

The Genetics of Potassium Acquisition and Utilisation by Plants

Philip J. White

(The James Hutton Institute, UK)

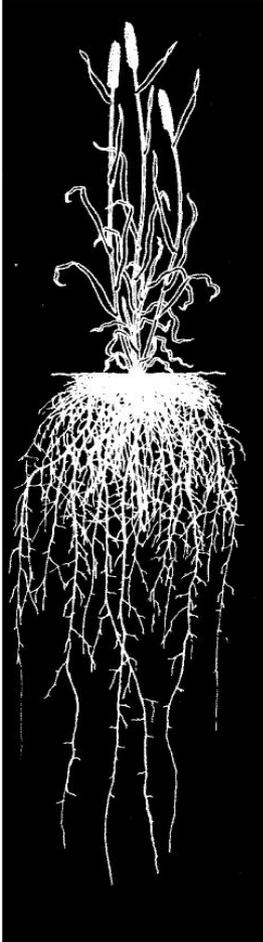
Michael J. Bell

(University of Queensland, Australia)



Frontiers in Potassium
Conference and Workshop,
Rome, Italy, 18 January 2017

Background

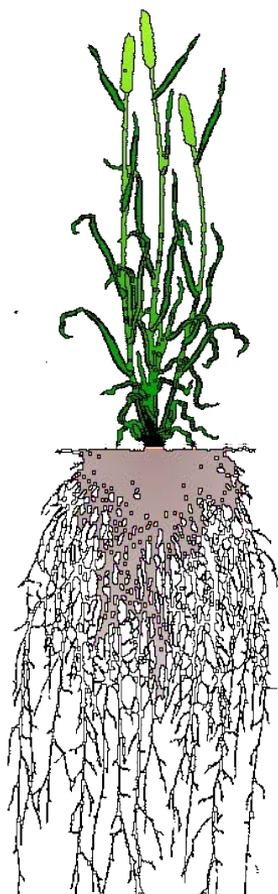


Potassium is an essential mineral element
Plants require tissue concentrations $>5-40 \text{ mg K g}^{-1} \text{ DM}$
Supply from soil is often insufficient to meet crop demand
Potassium added as inorganic and organic fertilisers

Potassium fertilisers are non-renewable,
and incur economic and environmental costs

Important to reduce application of K-fertilisers
through agronomic and genetic strategies

The Genetics of Potassium Acquisition and Utilisation by Plants



Potassium Uptake & Movement in Plants

Molecular Biology of Potassium Transporters

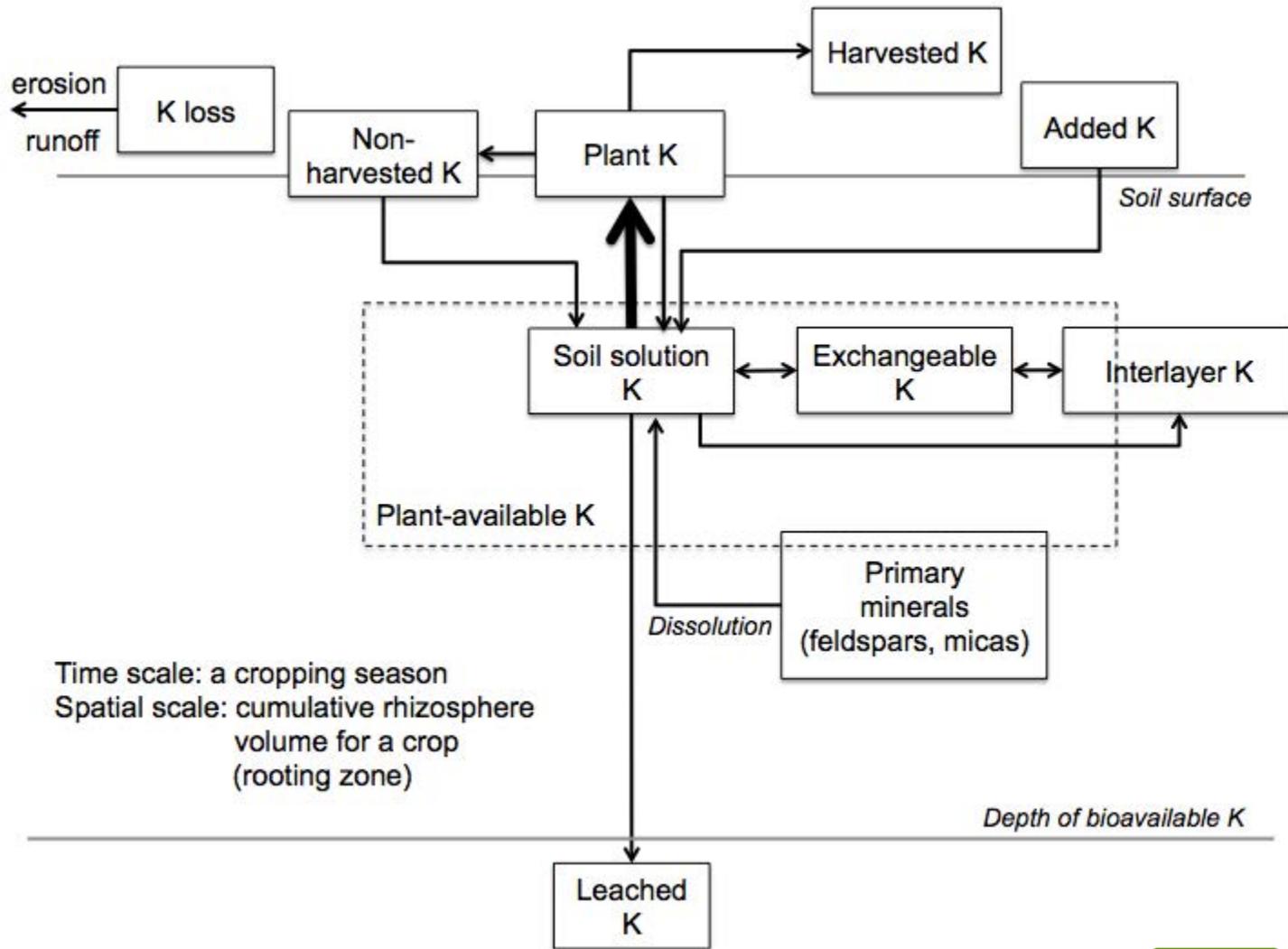
Definitions of Potassium Use Efficiency (KUE)

Variation Between and Within Plant Species

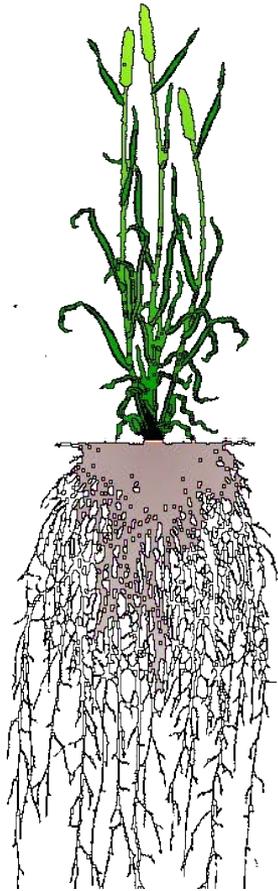
Plant Traits for Improving KUE

Genes Implicated in KUE

Potassium in Agriculture



Root Traits Increase Access to Nonexchangeable Potassium in Soils



Exudation of organic acids

Many plants exude organic acids, often citrate, oxalate and malate, which promote the dissolution of K-bearing silicates.

