leaves, 10 consecutive plants, homogeneous in size and development, were labeled in each plot. Phenology, leaf area, and leaf senescence measurements were performed on these plants. The number of fully expanded (visible ligule) and visible leaves (leaf tips) were determined weekly. Individual leaf area of fully expanded leaves was estimated by multiplying lamina length and maximum width, using a coefficient of 0.75 (Valentinuz and Tollenaar, 2006). A leaf was considered senesced when less than one-half of its leaf area was green based on visual assessment (Plénet et al., 2000; Jordan-Meille and Pellerin, 2004). Total leaf area of each plant during the period of leaf appearance was calculated as the sum of area of fully expanded leaves plus the area of the two following leaves, as suggested by Muchow and Carberry (1989), to include leaves that were still expanding. Individual leaf area refers to the area of each leaf starting from the bottom of the stem. Total leaf area was calculated as the sum of ILA of both green and senesced leaves. Senescence was expressed as a fraction of total leaf area (FSLAI = senesced LAI/total leaf area). Then, GLAI was estimated as the remaining leaf area.

Thermal time ($^{\circ}\text{C d}$) was calculated from emergence using a base temperature of 8°C (Ritchie and Nesmith, 1991). Linear functions were fitted to the relationship between visible leaves and thermal time from emergence (Eq. [2]), considering an intercept of 1, due to the fact that at thermal time zero, there is one visible leaf (Fletcher et al., 2008). The slope of this relationship was called the LAR (leaves $^{\circ}\text{C d}^{-1}$).

$$\text{Visible leaves} = 1 + \text{LAR}X \quad [2]$$

where X is thermal time from emergence.

Time course of leaf senescence (i.e., FSLAI as related to thermal time) was represented by an exponential function (Eq. [3]) (Muchow and Carberry, 1989):

$$\text{FSLAI} = Y_0 e^{kX} \quad [3]$$

where k is the rate of relative senescence ($^{\circ}\text{C d}^{-1}$), and Y_0 is FSLAI at thermal time zero (emergence). The FSLAI is null at emergence, but this parameter cannot be zero since the equation would return a zero FSLAI in the entire thermal time range. Equation [1] was used for describing leaf area distribution along the main stem. In all cases, when functions were fitted, statistical significance was tested and parameters of each function were compared between treatments using an F test (Mead et al., 2003). When no significant difference between treatments occurred, a single function was fit.

Aboveground Biomass, Nutrient Content, and Grain Yield

To understand the relative extent of P or K deficiencies, aboveground maize dry matter biomass was measured at five (V5, V12, R1, R2, and R6) and six (V4, V6, V11, R1, R2, and R6) stages of maize development (Ritchie and Hanway, 1982) in Exp. 1 and 2, respectively. Sampling area was 1.47 and 1.09 m^2 in Exp. 1 and 2, respectively, dried in an oven at 65°C with forced air circulation until a constant weight was reached and then weighed.

Samples were ground and passed through a 0.1-mm mesh, and P and K concentrations in grains and in stovers were determined. Both nutrients were extracted with an acid digestion using HNO_3 , H_2SO_4 , and HClO_4 . Phosphorus content was determined by colorimetry (Fiske and Subbarow, 1925), and K content was determined by flame photometry (Rich, 1965). Nutrient concentration of each structure was multiplied by the respective dry biomass and summed to obtain total P and K.

After physiological maturity, grain yield was determined by harvesting all plants in a 5- m^2 area and separating grains with a stationary thresher. Grain moisture was determined using a calibrated grain moisture meter and grain yield adjusted to a standard moisture content of 140 g kg^{-1} . Harvest occurred on 1 and 13 March for Exp. 1 and 2, respectively.

Statistical Analysis

Statistical analysis was conducted for each experiment separately, because most of the variables showed differences between experiments that did not allow a pooled analysis (i.e., lack of homogeneity of variances between experiments). An ANOVA was conducted for final leaf number, and GLAI was determined at each stage of maize development, where treatment (different combinations of P and K rates) was considered as a fixed effect and replication as a random effect. Orthogonal linear contrasts were made for evaluating P and K main effects and the $P \times K$ interaction (Petersen, 1994): (i) P0K0 and P0K2 vs. P2K0 and P2K2 for P main effect, (ii) P0K0 and P2K0 vs. P0K2 and P2K2 for K main effect, and (iii) P2K2 and P0K0 vs. P2K0 and P0K2 for the $P \times K$ interaction.

RESULTS

Weather Conditions

Weather conditions differed between Exp. 1 and 2. Average daily mean temperature in Exp. 1 was greater than in Exp. 2 (22.2 vs. 21.9°C), and so was the average daily radiation (23.3 vs. 20.7 MJ m^{-2}). Cumulative radiation in Exp. 1 was slightly less than in Exp. 2 (2365 and 2405 MJ m^{-2}) due to a longer crop growth period in Exp. 2 (nine more days). During the presilking period, average daily mean temperature was 19.1 and 17.2°C , and average daily radiation was 20.8 and 20 MJ m^{-2} for Exp. 1 and 2, respectively. These figures were lower than what was observed in the post-silking period, where average daily mean temperature was 24 and 24.2°C and average daily radiation was 24.7 and 23.9 MJ m^{-2} for Exp. 1 and 2, respectively.

