How long seed P reserve can support maximal growth rate of maize seedling?

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How long seed P reserve can support maximal growth rate of maize seedling?

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TCEM INRA Bordeaux, France

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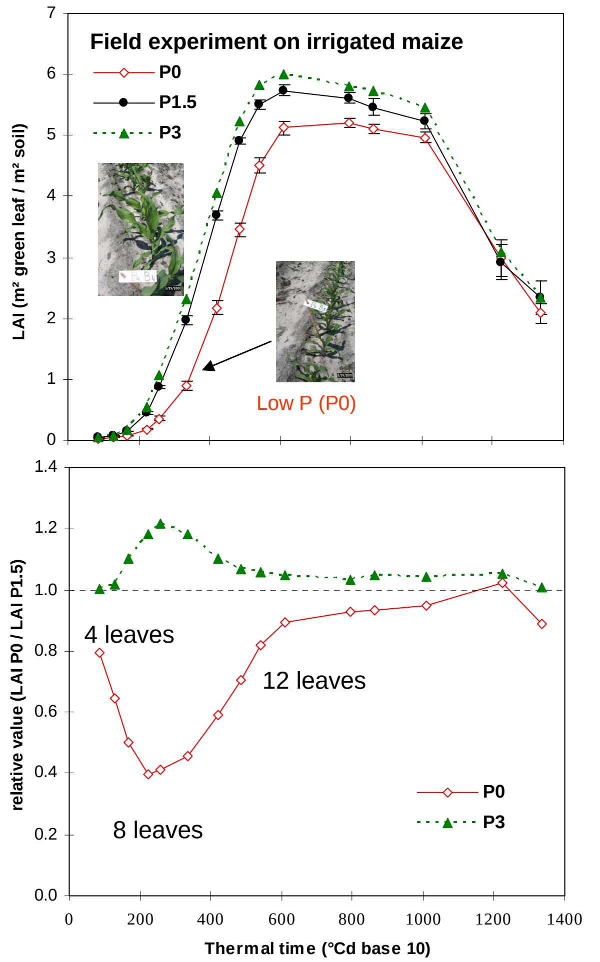
Effects of P limitation on crop growth

Consistent results reported in the literature have shown that under **moderate P deficiency :**

⇨the leaf area index is **early** reduced

- Slower rate of leaf appearance
- Reduce leaf size
- the lower leaf elongation rate was mainly associated with **a shorter leaf growth zone and reduced cell production rate in meristemic zone** (Assuero et al., 2003)



(Plenet et al., 2000)

Effects of P limitation on crop growth

Early growth is a key factor for the final crop yield (Grant et al., 2001, Sekiya et al 2010)

P deficiency reduced leaf appearance and expansion during early stages (Plenet et al 2000, Colomb et al., 2000) and subsequently reduced C assimilation.

Consequently, although root/shoot ratio is increased, root growth is reduced which have an **additional impact on P uptake capacity** (Mollier et al 1999)

So small early growth differences can cause big effects on plant P responsiveness (Wissuwa et al 2003)

~~~~~~~~~~~~~~~~~~~~~~~~~

Seed P is the only P source available to sustain the initial growth of seedlings.

Seed P content is positively correlated with SDW at 21 DAS of 18 cereal genotypes when soil P availability is severely restricted (Liao et al 2008).
The influence of seed P on biomass accumulation decreases with time.