Acidification of the Rhizosphere

Some plants, such as canola, acidify the rhizosphere appreciably, which promotes the dissolution of minerals, such as K-bearing silicates.

Reducing Rhizosphere Potassium Concentration

Most plants can reduce K^+ concentrations in the rhizosphere solution sufficient to release interlayer K in micaceous phyllosilicate minerals (illites, illite-like clay minerals & micas).

White (2013) *J. Plant Nutr. Soil Sci.* 176: 305-316

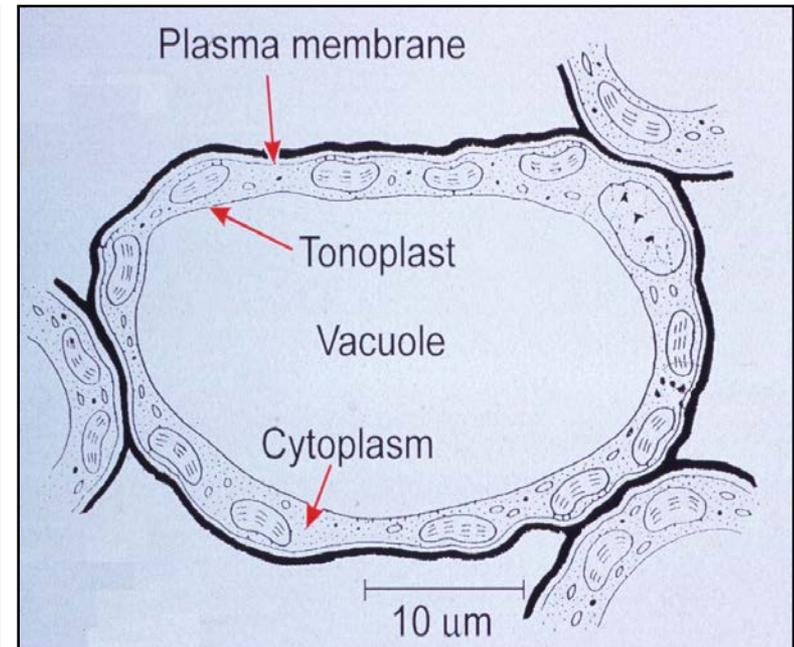
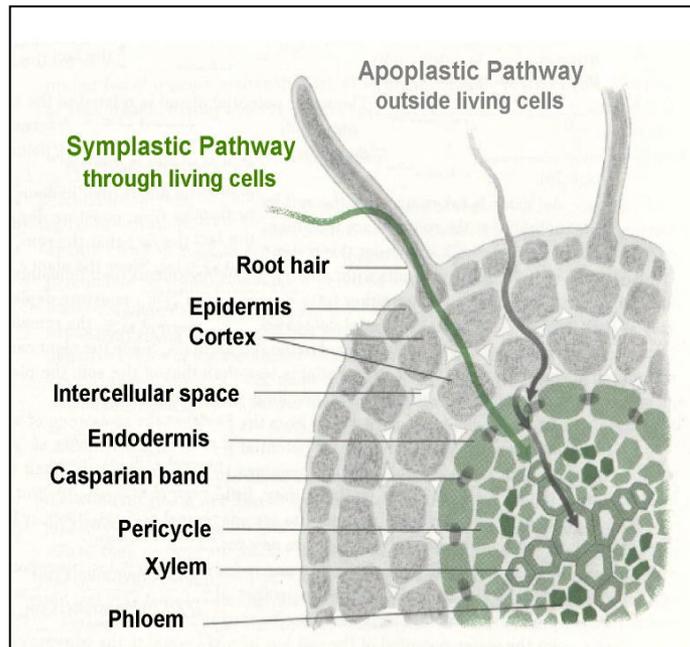
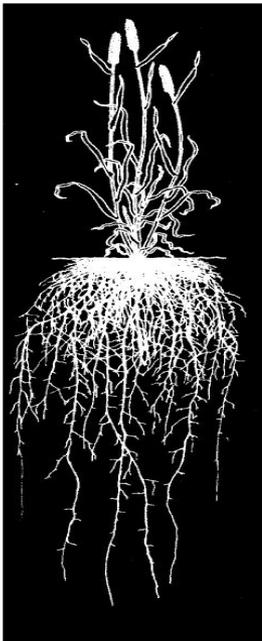
Hinsinger et al. (2017) *Proceedings Frontiers in Potassium*

Potassium Uptake by Root Cells

Potassium enters plant roots from the soil solution

Potassium follows a symplastic pathway to the xylem

Proteins facilitate their transport across the plasma membrane



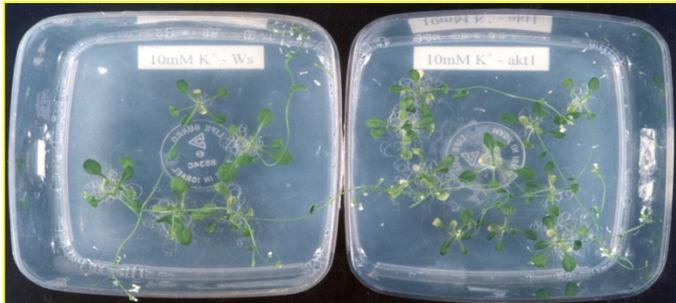
Molecular Biology of Potassium Transport