Aboveground Biomass, Grain Yield, and Nutrient Uptake

Aboveground biomass at physiological maturity in the P2K2 treatment was 18,600 and 19,900 kg ha^{-1} in Exp. 1 and 2, respectively. Phosphorus deficiency (i.e., P0K2 vs. P2K2) decreased biomass during early stages in both experiments (Fig. 1). The greatest differences were at V5 in Exp. 1 (57% reduction) and from V6 to R1 in Exp. 2 (46% average reduction). At physiological maturity, reductions in biomass due to P deficiency were 24 and

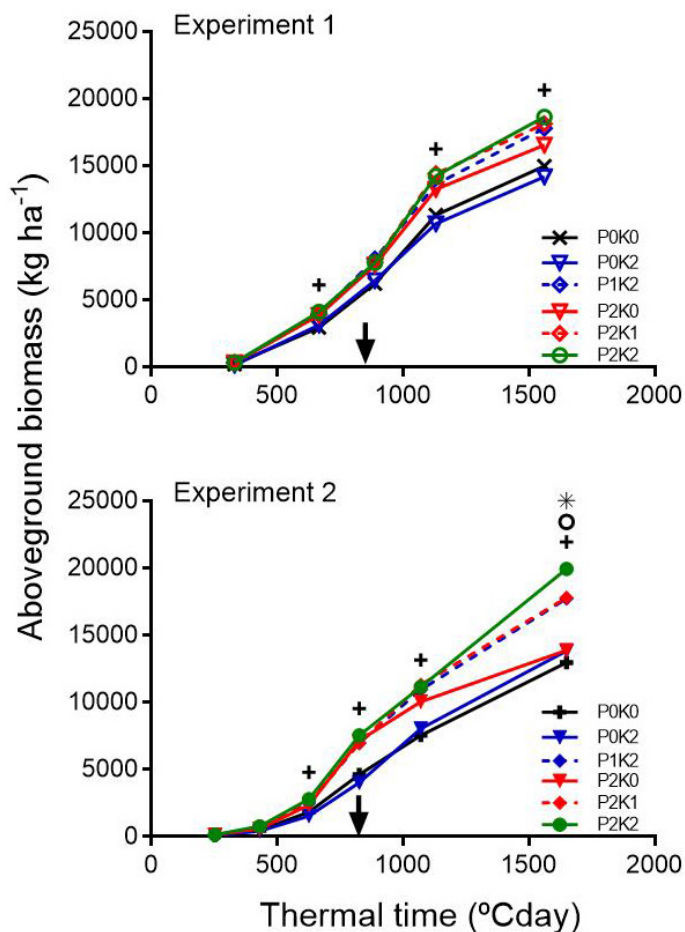


Fig. 1. Aboveground biomass as a function of thermal time from emergence to physiological maturity in maize under different levels of P and K fertilization in Exp. 1 and 2. Three levels of fertilizer P (0 [P0], 40 [P1], and 60 [P2] kg P ha⁻¹) and three levels of fertilizer K (0 [K0], 45 [K1], and 75 [K2] kg K ha⁻¹) were used. Black crosses indicate significant differences for each moment between P2K2 and P0K2 (i.e., response to P). Circles indicate significant differences between P2K2 and P2K0 (i.e., response to K), and asterisks significant P × K interaction (P2K2 and P0K0 vs. P2K0 and P0K2). Arrows indicate time of silking.

31% in Exp. 1 and 2, respectively. Potassium addition (i.e., P2K0 vs. P2K2) did not cause biomass changes during the crop cycle in Exp. 1, but a trend with an 11% reduction ($p < 0.08$) was observed at physiological maturity (Fig. 1). This K deficiency effect was larger in Exp. 2, with a 30% reduction at physiological maturity (Fig. 1).

Phosphorus deficiency (i.e., P0K2 vs. P2K2) reduced grain yield by 26 and 30% in Exp. 1 and 2, respectively (Table 1). On the other hand, K deficiency (i.e., P2K0 vs. P2K2) did not affect grain yield in Exp. 1 but reduced it by 35% in Exp. 2.

Averaging across experiments, P deficiency reduced P uptake by 43% and stover P by 26%, whereas grain P was significantly reduced by 32 only in Exp. 1. Due to its effects on biomass accumulation, P deficiency also reduced K uptake by 26 and 34% in Exp. 1 and 2, respectively. Potassium deficiency reduced K uptake by 42% in Exp.

2 without effects in Exp. 1. Potassium deficiency did not modify grain K but reduced stover K in both experiments. Due to its effects on biomass accumulation, K deficiency also reduced P uptake by 30% in Exp. 2.

Leaf Appearance Rate and Final Leaf Number

Leaf appearance rate was similar in P2K2 in Exp. 1 and 2 (0.0224 and 0.0232 leaves °C d⁻¹, respectively). Phosphorus deficiency (P0K2 vs. P2K2) significantly decreased LAR by 7% in Exp. 1 (Fig. 2). In Exp. 2, LAR was significantly reduced in the P0K0 and P0K2 treatments by 10% with respect to P2K2. No effect of K addition was observed in both experiments. In both experiments, final leaf number did not differ among all treatments and averaged ~17 leaves (Table 2).