Table 5. Liao et al 2008 Correlation coefficient between seed-P content and shoot dry weight and shoot P content

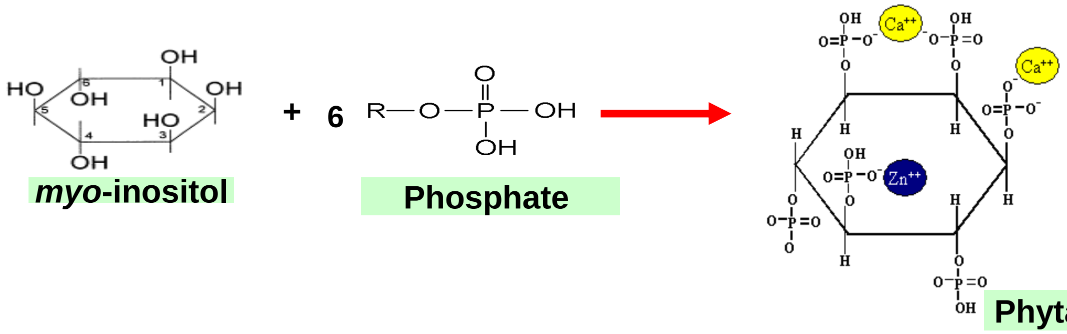
P treatment	Ferrosol				Kandosol			
	21 DAS		35 DAS		21 DAS		35 DAS	
	SDW	SP	SDW	SP	SDW	SP	SDW	SP
Low P	0.49**	0.45**	0.58**	0.41**	0.31*	0.06	0.01	0.01
High P	0.04	0.01	0.01	0.03	0.04	0.02	0.01	0.01

Seed P reserves

30%-90% of seed P occurs in form of phytate

(Lott et al., 1995 Frossard et al 2000, Reddy 2002)

Phytate is a complex salt of *myo*-inositol hexa*kis*phosphoric acid : *myo*-inositol 1, 2, 3, 4, 5, 6-hexa*kis*phosphate (Park et al., 2006)



***myo*-inositol** **Phosphate** **Phytate** ($C_6H_{18}O_{24}P_6$)

During germination, phytate is broken down by the action of phytase (Pilu et al., 2003) and phosphate is transferred to growing seedling compartments

In maize, phytase activity increased from 1-5 days, reaches a plateau between day 5 and 7 (Laboure et al., 1993)
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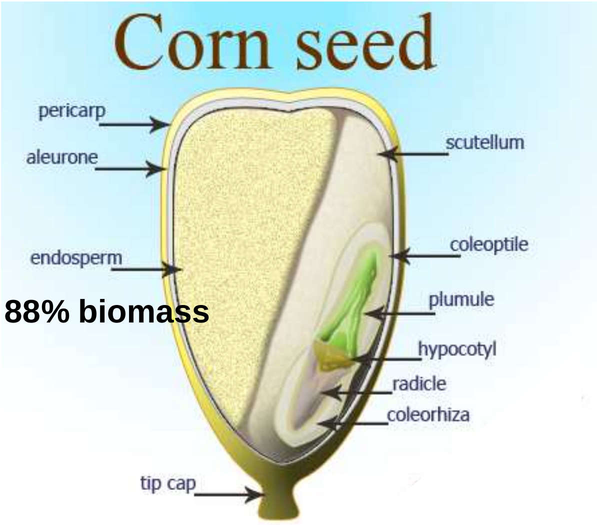
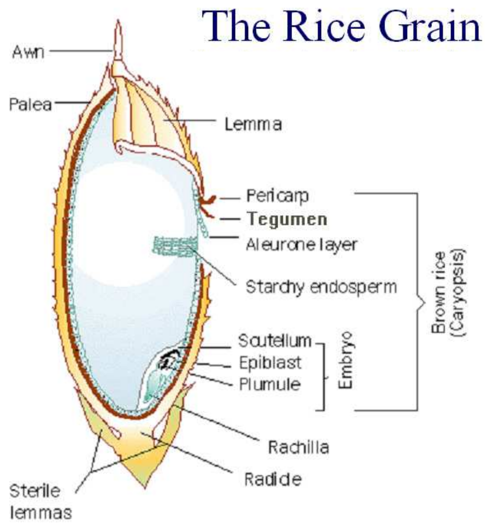
Localization of seed P reserves





Phytate P localization in the seed

	Corn seed	Rice seed
Embryo	**90%** ***(in scutellum)***	**10%**
Aleurone layer	**10%**	**90%**
Endosperm	**<1%**	**<1%**

Lott et al., 1995
Park et al., 2006
Zhu et al., 2001

Objectives of our study

From this brief review on early effects of P limitation, the following questions arise :

➢ Are seed P reserves contribute significantly to seedling P nutrition until external P uptake by roots starts?

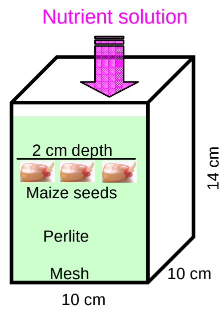
➢ Is seed P remobilization a limiting step for seedling P nutrition? How long seed P reserves can support seedling P requirement?

➢ High seed P reserves selection and remobilization improvement are they valuable opportunities to improve seedling growth under low P conditions?

