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



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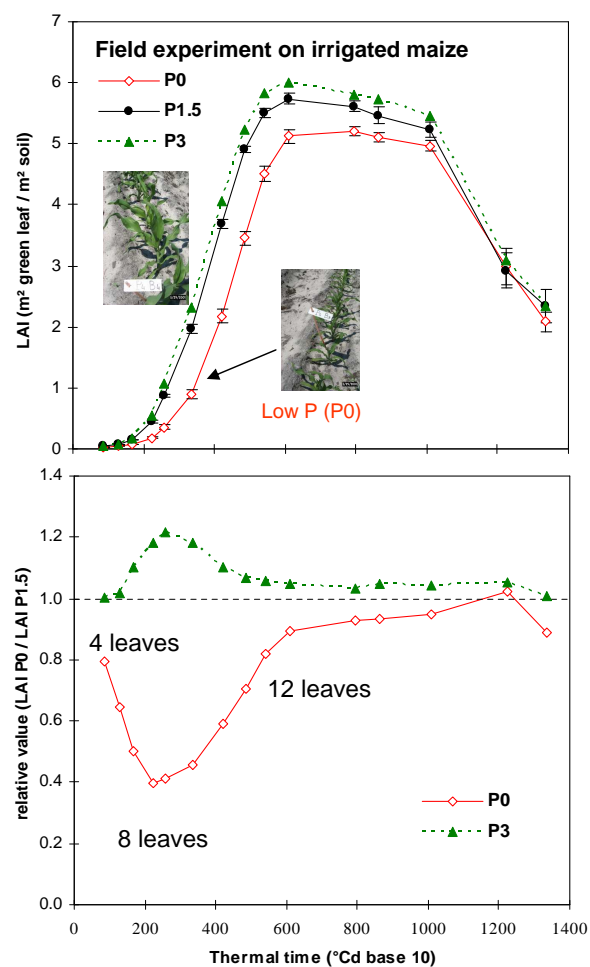
JIRCAS Workshop: Improving phosphorus efficiency in Rice: novel traits and underlying genes, 25-27<sup>th</sup> November 2013

## 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**

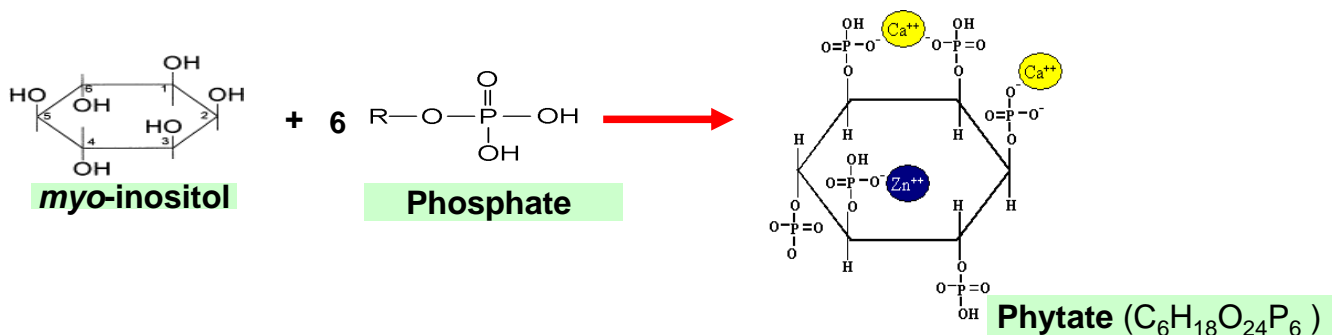
P treatment	Ferrosol				Kandosol			
	21 DAS		35 DAS		21 DAS		35 DAS	
	SDW	SP	SDW	SP	SDW	SP	SDW	SP
Low P	0.49**	0.45**	0.58**	0.41**	0.31*	0.06	0.01	0.01
High P	0.04	0.01	0.01	0.03	0.04	0.02	0.01	0.01