Individual Leaf Area

Both P and K deficiencies decreased ILA within each position in the stem. The effect of P deficiency (P0K2 vs. P2K2) was greater (a decrease of 14 and 22% in ILA, on average, in Exp. 1 and 2, respectively) than K deficiency (P2K0 vs. P2K2) (11 and 16% in Exp. 1 and 2). Equation [1] satisfactorily described ILA along the main stem, with r^2 values >0.98 (Fig. 3). Phosphorus and K deficiencies significantly affected the parameters of Eq. [1] (Table 3). Parameter A_0 (area of the largest leaf) significantly decreased in P0K0 (13 and 25%), P0K2 (15 and 20%), and P2K0 (7 and 10%) with respect to P2K2 in Exp. 1 and 2, respectively. In Exp. 2, a significant increase (17%) in parameter b (amplitude) was observed in treatments without P addition (P0K0 and P0K2 vs. P2K2). These results, together with the lack of changes in parameter c (degree of skewness), demonstrated no shifts in the symmetry of the curve by P or K deficiencies.

Leaf Senescence

The parameter Y_0 in Eq. [3], which represents the fraction of senesced leaf area at thermal time zero (emergence), did not differ significantly between treatments. Therefore, a common value was considered in each experiment for this parameter (1.68×10^{-5} and 1.12×10^{-3} in Exp. 1 and 2, respectively). In Exp. 1, the relative senescence rate (parameter k in Eq. [3]) was higher than in Exp. 2 (Fig. 4). Senescence progressed slowly until ~1100°C d (the start of effective grain filling), showing FSLAI values <0.1 in both experiments at that moment. Phosphorus deficiency (P0K2 vs. P2K2) slightly reduced the rate of leaf senescence by 2% ($p < 0.05$) in Exp. 1 and showed the same trend ($p < 0.10$) in Exp. 2 (Table 4). In Exp. 1, P2K1 was the only treatment that had a slightly higher senescence rate than P2K2 (1%). In Exp. 2, all treatments with intermediate levels or without K addition (i.e., P0K0, P2K1, and P2K0) had higher leaf senescence rates than P2K2. Treatment P2K0 had with the highest increase in leaf

Table 1. Grain yield and nutrient absorption and concentration at plant maturity with different levels of P and K.

Treatment†	Grain yield	Total P	Total K	Grain P	Stover P	Grain K	Stover K
		kg ha ⁻¹		mg g ⁻¹			
Exp. 1							
P0K0	7,099a‡	16a	72a	1.70a	0.31a	4.62	5.04
P0K2	7,092a	16a	72a	1.87ab	0.30a	4.63	5.63
P1K2	8,858b	27b	95b	2.59cd	0.36ab	4.86	5.86
P2K0	8,759b	30b	82ab	3.04d	0.40b	4.95	4.96
P2K1	9,269b	26b	91b	2.32bc	0.41b	4.65	5.28
P2K2	9,577b	28b	98b	2.52cd	0.33a	4.72	5.89
<i>p</i> value							
Treatment effect	<0.01	<0.01	0.01	<0.01	0.04	0.13	0.16
Contrasts§							
P main effect	<0.01	<0.01	<0.01	<0.01	0.03	0.04	0.76
K main effect	0.26	0.60	0.17	0.37	0.14	0.29	0.02
P × K interaction	0.26	0.62	0.19	0.08	0.35	0.22	0.57
Exp. 2							
P0K0	7,298a	16a	63a	1.98	0.35a	4.50	5.27ab
P0K2	7,340a	17a	72ab	1.89	0.38ab	4.50	6.07b
P1K2	9,532b	23abc	94cd	1.92	0.54c	4.69	6.05b
P2K0	6,817a	21ab	63a	2.29	0.59c	4.57	4.50 a
P2K1	9,733b	25bc	90bc	2.13	0.49bc	4.37	5.86b
P2K2	10,515b	30c	109d	2.37	0.50bc	4.63	6.43b
<i>p</i> value							
Treatment effect	<0.01	0.01	<0.01	0.68	0.01	0.52	0.03
Contrasts							
P main effect	<0.01	<0.01	<0.01	0.14	<0.01	0.39	0.60
K main effect	<0.01	0.06	<0.01	0.97	0.54	0.77	<0.01
P × K interaction	<0.01	0.10	0.01	0.73	0.17	0.77	0.16

† P0, 0 kg P ha⁻¹; P1, 40 kg P ha⁻¹; P2, 60 kg P ha⁻¹; K0, 0 kg K ha⁻¹; K1, 45 kg K ha⁻¹; K2, 75 kg K ha⁻¹.

‡ Within columns, means followed by a common letter are not significantly different (LSD, *p* = 0.05).

§ P main effect: P0K0 and P0K2 vs. P2K0 and P2K2, K main effect: P0K0 and P2K0 vs. P0K2 and P2K2, P × K interaction: P0K0 and P2K2 vs. P0K2 and P2K0.