To address these questions we need to accurately quantify :

- Kinetics of seed P remobilization during germination
- Exact time of exogenous P uptake by seedling roots
- The relative contribution of endogenous seed P and exogenous P uptake to seedling P nutrition
- Interactions between seed P remobilization and exogenous P uptake

Experimental approach



Individual Pot

First experiment

- Objectives

  1. Exact kinetics of seed P remobilization and exogenous P uptake
  2. Relationship among C, N and P remobilization in seeds
  3. Relative contribution of both processes to seedling P nutrition

Maize seed P (686 µg P seed^{-1}) & complete nutrient solution P (500 µM)

Second experiment

- Objectives

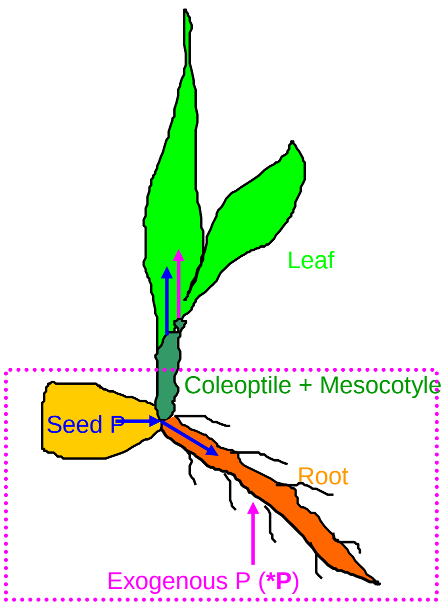
  1. Does the relative contribution of seed P remobilization and exogenous P uptake to seedling P nutrition depend on endogenous or exogenous P availability?
  2. Do both processes have an effect on each other?

Exogenous P	Seed P	
	LS	**HS**
0P	0PLS	0PHS
LP	**LPLS**	**LPHS**
HP	**HPLS**	**HPHS**

Initial seed P (LS : **506** & HS : **952** µg seed^{-1})
Nutrient solution P (0P: **0** , LP : **100** & HP : **1000** µM)

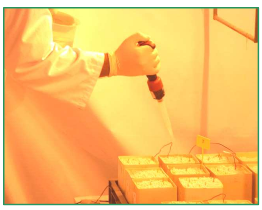
Labelling of nutrient solution with ^{32}P

- The nutrient solution was labelled with ^{32}**P** to identify and quantify the two P fluxes in growing seedlings
- The specific activity of P uptaken by seedlings is equal to the specific activity of P in nutrient solution, it implies that there is no isotopic discrimination during P uptake (Fardeau 1993)



$$({}^{31}P_{seedling})_t = ({}^{32}P_{seedling})_t \,/\, ({}^{32}P_{NS} / {}^{31}P_{NS})_t$$

- P sorption on seedling roots (less than 0.009 µg P cm^{-1})
- *P sorption on perlite (~0)*


Irrigation on each day

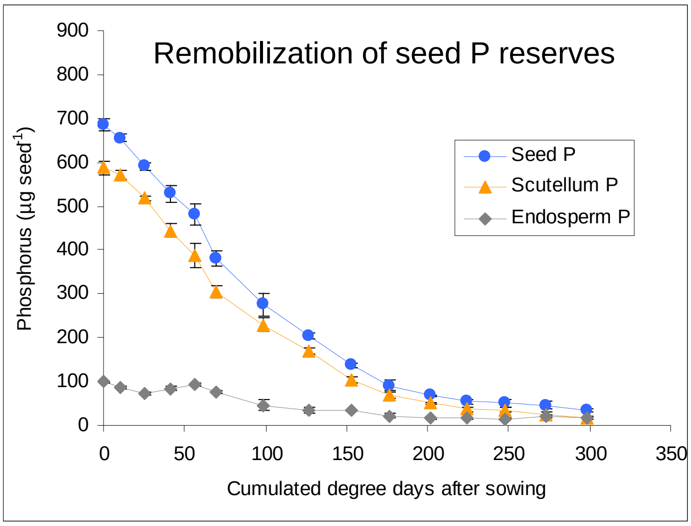

17 days old seedlings


Seedling preparation

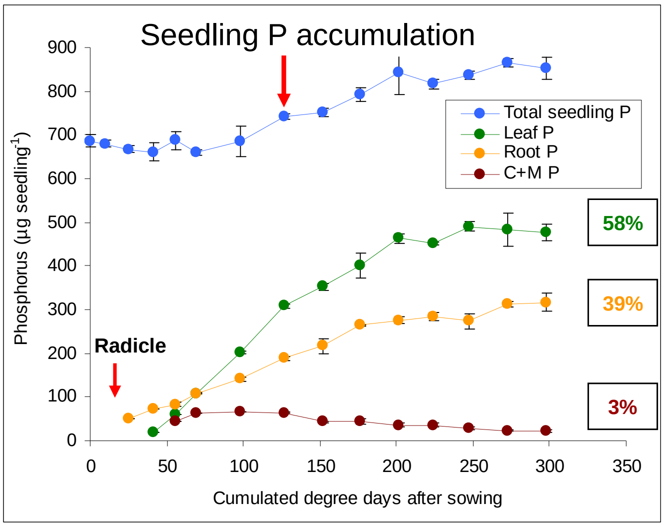

Endosperm, scutellum, C+M, roots, leaves

Allocation and changes of seed and seedling P?