## Seed P reserves

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

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

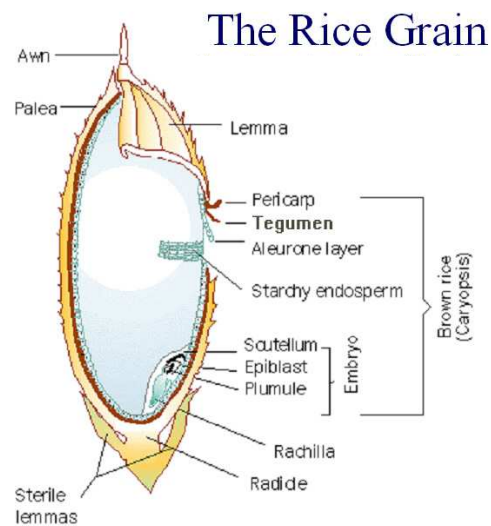
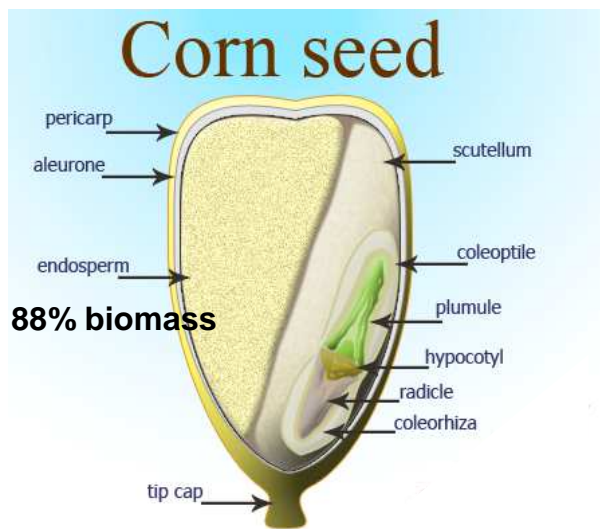
Phytate is a complex salt of *myo*-inositol hexakisphosphoric acid : *myo*-inositol 1, 2, 3, 4, 5, 6-hexakisphosphate (Park et al., 2006)



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)

# Localization of seed P reserves



## Phytate P localization in the seed

	Corn seed	Rice seed
Embryo	<b>90%</b> (in scutellum)	<b>10%</b>
Aleurone layer	<b>10%</b>	<b>90%</b>
Endosperm	<b>&lt;1%</b>	<b>&lt;1%</b>

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

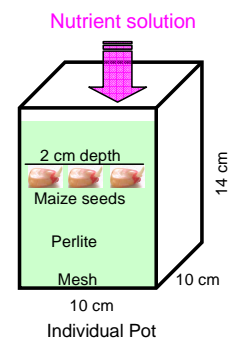
# Experimental approach

## 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  $\mu\text{g P seed}^{-1}$ ) & complete nutrient solution P (500  $\mu\text{M}$ )



## 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?

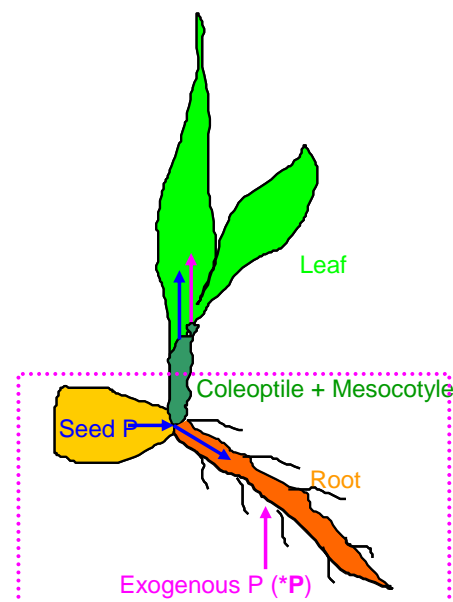
Initial seed P (LS : **506** & HS : **952**  $\mu\text{g seed}^{-1}$ )  
 Nutrient solution P (0P: **0** , LP : **100** & HP : **1000**  $\mu\text{M}$ )

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

## Labelling of nutrient solution with $^{32}\text{P}$

- ❖ The nutrient solution was labelled with  $^{32}\text{P}$  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)

$$(^{31}\text{P}_{\text{seedling}})_t = (^{32}\text{P}_{\text{seedling}})_t / (^{32}\text{P}_{\text{NS}} / ^{31}\text{P}_{\text{NS}})_t$$



- ❖ P sorption on seedling roots (less than  $0.009 \mu\text{g P cm}^{-1}$ )
- ❖ P sorption on perlite ( $\sim 0$ )