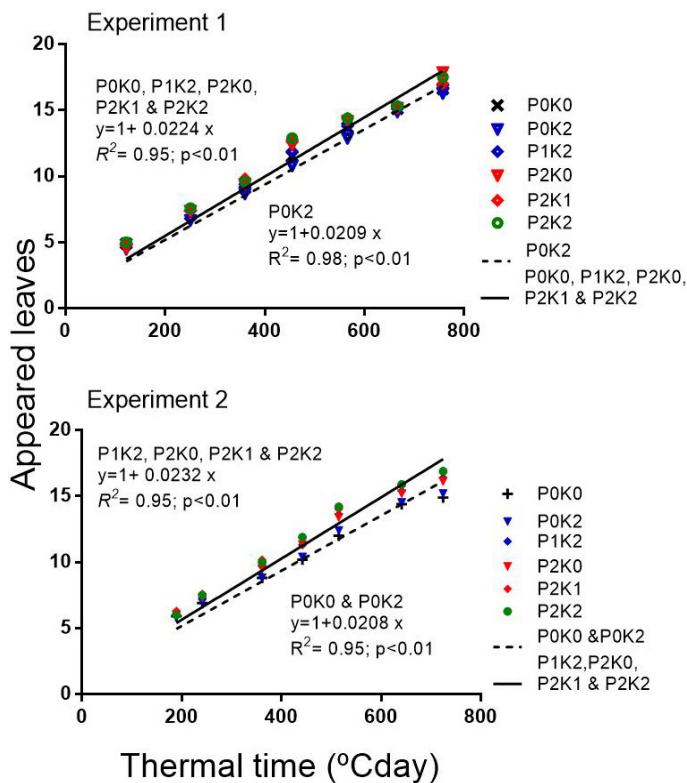


Fig. 2. Visible leaves as a function of thermal time in Exp. 1 and 2. Treatments that did not differ were grouped and a common fit is shown. Three levels of fertilizer P (0 [P0], 40 [P1], and 60 [P2] kg P ha⁻¹) and three levels of fertilizer K (0 [K0], 45 [K1], and 75 [K2] kg K ha⁻¹) were used.

senescence rate with respect to P2K2 (12%). Furthermore, a P × K interaction was observed, since the response to K shortage depended on P level, as P0K0 had a significantly lower leaf senescence rate than P2K0 (Table 4).

Green Leaf Area Index Evolution

Maximum GLAI in the fully fertilized treatment (P2K2) was similar between experiments (3.6 and 3.2 in Exp. 1 and 2, respectively) and was reached around silking at 757

Table 2. Final leaf number per plant in maize fertilized with different levels of P and K.

Treatment†	Exp. 1	Exp. 2
P0K0	17.3	16.9
P0K2	17.2	17.0
P1K2	17.1	17.0
P2K0	17.1	16.9
P2K1	17.1	17.0
P2K2	17.2	17.0
<i>F</i> test probability		
Treatment effect	0.56	0.39
Contrasts‡		
P main effect	0.40	0.58
K main effect	0.61	0.11
P × K interaction	0.40	0.27

† P0, 0 kg P ha⁻¹; P1, 40 kg P ha⁻¹; P2, 60 kg P ha⁻¹; K0, 0 kg K ha⁻¹; K1, 45 kg K ha⁻¹; K2, 75 kg K ha⁻¹.

‡ P main effect: P0K0 and P0K2 vs. P2K0 and P2K2, K main effect: P0K0 and P2K0 vs. P0K2 and P2K2, P × K interaction: P0K0 and P2K2 vs. P0K2 and P2K0.

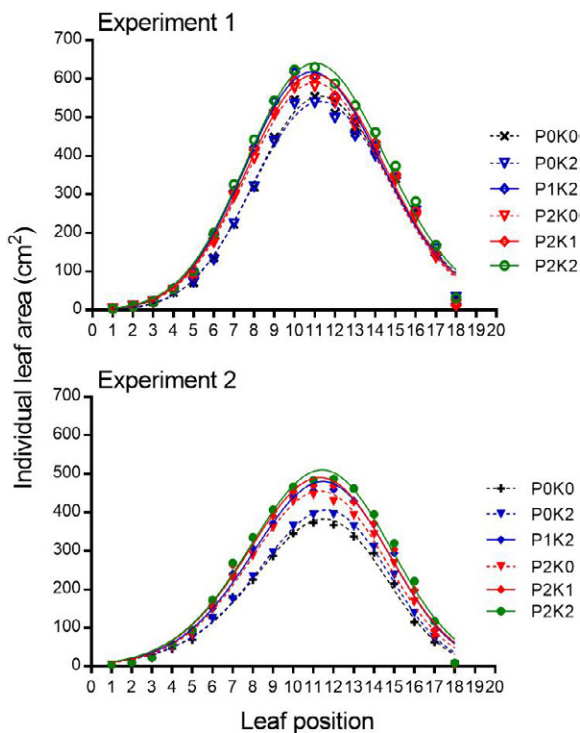


Fig. 3. Individual leaf area as a function of leaf number in Exp. 1 and 2. Lines are the fitted Eq. [1]. Statistical analysis of the parameters of the function is shown in Table 2. Three levels of fertilizer P (0 [P0], 40 [P1], and 60 [P2] kg P ha⁻¹) and three levels of fertilizer K (0 [K0], 45 [K1], and 75 [K2] kg K ha⁻¹) were used.