1^{st} experiment



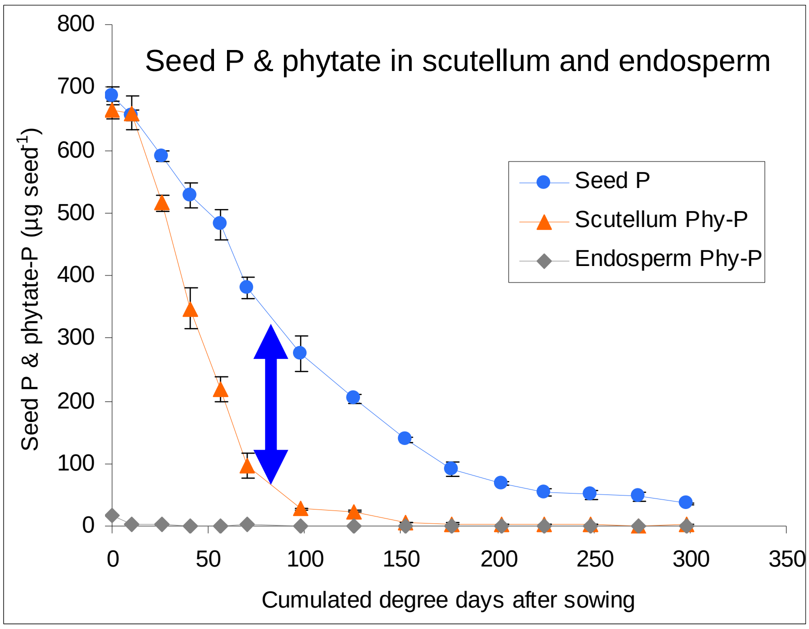
Nadeem et al. 2011a



Nadeem et al. 2011a

- ❖ Main part of initial seed P reserves were stored in scutellum (86%)
- ❖ Up to 202 °C DAS (15^{th} DAS), 92% of scutellum and 84% of endosperm P were remobilized
- ❖ Seedling P accumulation was started soon after radicle emergence and was significant after 7-9^{th} DAS

Changes in seed P, scutellum & endosperm phytate-P

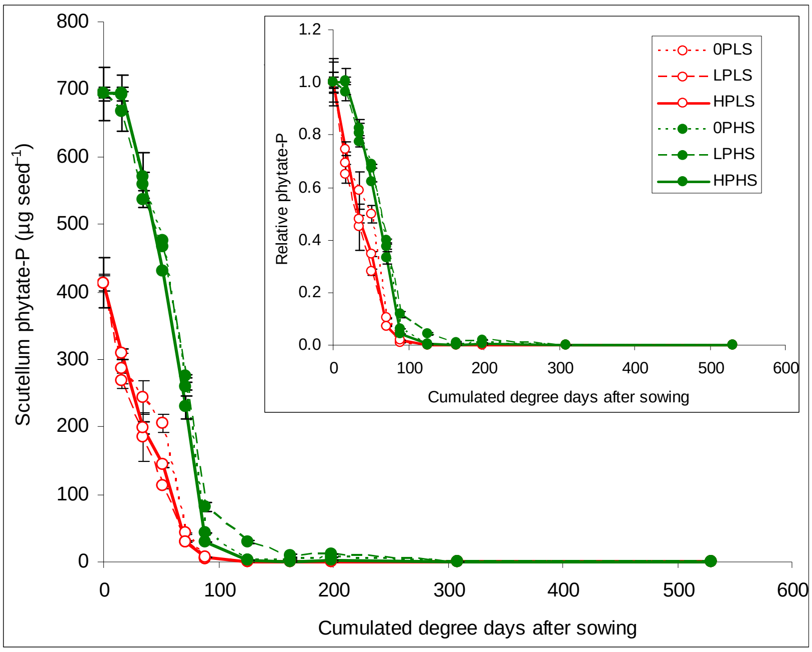


Nadeem et al. 2011a

- ❖ P in seed is mainly stored in the form of phytate-P and is present in scutellum
- ❖ A quick hydrolysis of phytate-P was observed till 126 °C DAS (9^{th} DAS)
- ❖ Quick phytate-P hydrolysis favours the increase in non phytate-P from 26 - 126 °C DAS (1^{st}-9^{th} DAS)

Effect of P treatments on phytate-P hydrolysis?