Irrigation on each day



17 days old seedlings



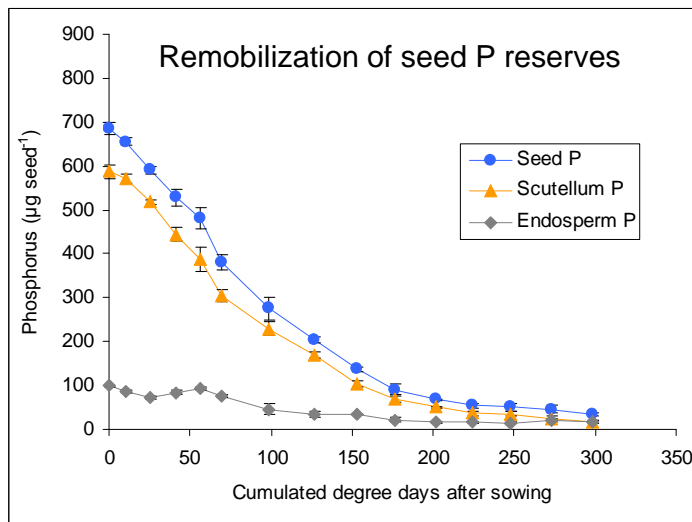
Seedling preparation



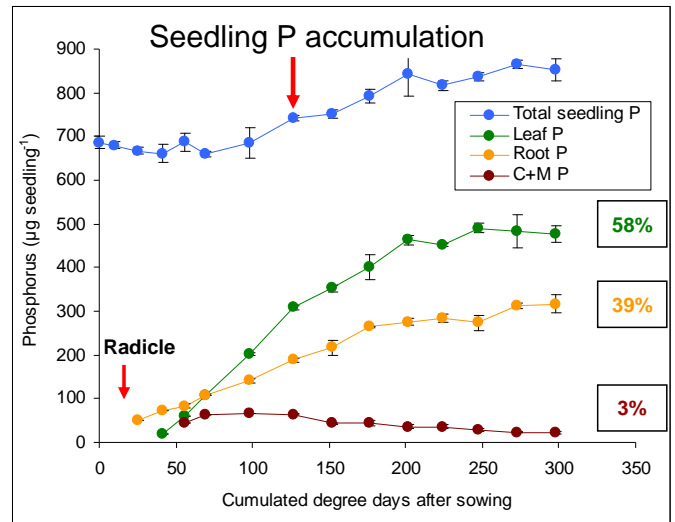
Endosperm, scutellum, C+M, roots, leaves

# Allocation and changes of seed and seedling P?

## 1<sup>st</sup> experiment



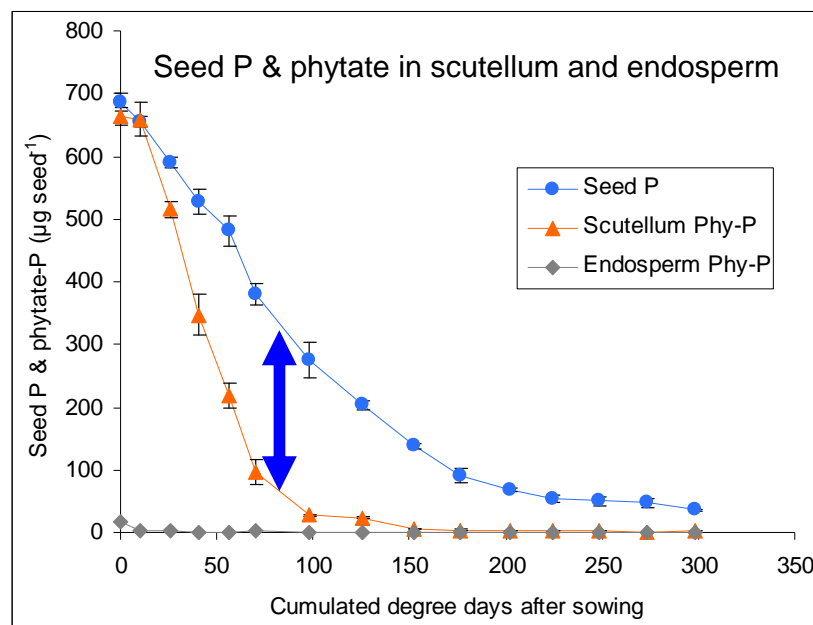
Nadeem et al. 2011a



Nadeem et al. 2011a

- ❖ Main part of initial seed P reserves were stored in scutellum (86%)
- ❖ Up to 202 °C DAS (15<sup>th</sup> 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<sup>th</sup> DAS