and 776°C d in Exp. 1 and 2, respectively (Fig. 5). Phosphorus deficiency (P0K2 vs. P2K2) reduced GLAI by 20 and 32%, averaged across all sampling dates in Exp. 1 and 2, respectively. Reductions in GLAI due to K deficiencies (P2K0 vs. P2K2) were relatively small, averaging 13 and 25% in Exp. 1 and 2, respectively. A significant P × K interaction was observed in intermediate stages, between 666 and 1200°C d and between 515 and 1400°C d in Exp. 1 and 2, respectively. The relative reduction in GLAI due to P deficiency declined during the crop cycle, whereas the reduction due to K deficiency increased with time (Fig. 5). In relative terms, under no K deficiency (K2), P0 and P1 showed a relative decrease of 34 and 38% and 10 and 14% in GLAI, with respect to P2 before silking. After this stage, this decrease was 7 to 26 and 0 to 8% for P0 and P1, respectively in both experiments. Under no P deficiency (P2), K0 and K1 showed a stronger relative reduction in GLAI after silking (13 to 29% in K0 and 10 to 11% in K1) than before silking (12 to 20% in K0 and 4 to 2% in K1).

In both experiments, a similar trend in relative GLAI (with respect to P2K2) was observed between treatments, independent of the differences in absolute values (Fig. 6). P0K0 and P0K2 showed similar relative GLAI early in the crop cycle. In contrast, relative GLAI values in P0K0 were similar to those in P2K0 towards the end of the cycle. This would indicate that P was more limiting early in the crop cycle, whereas K was more restrictive for GLAI

Table 3. Parameters of Eq. [1], fit to the individual leaf area profile in maize with different levels of P and K fertilization.

Treatment‡	Parameter†			
	A ₀	b	X ₀	c
Exp. 1	cm ²			
P0K0	554.7**	0.044	11.30	7.3 × 10 ⁻⁴
P0K2	541.1**	0.043	11.28	7.9 × 10 ⁻⁴
P1K2	617.8	0.043	10.86	8.2 × 10 ⁻⁴
P2K0	589.9**	0.043	10.99	5.8 × 10 ⁻⁴
P2K1	610.9	0.043	11.02	5.5 × 10 ⁻⁴
P2K2	640.6	0.041	11.02	6.6 × 10 ⁻⁴
Exp. 2				
P0K0	383.0**	0.048*	11.52	-1.6 × 10 ⁻³
P0K2	406.3**	0.048*	11.63	-1.6 × 10 ⁻³
P1K2	480.1§	0.043	11.47	-8.6 × 10 ⁻⁴
P2K0	456.0**	0.044	11.34	-8.5 × 10 ⁻⁴
P2K1	490.5	0.041	11.33	-6.6 × 10 ⁻⁴
P2K2	510.1	0.041	11.43	-6.5 × 10 ⁻⁴

* Significant at the 0.05 probability level compared with P2K2.

** Significant at the 0.01 probability level compared with P2K2.

† A₀, area of the largest leaf; b, degree of breadth; c, degree of skewness; X₀, position of the largest leaf.

‡ P0, 0 kg P ha⁻¹; P1, 40 kg P ha⁻¹; P2, 60 kg P ha⁻¹; K0, 0 kg K ha⁻¹; K1, 45 kg K ha⁻¹; K2, 75 kg K ha⁻¹.

§ Significant at the 0.1 probability level compared with P2K2.

when approaching physiological maturity. Around the middle of the crop cycle, when P and K effects were relatively similar, the P × K interaction was significant.

DISCUSSION

Relative P deficiency, as quantified by the relative decrease in aboveground biomass, was 24 to 31% in both experiments. In terms of P uptake, this deficiency was larger (~43%). These results indicate a similar P shortage as observed by Fletcher et al. (2008), which showed 30 to 38% decrease in biomass, but a more severe P deficiency than in maize studies by Plénet et al. (2000) which showed 8 to 17% reductions. Potassium deficiency in Exp. 2 (i.e., 30% reduction in aboveground biomass and a concomitant 42% decrease in K uptake) was higher than those observed in maize Bordoli and Mallarino (1998) and Wu et al. (2013), who observed 4 to 19% reductions in biomass. Therefore, P deficiency was severe in both years in the present experiments, and for K in Exp. 2. Also, the present study showed that K deficiencies decreased maize growth late in the season, as opposed to P deficiency that was evident beginning in early stages. Grant et al. (2001) indicated higher relative reductions in biomass early in the cycle in P-deficient crops. Mallarino et al. (1999) found that increases in early growth in response to P fertilization in maize (V5–V6) are rarely of similar magnitude when evaluating grain yield. These authors observed no responses to K fertilization in early growth, but low and frequent responses in grain yield.

Phosphorus deficiency delayed leaf appearance, in coincidence with previous studies performed not only in