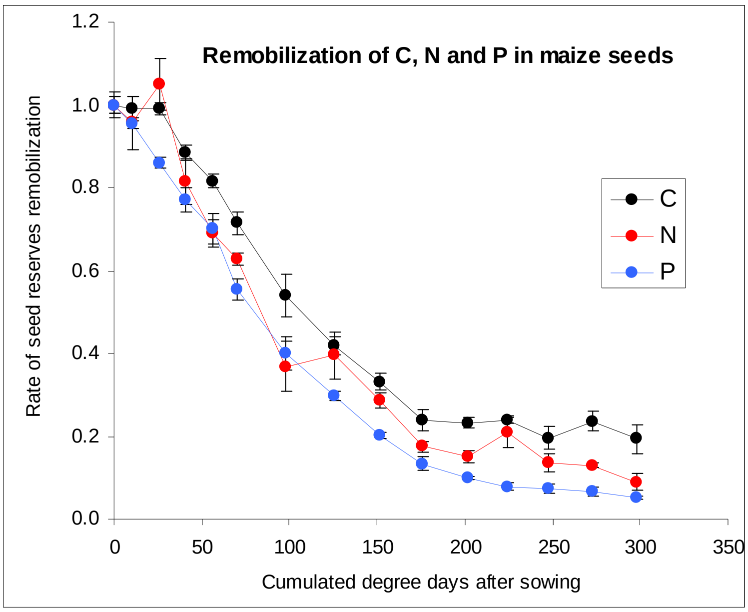
2nd experiment



Nadeem et al. 2011b

- ❖ The phytate-P reserves differe in LS and HS seeds due to initial seed P reserves
- ❖ 98% of phytate-P was hydrolysed till 89 °C DAS in all P treatments
- ❖ Exogenous P has no effect on phytate-P hydrolysis kinetics. Slight effect of endogenous P on phytate hydrolysis kinetics.

Relationship among C, N and P remobilization in seeds?

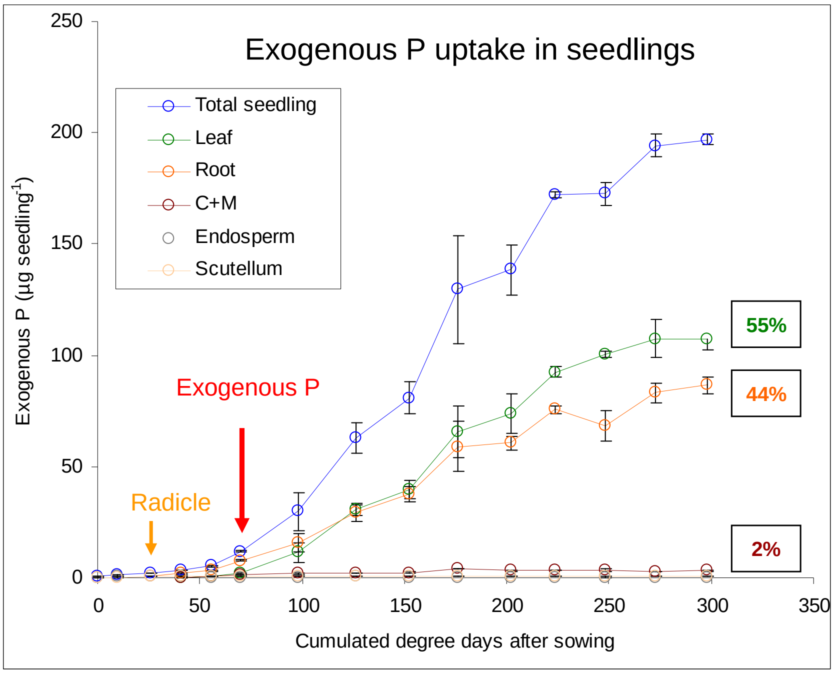


Nadeem et al. 2011a

C and N in endosperm while P in scutellum

❖ P, C and N follows the similar remobilization kinetics during germination and early growth, although they are located in different compartments of maize seed