## Changes in seed P, scutellum & endosperm phytate-P

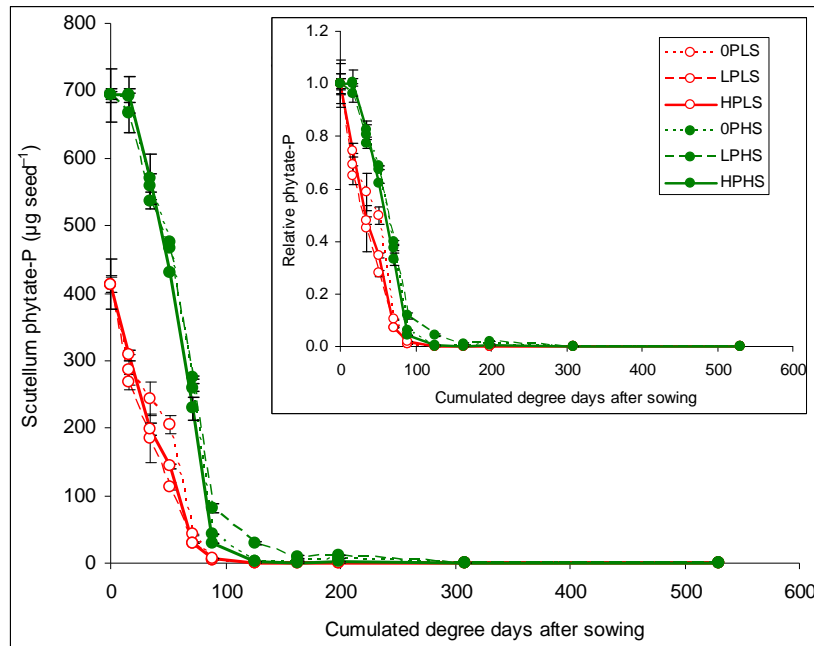


Nadeem et al. 2011a

- ❖ 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<sup>th</sup> DAS)
- ❖ Quick phytate-P hydrolysis favours the increase in non phytate-P from 26 - 126 °C DAS (1<sup>st</sup>-9<sup>th</sup> DAS)

# Effect of P treatments on phytate-P hydrolysis?

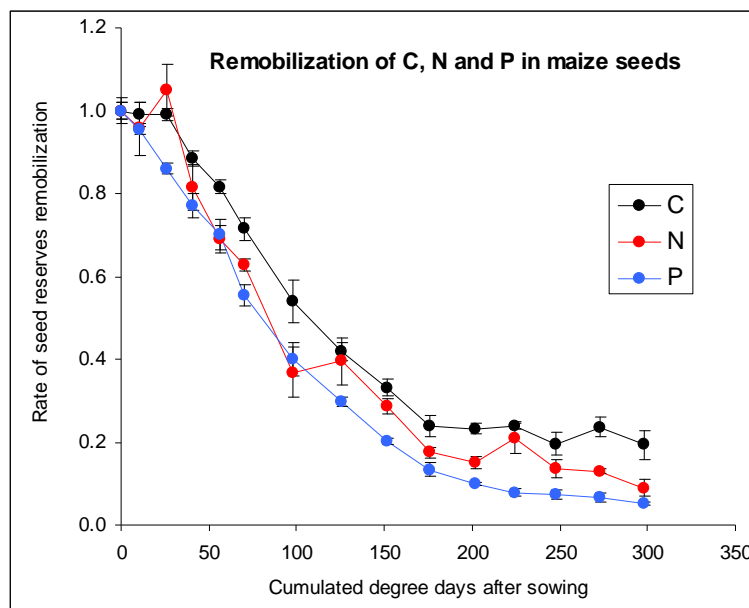
## 2<sup>nd</sup> experiment



Nadeem et al. 2011b

- ❖ The phytate-P reserves differ 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?