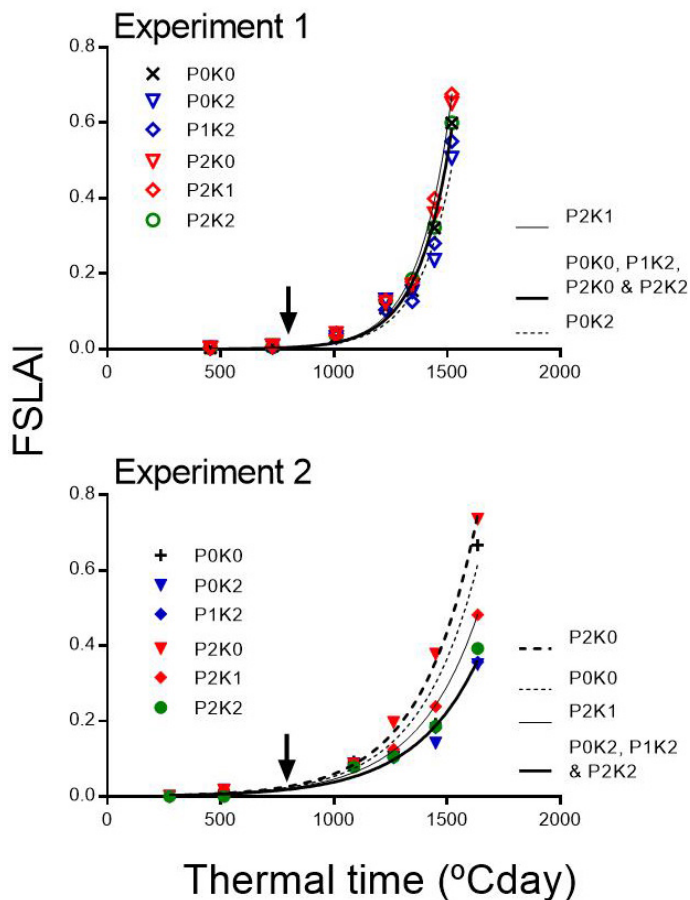


Fig. 4. Fraction of senesced leaf area index (FSLAI) as a function of thermal time from emergence in Exp. 1 and 2. Three levels of fertilizer P (0 [P0], 40 [P1], and 60 [P2] kg P ha⁻¹) and three levels of fertilizer K (0 [K0], 45 [K1], and 75 [K2] kg K ha⁻¹) were used. Treatments that did not differ ($p > 0.05$) were grouped and a common fit is shown. Arrows indicate silking date. Y_0 (FSLAI at thermal time zero [emergence]) was pooled for all treatments in each experiment (1.68×10^{-5} and 1.12×10^{-3} in Exp. 1 and 2, respectively). Values of parameter k (relative senescence rate) in Exp. 1 were P0K2 = 6.75×10^{-3} ; P0K0, P1K2, P2K0, and P2K2 = 6.87×10^{-3} ; P2K1 = 6.97×10^{-3} ; in Exp. 2, they were P0K2, P1K2, and P2K2 = 3.53×10^{-3} ; P0K0 = 3.85×10^{-3} ; P2K0 = 3.97×10^{-3} ; P2K1 = 3.70×10^{-3} . For all fitted functions, $R^2 > 0.93$ and $p < 0.01$.

Table 4. Parameter k of Eq. [3] (leaf senescence rate) that fits the evolution of FSLAI (senescence expressed as a fraction of total leaf area) in maize with different levels of P and K fertilization.

Treatment†	Exp. × 10 ⁻³ °C d ⁻¹	
	Exp. 1	Exp. 2
P0K0	6.82	3.92**
P0K2	6.69*	3.55‡
P1K2	6.75‡	3.58
P2K0	6.88	4.03**
P2K1	6.91**	3.77**
P2K2	6.83	3.63

* Significant at the 0.05 probability level compared with P2K2.

** Significant at the 0.01 probability level compared with P2K2.

† P0, 0 kg P ha⁻¹; P1, 40 kg P ha⁻¹; P2, 60 kg P ha⁻¹; K0, 0 kg K ha⁻¹; K1, 45 kg K ha⁻¹; K2, 75 kg K ha⁻¹.

‡ Significant at the 0.1 probability level compared with P2K2.

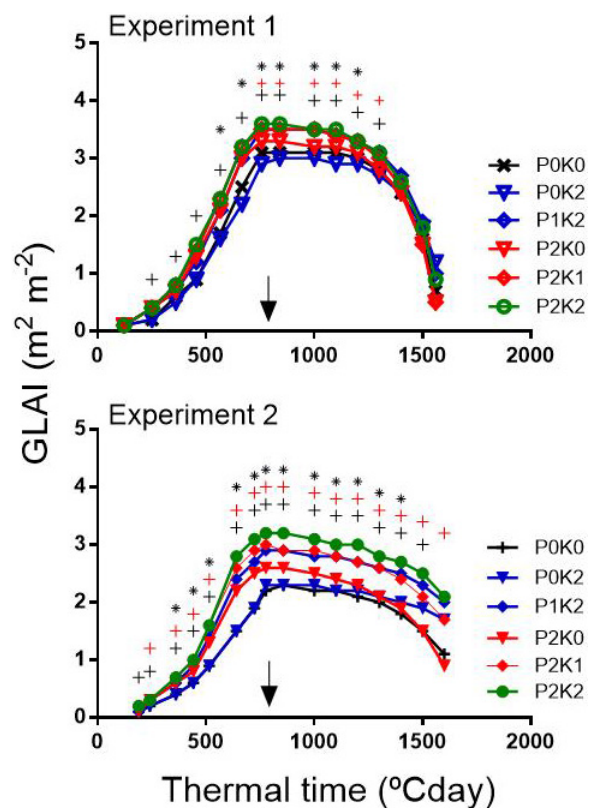


Fig. 5. Green leaf area index (GLAI) as a function of thermal time from emergence in Exp. 1 and 2. Three levels of fertilizer P (0 [P0], 40 [P1], and 60 [P2] kg P ha⁻¹) and three levels of fertilizer K (0 [K0], 45 [K1], and 75 [K2] kg K ha⁻¹) were used. Black crosses indicate significant ($p < 0.05$) differences for each moment between P2K2 and P0K2 (P deficiency), red crosses indicate differences between P2K2 and P2K0 (K deficiency), and asterisks indicate significant interaction (P2K2 and P0K0 vs. P2K0 and P0K2). Arrows indicate silking date.