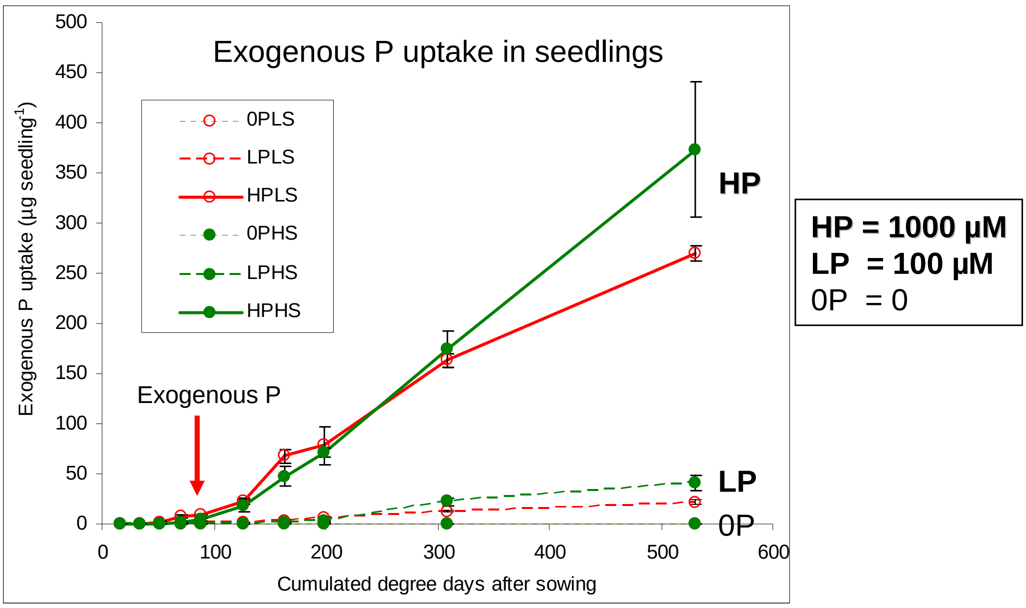
When seedling roots start exogenous P uptake?



Nadeem et al. 2011a

❖ The seedling roots start to uptake P on 70 °C DAS (5th DAS)

Effect of P treatments on exogenous P uptake?



Nadeem et al. 2011b

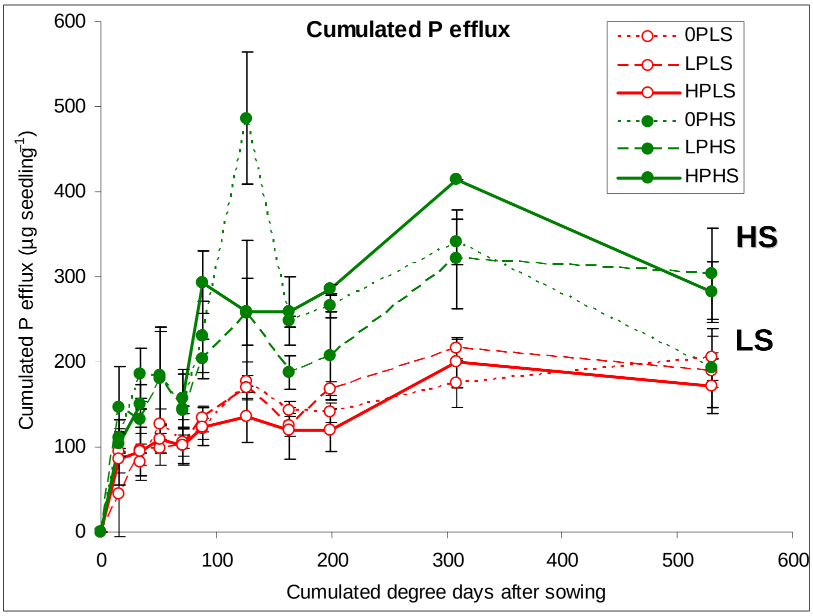
❖ The seedlings start to uptake P on 71 °C DAS (5th DAS) for **all P treatments**

❖ More P uptake in high (HP) as compared to low (LP) exogenous P

❖ Similar P absorption influx was observed in LS and HS seedlings

Effect of P treatments on P efflux from germinating seeds?