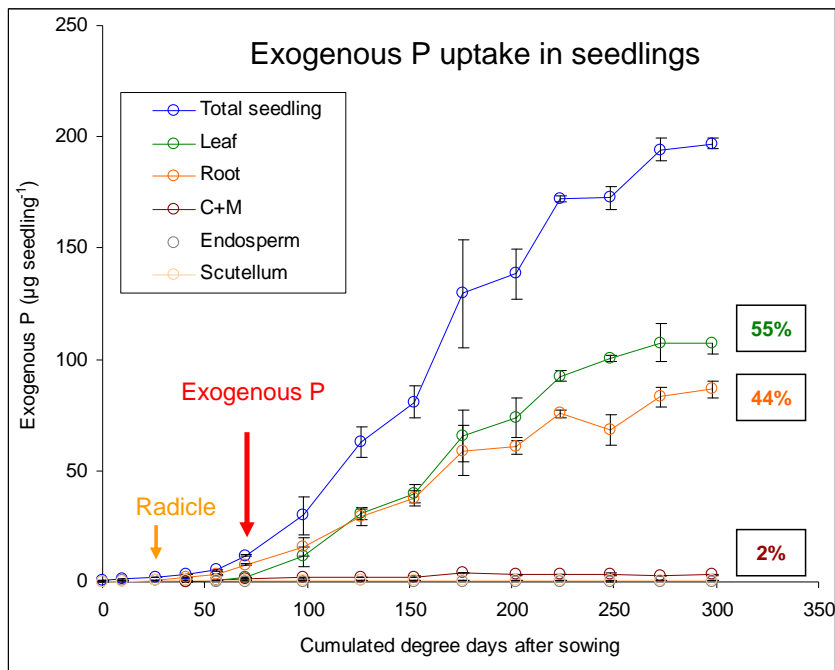


C and N in endosperm  
while P in scutellum

Nadeem et al. 2011a

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

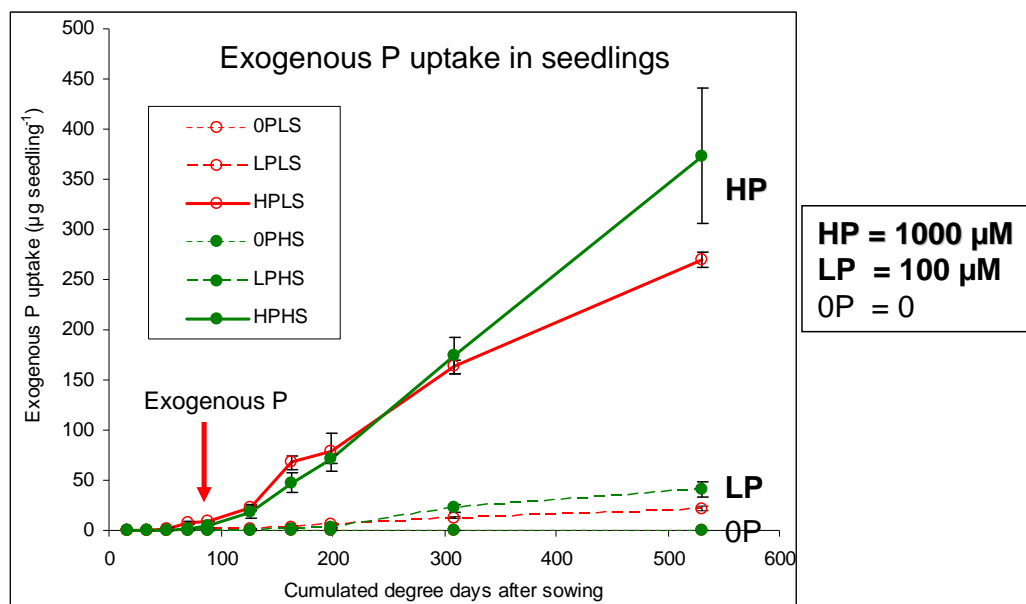
# When seedling roots start exogenous P uptake?