maize (Plénet et al., 2000), but also in wheat (Gutiérrez-Boem and Thomas, 1998; Rodríguez et al., 1998b) and barley (*Hordeum vulgare* L.; Prystupa et al., 2003) under controlled conditions. In the present study, decreases in LAR in response to K deficiency were not significant, as opposed to Jordan-Meille and Pellerin (2004), who observed small differences in this rate under K-deficient conditions in field-grown maize. The inverse of the LAR, the phyllochron, is determined by the timing of leaf initiation at the stem apex and duration of leaf tip elongation through the whorl of mature sheaths. The duration of leaf tip elongation through the whorl depends on the elongation rate and sheath length (Skinner and Nelson, 1995). An increase in phyllochron may be a consequence of a reduction in leaf expansion rate, as was observed with P deficiency in maize (Colomb et al., 2000; Plénet et al., 2000). In P-deficient wheat, Rodríguez et al. (1998b) determined that increases in phyllochron were due to a reduction in leaf differentiation rate and leaf elongation rate through the whorl. In the present study, it is likely that the reduced LAR was a consequence of a reduced leaf expansion rate.

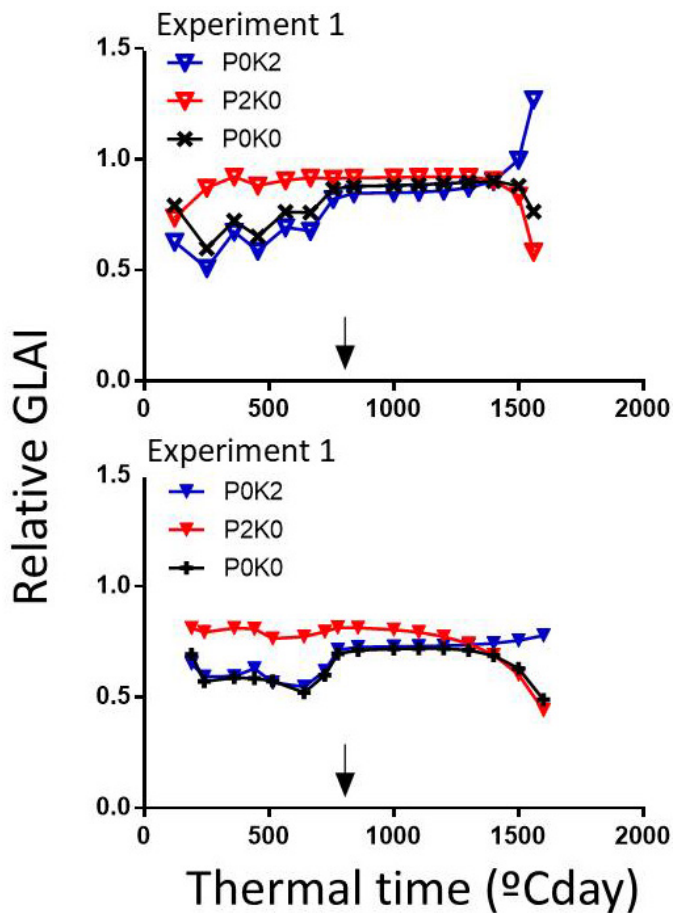


Fig. 6. Relative green leaf area index (GLAI) with respect to P2K2, as a function of thermal time from emergence in Exp. 1 and 2. Arrows indicate silking date. Three levels of fertilizer P (0 [P0], 40 [P1], and 60 [P2] kg P ha⁻¹) and three levels of fertilizer K (0 [K0], 45 [K1], and 75 [K2] kg K ha⁻¹) were used.

Final leaf number in maize is sensitive to changes in factors affecting crop development such as photoperiod (Muchow and Carberry, 1989) and temperature (Tollenaar and Hunter, 1983). Some studies showed no changes in final leaf number as modified by water (Muchow and Carberry, 1989) or N (Uhart and Andrade, 1995) shortage. Phosphorus (Colomb et al., 2000; Plénet et al., 2000; Fletcher et al., 2008) or K (Jordan-Meille and Pellerin, 2004) deficiency did not alter final leaf number in maize. In wheat, some studies have shown that final leaf number on the main stem was not altered under P deficiency; however, total leaf area decreased because of a reduction in tiller number (Gutiérrez-Boem and Thomas, 1998; Rodríguez et al., 1998b). In the present study, neither P, K, nor their interaction modified final leaf number. It is likely that the magnitude of nutrient deficiency in prevailing field conditions was not so severe as to affect this process, as was observed by Salvagiotti and Miralles (2007) with S deficiency in wheat.