P efflux = [seed P loss + root P uptake] – [Seedling P accumulation]



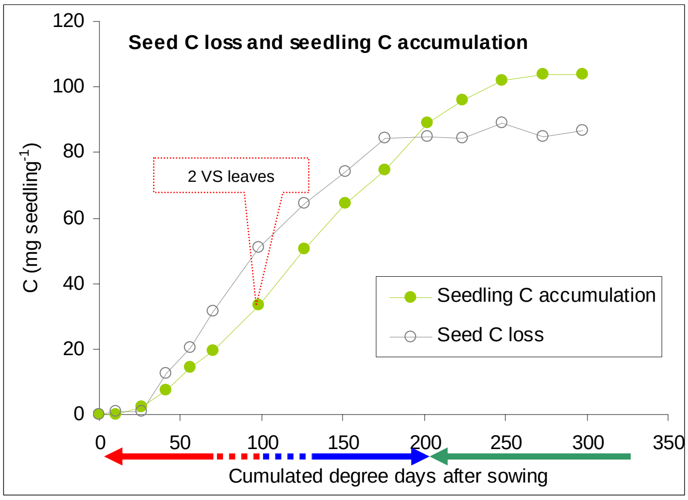
Nadeem et al. 2011b

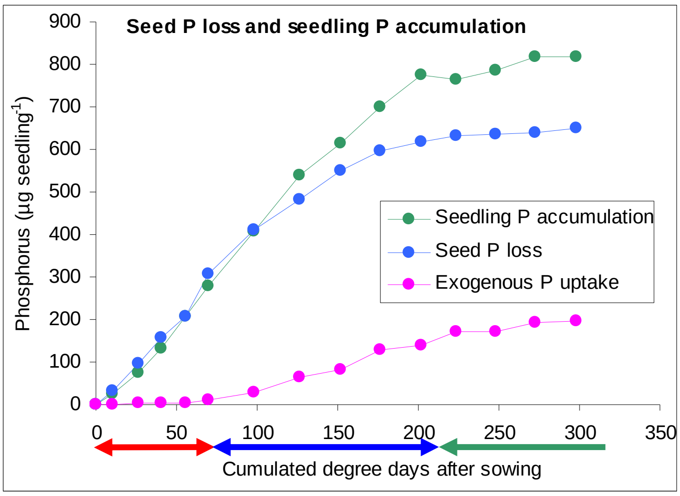
The P efflux starts to increase from 16 °C DAS in all P treatments between seed imbibition and root emergence

The P efflux dependents on initial endogenous seed P

The P efflux is not influenced by external P availability

Heterotrophy, transition and autotrophy stages for P?





Heterotrophy/ remobilized C

Transitional/ remobilized C+ photosynthesis

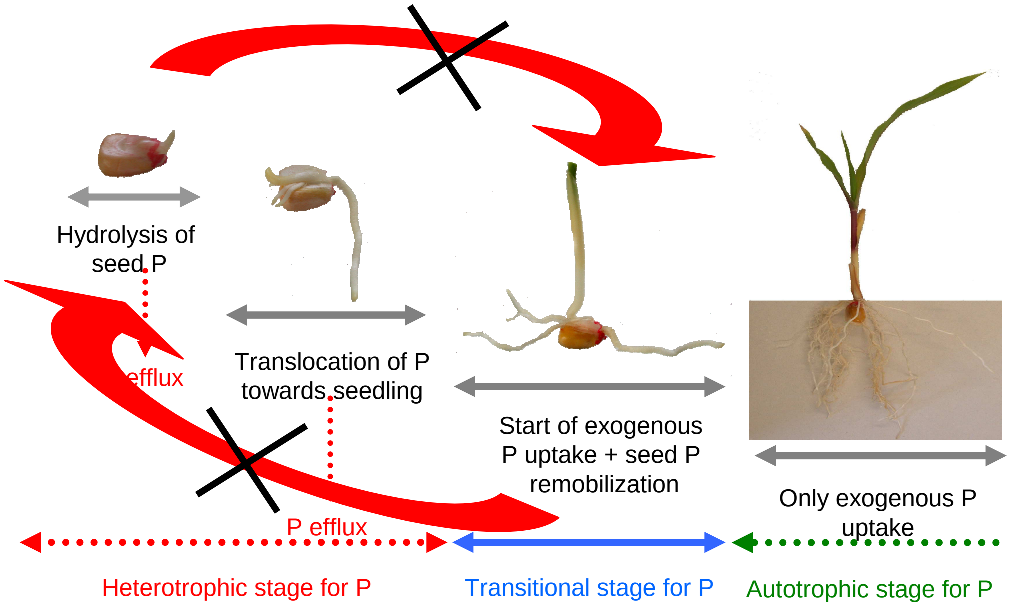
Autotrophy/ Photosynthesis

Heterotrophy/ remobilized P

Transitional/ remobilized P+ exogenous P uptake

Autotrophy/ exogenous P uptake

General representation of results



How long seed P reserve can support maximal growth rate?