Uptake by Plant Roots: AKT1 & HAK5

Wild-type

akt1

10 mM K⁺



0.1 mM K⁺

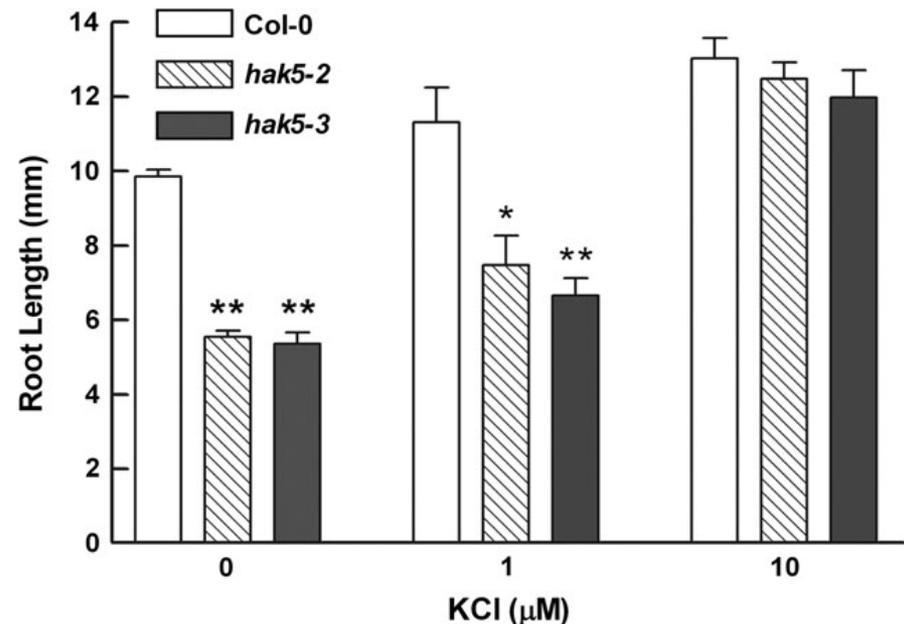


0.03 mM K⁺



Plants lacking AKT1 do not grow at low K⁺
(AKT1 is a plasma membrane K⁺ channel)

Plants lacking HAK5 do not grow at low K⁺
(HAK5 is a plasma membrane H⁺/K⁺ symporter)