Nadeem et al. 2011a

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

# Effect of P treatments on exogenous P uptake?



Nadeem et al. 2011b

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

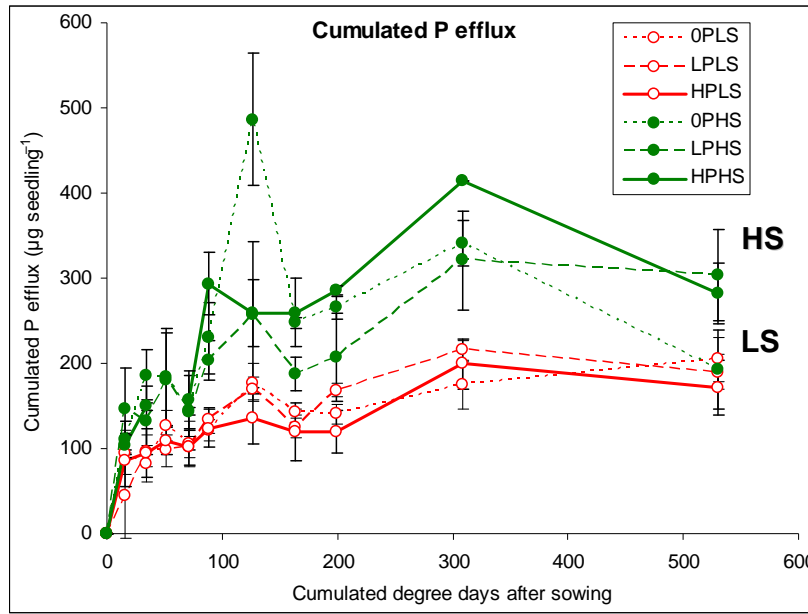
❖ More P uptake in high (HP) as compared to low (LP) exogenous P

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



# Effect of P treatments on P efflux from germinating seeds?

$$P \text{ efflux} = [\text{seed P loss} + \text{root P uptake}] - [\text{Seedling P accumulation}]$$



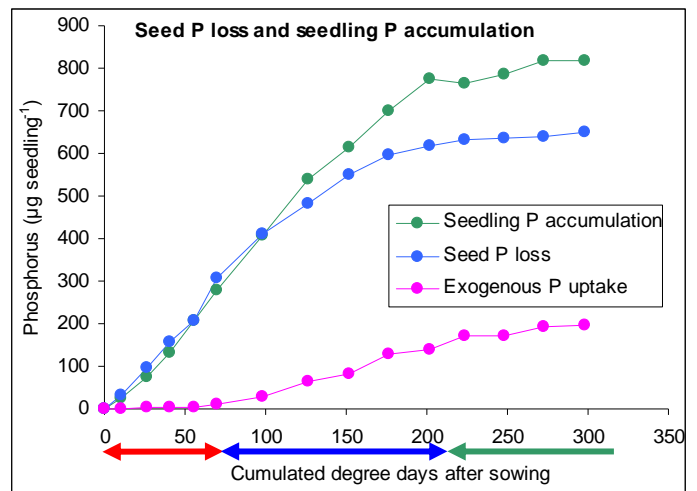
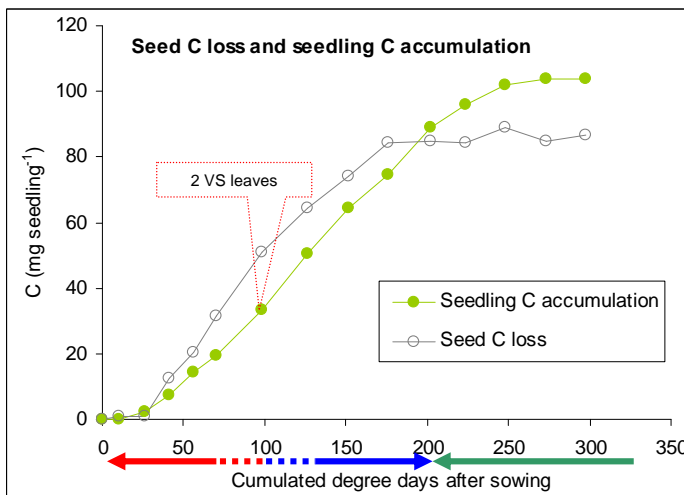
Nadeem et al. 2011b