Growth function (mg DM)	DM=a e $^{RGR.t}$
Optimal P concentration (mg P/ g DM)	$[P]_{opt}$
Seed P content (mg P / seed)	SeedP
Critical time (days)	t_c

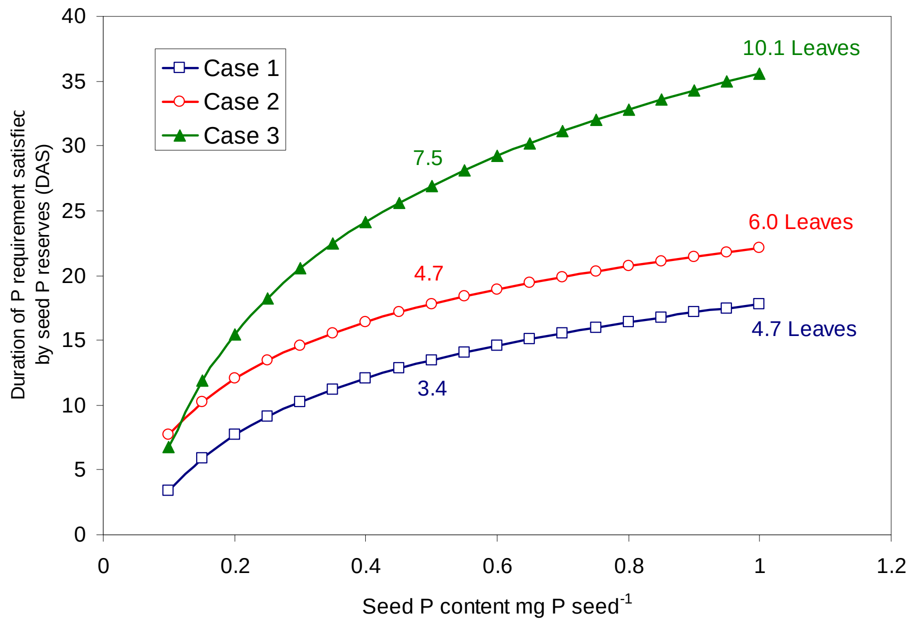
$$t_c = \frac{1}{RGR} \ln\left(\frac{SeedP}{a[P]_{opt}}\right)$$

Leaf appearance after 2 d, leaf base temperature 10°C, phyllochron 60°C d

Case 1 RGR=0.16; a=0.029 g
$[P]_{opt}$ = 2 mg/g

Case 2 Lower P requirement
RGR=0.16; a=0.029 g
$[P]_{opt}$ = 1.5 mg/g

Case 3 Lower RGR
RGR=0.08; a=0.029 g
$[P]_{opt}$ = 2 mg/g



Adapted from White and Veneklaas, 2012

Summary

- **P is stored in maize scutellum** rather than embryo and mainly in the form of phytate

- Remobilization of **C, N and P follows the similar kinetics** although they have different origin

- **Phytate hydrolysis process is not a limiting step** for seedling P nutrition

- **P losses by efflux** may represent 30% of initial seed P content during seed imbibition

- **Exogenous P uptake by roots begin 5-7 DAS and is not influenced by endogenous seed P content** but mainly depends on exogenous P availability. We don’t know why root P uptake is delayed (low abundance or activity of P transporters? Lack of systemic signal from the shoots?)

- P supplied by seed phytate hydrolysis is enough to satisfy the early seedling P demand for at least 3 weeks. Similar conclusions were drawn from theoretically calculations (White et Veneklass 2012).

- Greater seed P content enables seedlings to establish faster and contributes to reduce further effects of external P uptake limitation

Sowing high seed P helps seedling establishment in P deficient soils, but other strategies exist to improve PUE : selection of genotypes with low seed P accumulation (see Terry’s presentation) ?