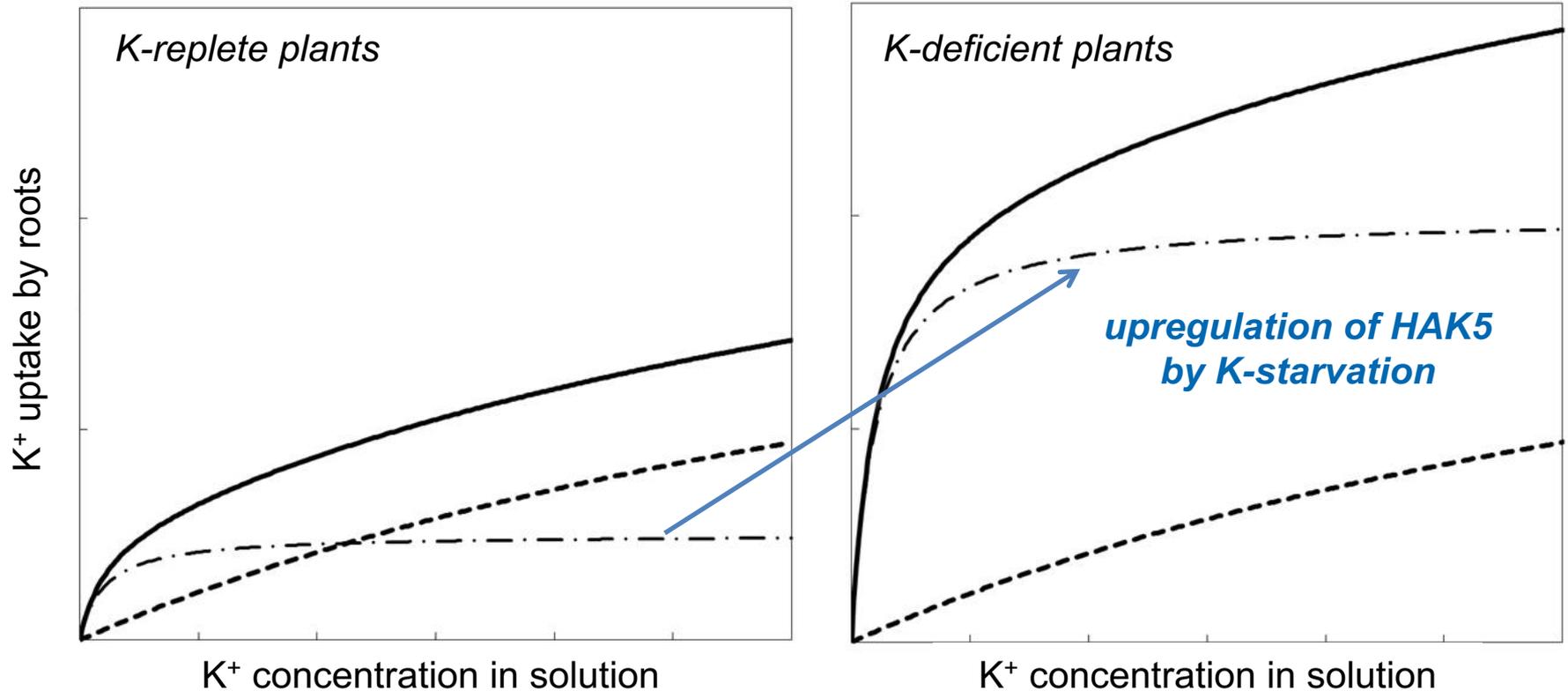


Broadley et al. (2001)
J. Exp. Bot. 52:839-844

Qi et al. (2008)
J. Exp. Bot. 59:595-607

Molecular Biology of Potassium Transport

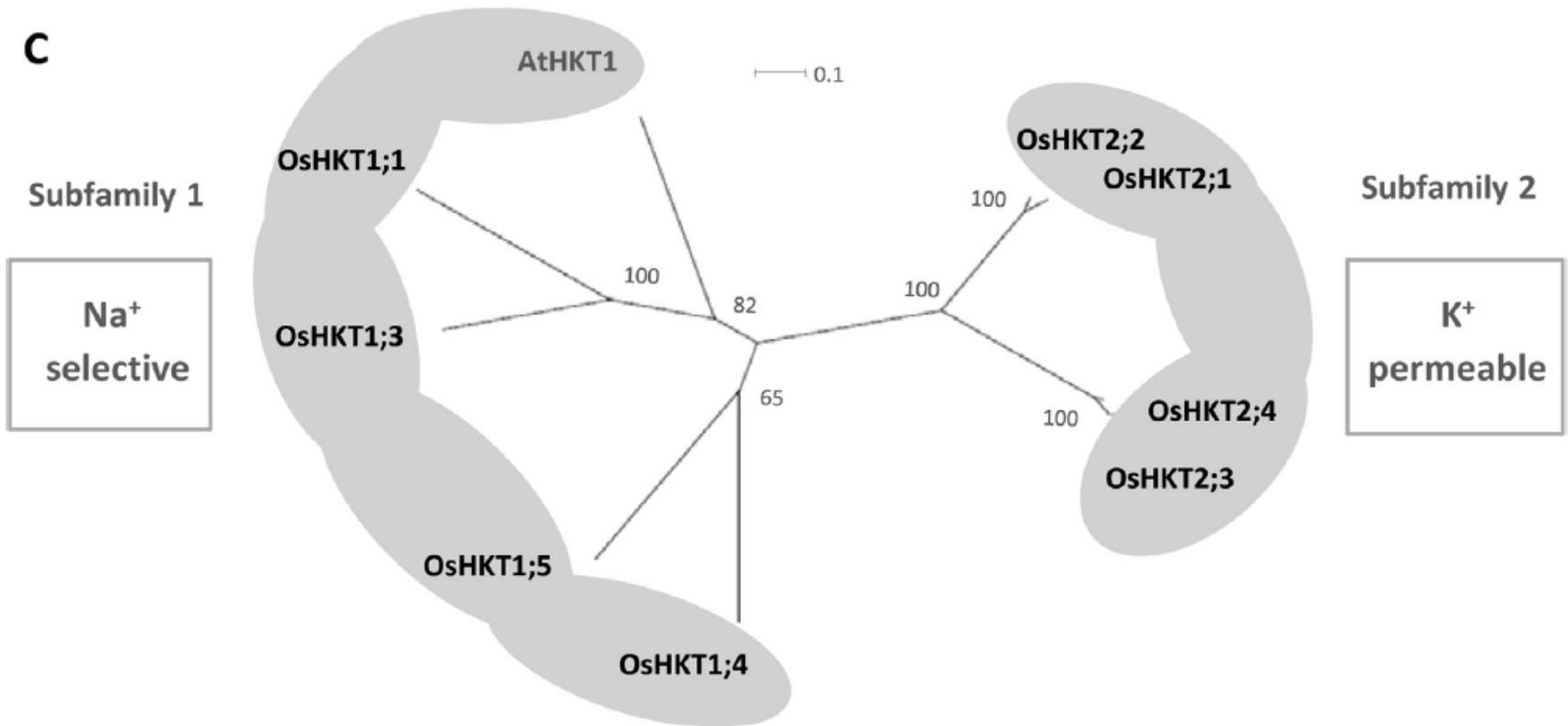
Regulation by Plant Potassium Status



White & Greenwood (2012) In: *Russell's Soil Conditions and Plant Growth (12th Edition)*. Wiley/Blackwell.

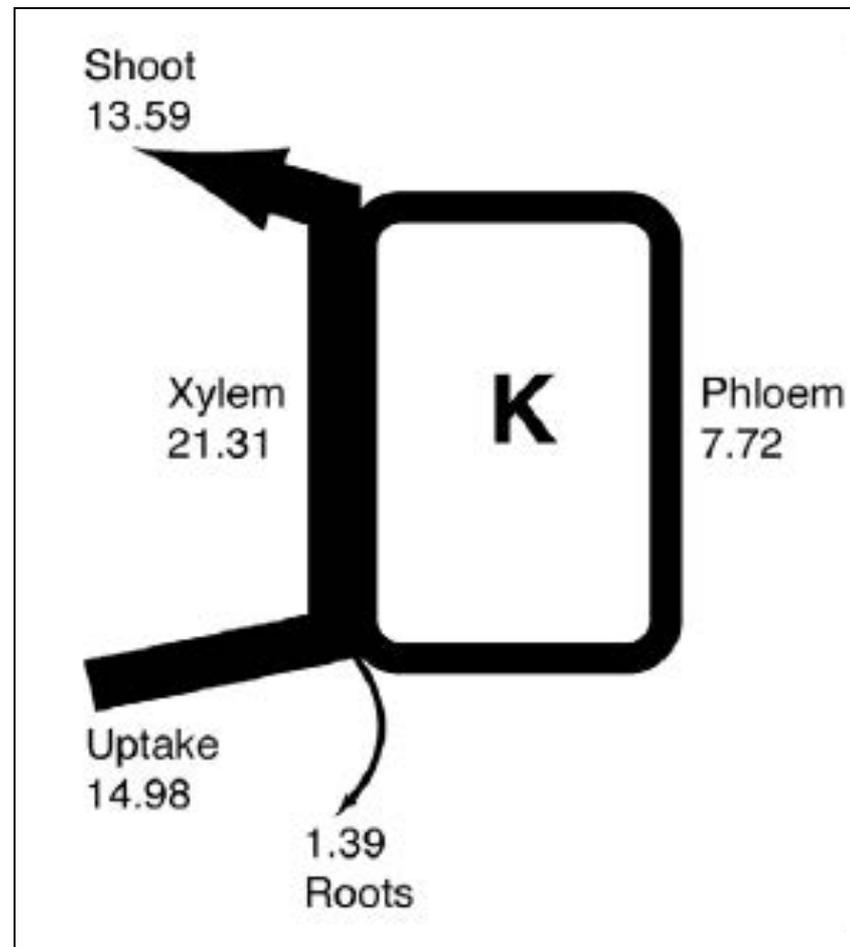
Molecular Biology of Potassium Transport