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

The P efflux depends on initial endogenous seed P

The P efflux is not influenced by external P availability

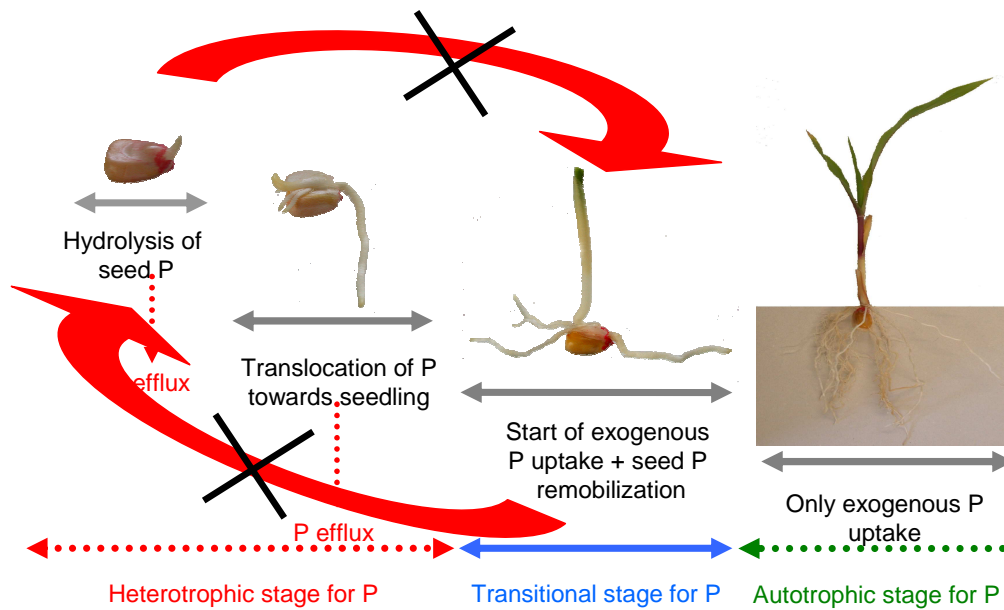
# Heterotrophy, transition and autotrophy stages for P?



**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)

Optimal P concentration (mg P/ g DM)

Seed P content (mg P / seed)

Critical time (days)

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

$$DM = a e^{RGR \cdot t}$$

$$[P]_{opt}$$

$$SeedP$$

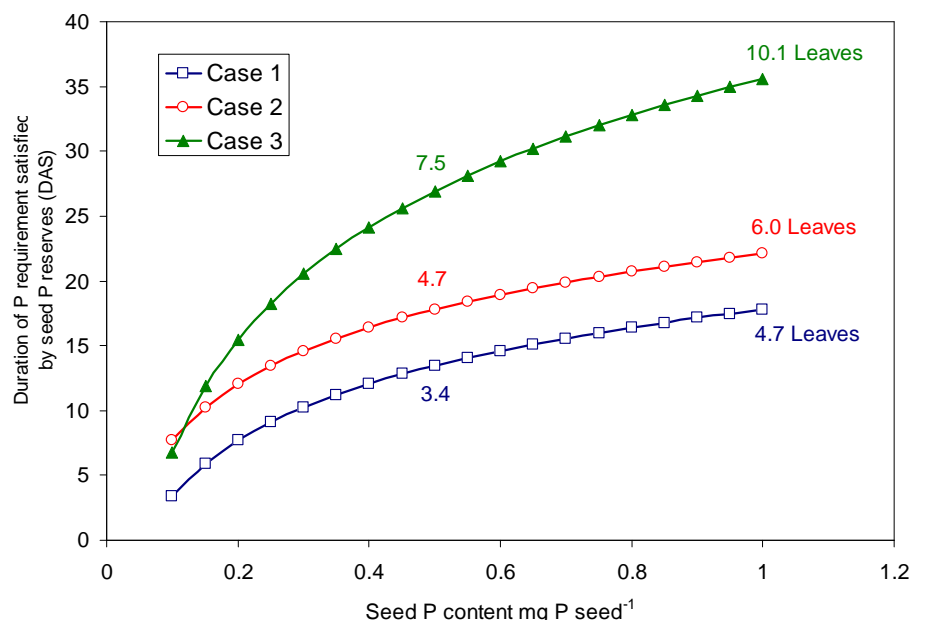
$$t_c$$

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

**Case 1** RGR=0.16; a=0.029 g  
[P]<sub>opt</sub> = 2 mg/g

**Case 2** Lower P requirement  
RGR=0.16; a=0.029 g  
[P]<sub>opt</sub> = 1.5 mg/g

**Case 3** Lower RGR  
RGR=0.08; a=0.029 g  
[P]<sub>opt</sub> = 2 mg/g



## 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) ?

# Thanks

I hope that seeds sown during this workshop will germinate and yield to successful projects