Individual leaf area in each leaf position was strongly decreased by P deficiency and, to a lesser extent, by K deficit, even in Exp. 2 where P and K deficiency were

similar in terms of growth and nutrient uptake. Previous evidence also showed that both P (Plénet et al., 2000) and K shortage (Jordan-Meille and Pellerin, 2004) reduce ILA. The size of the largest leaf (parameter A_0 in Eq. [1]) was the most affected by P and K shortage. No effects of P and K deficiency were detected on the symmetry of the leaf area profile. Yang and Alley (2005) proposed that in addition to genetic control, assimilate availability for leaf growth depends on photosynthates produced by previous expanded leaves (determining the raising part of the curve) and the strength of other sinks such as stem, roots, or ears (which determines the declining part of this curve). Beyond these theoretical assumptions, there is a wide correlation among parameters of Eq. [1] (Keating and Wafula, 1992; Yang and Alley, 2005). This correlation, together with the greater stability of parameters other than A_0 , has allowed accurate modeling of leaf area per plant, only by knowing A_0 (Fournier and Andrieu, 1998; Valentinuz and Tollenaar, 2006; Boomsma et al., 2009). In line with this, our results show that P and K deficiencies affect mostly A_0 . An alternative approach for modeling leaf area of P- and K-stressed crops could be linking A_0 with an indicator of stress, such as the P stress factor of the Agricultural Production Systems simulator (APSIM) model (Delve et al., 2009). In this way, leaf area expansion and C routine could be decoupled, which is important because of the differential effect of many factors on expansion and growth (Tardieu et al., 1999).

Potassium shortage significantly accelerated senescence in the present study. This result is opposed to earlier evidence in maize (Jordan-Meille and Pellerin, 2004) that detected little increase (around 5%) on senescence during early stages in the crop cycle, disappearing by silking, and sharp reductions on leaf area expansion. In agreement with the present study, a similar senescence pattern with time in response to K deficiency was observed in cotton (*Gossypium hirsutum* L.; Brouder and Cassman, 1990; Wright, 1999). Soil constraints (Brouder and Cassman, 1990) or source-sink imbalances caused by large growing sinks (Wright, 1999) were postulated as feasible explanations of this late expression of senescence. From the plant physiological perspective, K deficiency may reduce assimilate transport to the roots, since K is required for sucrose loading in the phloem (Cakmak et al., 1994; Marschner et al., 1996; Hermans et al., 2006) that may lead to a decrease in root/shoot ratio (Hermans et al., 2006). Ma et al. (2013) showed that a drop in root/shoot ratio was enhanced during reproductive stages in K deficient wheat plants. In a study of sunflower (*Helianthus annuus* L.) hybrids differing in the stay-green trait that were irrigated or subjected to terminal drought, loss of root functionality preceded canopy senescence (Lisanti et al., 2013). It is likely that K deficiency impaired root functionality and triggered canopy senescence. Beyond this possible explanation, soil K availability in the present study may have decreased during late stages

of the crop cycle, since it had low concentrations of both exchangeable and nonexchangeable K (Horra et al., 2000).

The slight decrease in the rate of leaf senescence observed in P-deficient maize in the present study is consistent with previous research by Colomb et al. (2000) and Plénet et al. (2000), where final biomass reduction was ~15%. However, Fletcher et al. (2008) did not observe differences in senescence in P-deficient in sweet corn, even with larger deficiencies achieved (final biomass reduction of ~30%). This differential effect on senescence could be related to the crop type (reduced demand by grain) or environmental conditions. In P-deficient soybean [*Glycine max* (L.) Merr.] plants growing in pots, with biomass and yield reductions of 30%, no trend was found in multiple functional features of senescence (Crafts-Brandner, 1992).

Green leaf area is the consequence of the counteracting processes of expansion and senescence. Phosphorus deficiency had greater effects on GLAI early in the crop cycle by reducing LAR and ILA. In contrast, K deficiencies slightly decreased GLAI in earlier stages and sharply decreased it during later stages of the crop cycle, because of a rise in leaf senescence rate. These results offer insights for physiological breeding for P and K stress tolerance. Plant green cover is a trait able to be screened with remote sensing phenotyping methods (Araus and Cairns, 2014). A more sensitive period for phenotyping P stress tolerance in maize would be in the mid-vegetative stages, between 300 and 700°C d (V9–V15 stages). Potassium stress should be phenotyped in effective grain filling, from 1200°C d up to physiological maturity.

In summary, we rejected the hypothesis, as effects of K and P shortage on leaf development in maize were different, even when both had similar dynamics in the soil. Phosphorus deficiency strongly decreased LAR and ILA, whereas K deficiency reduced ILA to a lesser extent. However, K deficiency had an important effect on leaf senescence. As a result of the counteracting processes of expansion and senescence, the effect of P deficiency on GLAI tended to attenuate as crop cycle progressed, whereas K deficiency showed important effects late in the crop cycle. Interaction of P × K was significant for GLAI at intermediate stages, where both deficiencies converged.

The results of the present study, in agreement with previous research, show that LAR and senescence were affected by P or K shortage; however, this study shows for the first time the interaction between both nutrients in determining these traits and also that both nutrients affect green leaf area in different moments of the crop growth cycle.

Conflict of Interest

The authors declare that there is no conflict of interest.

Acknowledgments

We thank INTA Mercedes staff, especially Juan Ramón Fernández and Rubén Molina, for field assistance. This work was

funded by INTA Argentina (Instituto Nacional de Tecnología Agropecuaria) and IPNI (International Plant Nutrition Institute) Southern Cone.

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