HKT Transporters in Cereals



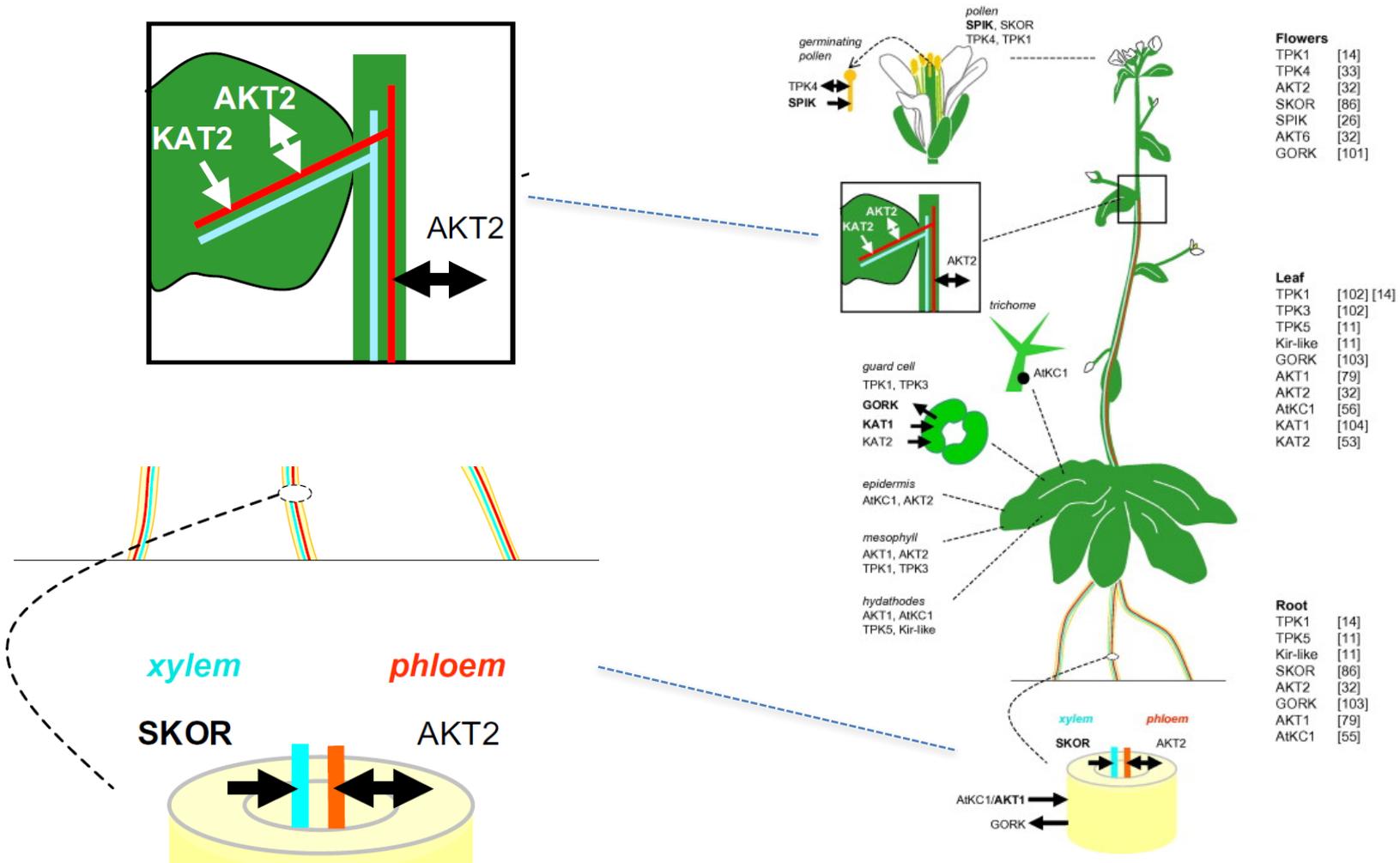
Véry et al. (2014) *J. Plant Physiol.* 171: 748-769.
Chérel et al. (2014) *J. Exp. Bot.* 65: 833-848.

Potassium Recirculates Within the Plant



Karley & White (2009) *Curr. Opinion Plant Biol.* 12, 291-298
White & Karley (2010) In: *Plant Cell Monographs* 17, 199-224

Molecular Biology of Potassium Transport Loading Xylem (SKOR) and Phloem (AKT2)



Molecular Biology of Potassium Transport (*Arabidopsis thaliana*)

Gene Family	#	Membrane Location	Transport Mechanism	Regulation by K-starvation
Shaker-type	9	PM	K ⁺ channel	AtSKOR (down)
GLR	20	PM	Cation channel	AtGLR1.1 (up)
CNGC	20	PM	Cation channel	
KT/HAK/KUP	13	PM, TP, ER, CP	K ⁺ /H ⁺ symport	KUP3, HAK5 (up)
TPK/KCO	6	PM, TP, CP	K ⁺ channel	
CPA1 (NHX)	8	PM, TP, EN	Cation/H ⁺ antiport	
CPA2 (CHX)	28	PM, TP, EN	Cation/H ⁺ antiport	
CPA2 (KEA)	6	CP	K ⁺ /H ⁺ antiport	
CaCA (CCX)	5	(PM), TP	K ⁺ (/H ⁺) transporter	
MFS (ZIFL)	2	PM, TP	K ⁺ /H ⁺ transporter	

Broadley & White (2012) *Plant & Soil* 355:23-27.
White & Bell (2017) *Proceedings Frontiers in Potassium*

Potassium (K) Use Efficiency

$$KUE = KUpE \times KUtE$$

Agronomic K Use Efficiency =

K Uptake Efficiency \times K Utilisation Efficiency

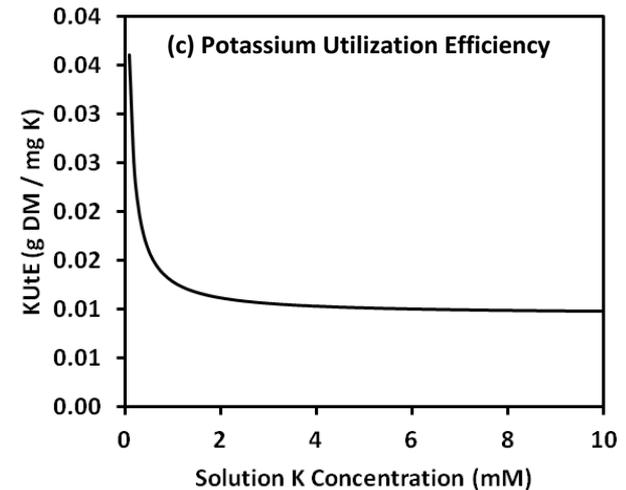
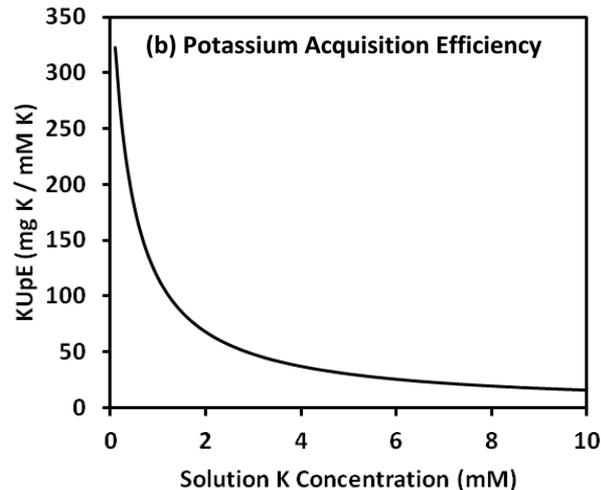
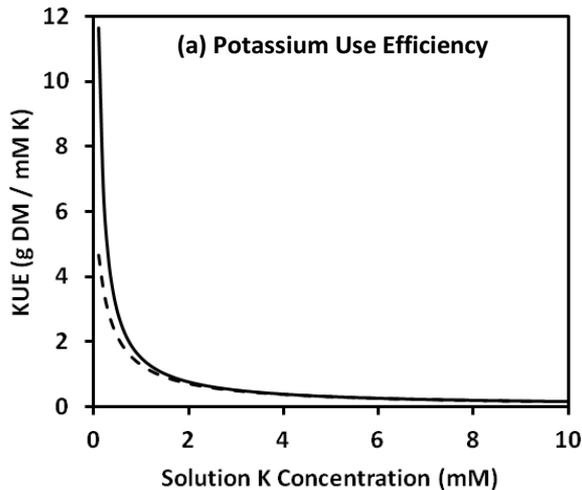
(yield / available K) =

(K acquired / available K) \times (yield / K acquired)

Potassium Use/Uptake/Utilisation Efficiencies Vary With Potassium Supply

Agronomic Potassium Use Efficiency (KUE) =
Potassium Acquisition Efficiency (KUpE) x Potassium Utilisation Efficiency (KUtE)

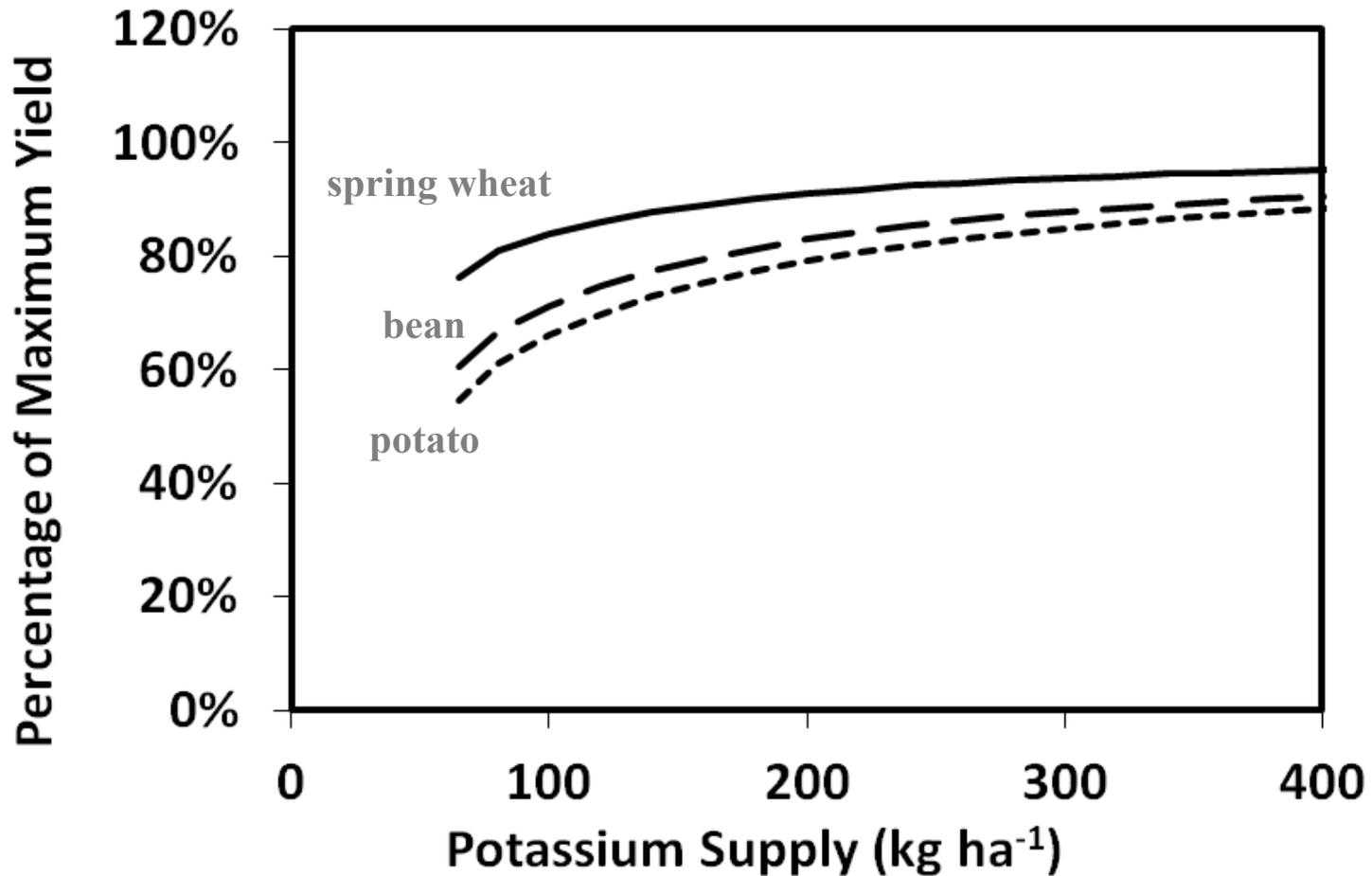
Barley Genotype
Prisma ———
Volla - - - -



White (2013) *J. Plant Nutr. Soil Sci.* 176: 305-316.

White et al. (2016) *Comm. Soil Sci. Plant Anal.* 47(S1): 104-111.

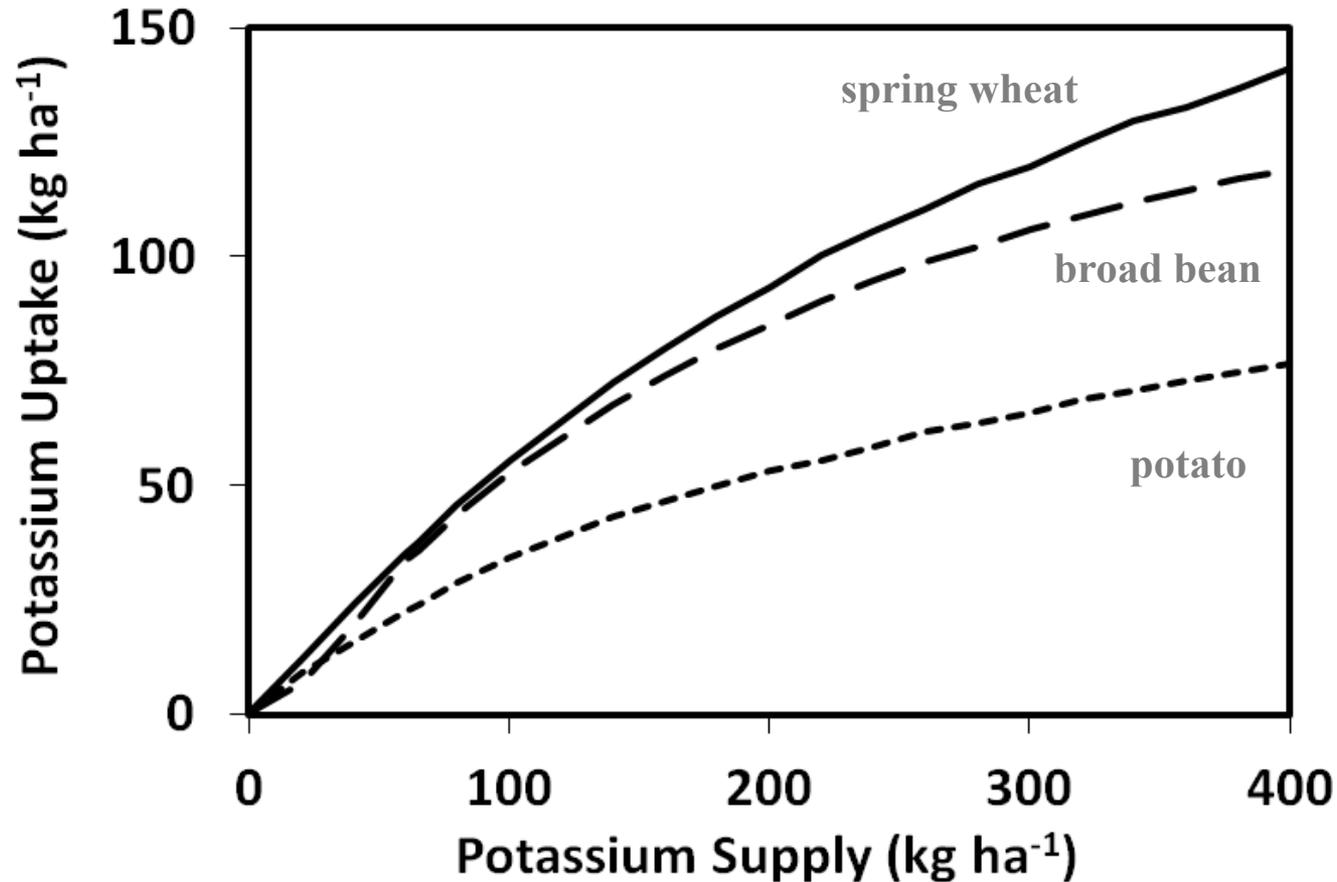
Variation Between Crop Species Yield Responses to K Supply (KUE)



White (2013) *J. Plant Nutr. Soil Sci.* 176: 305-316

Variation Between Crop Species

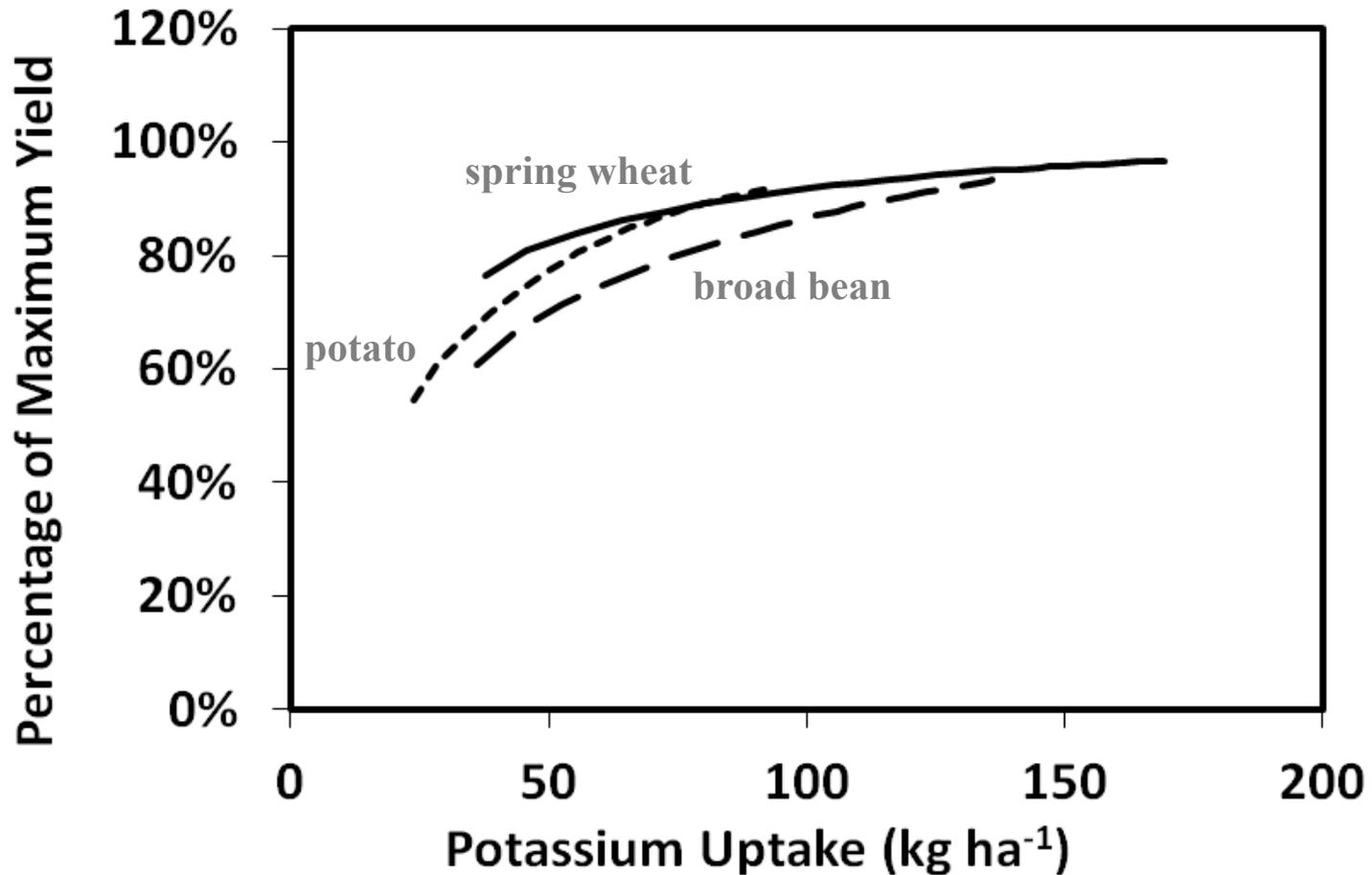
K Uptake Responses to K Supply (KUpE)



White (2013) *J. Plant Nutr. Soil Sci.* 176: 305-316

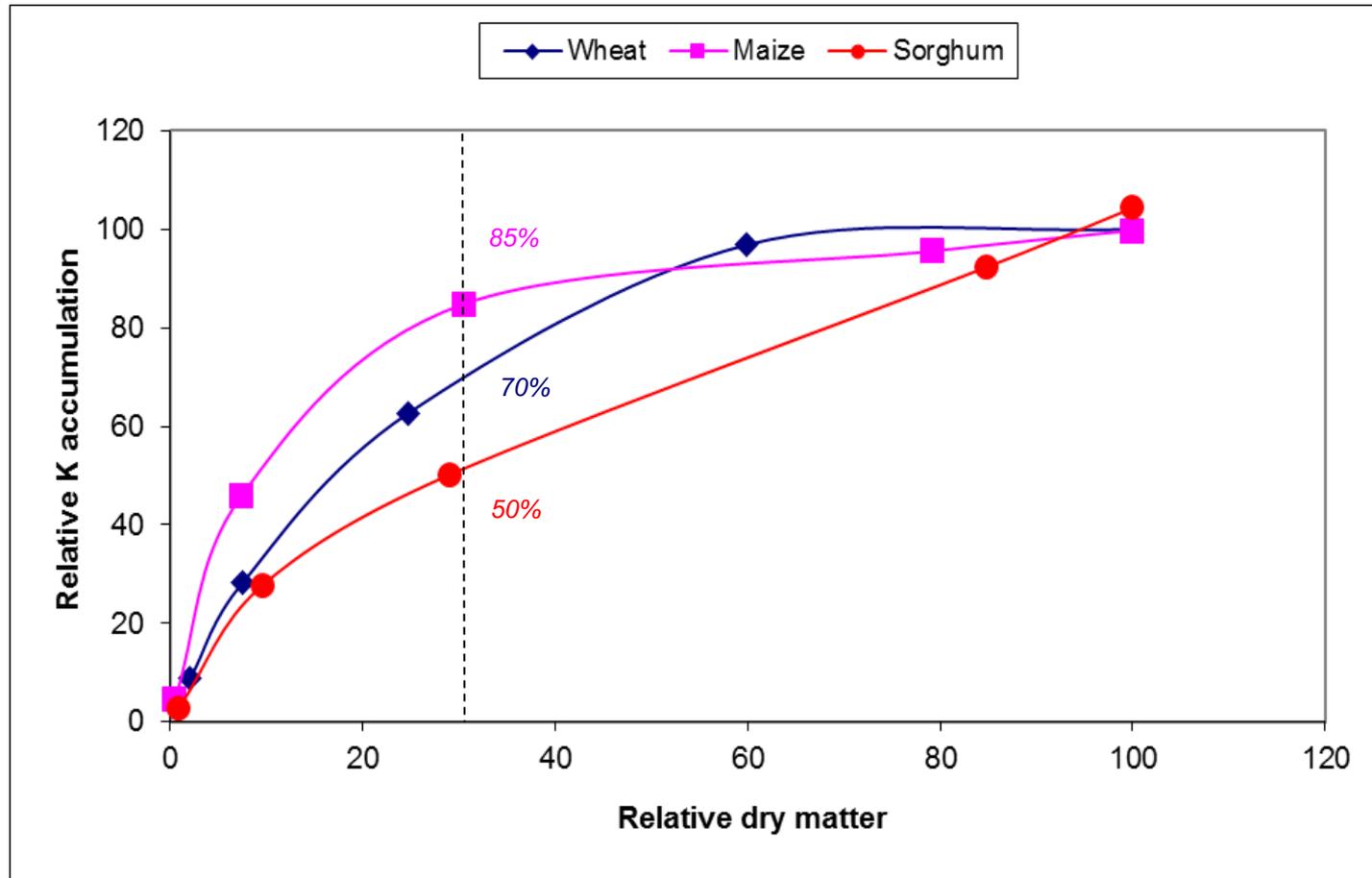
Variation Between Crop Species

K Utilisation Responses to K Supply (KUtE)



White (2013) *J. Plant Nutr. Soil Sci.* 176: 305-316

Variation in Timing of Potassium Acquisition Between Crops



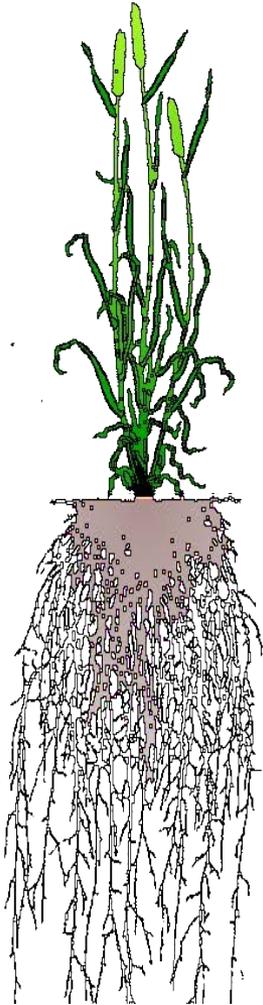
Bell et al., unpublished data.

Genotypic Variation in KUE in Crop Species

crop	yield or biomass response to K supply	KUpE	KUtE
Rice (<i>Oryza sativa</i>)	1.41 - 5.92	1.42 - 1.98	1.46 - 5.94
Wheat (<i>Triticum aestivum</i>)	1.14 - 1.76	1.80 - 6.52	1.34 - 2.34
Barley (<i>Hordeum vulgare</i>)	1.74 - 6.46	1.71 - 5.54	1.23 - 2.84
Sorghum (<i>Sorghum bicolor</i>)	-	-	1.91
Maize (<i>Zea mays</i>)	-	1.86	1.33 - 2.55
Common bean (<i>Phaseolus vulgaris</i>)	1.93	4.36 - 6.04	1.44 - 8.46
Soybean (<i>Glycine max</i>)	1.60	-	-
Lupin (<i>Lupinus angustifolius</i>)	1.76	1.23	1.57
Alfalfa (<i>Medicago sativa</i>)	-	-	1.63
Canola, OSR (<i>Brassica napus</i>)	1.12 - 2.40	1.58 - 3.50	1.52 - 3.13
<i>Brassica oleracea</i>	-	17.9	1.67 - 3.37
Chinese cabbage (<i>Brassica rapa</i>)	-	-	2.30
Indian mustard (<i>Brassica juncea</i>)	-	1.54	1.44
Spinach (<i>Spinacia oleracea</i>)	-	-	3.90
Cassava (<i>Manihot esculenta</i>)	1.69	-	1.32
Sweet potato (<i>Ipomoea batatas</i>)	-	9.46	3.18
Tomato (<i>Solanum lycopersicum</i>)	1.94 - 2.06	1.05 - 1.84	1.24 - 1.82
Potato (<i>Solanum tuberosum</i>)	1.51 - 2.15	1.18 - 2.83	1.54 - 3.68
Cotton (<i>Gossypium hirsutum</i>)	2.08 - 5.80	1.99 - 8.87	1.25 - 1.45

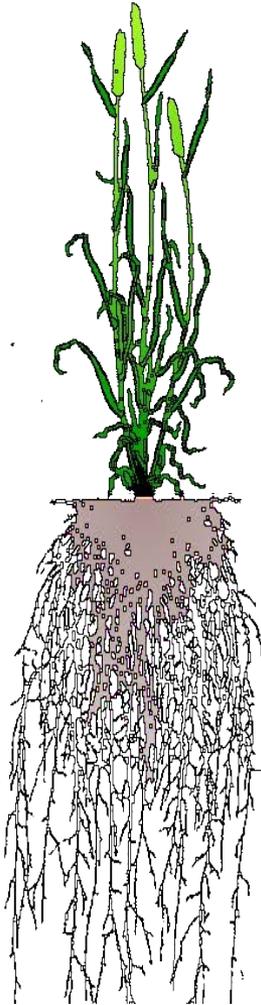
Potassium Use Efficiency

Improving Potassium Acquisition & Utilisation



$$KUE = KUpE \times KUtE$$

Plant Traits Influencing Potassium Acquisition Efficiency (KUpE)

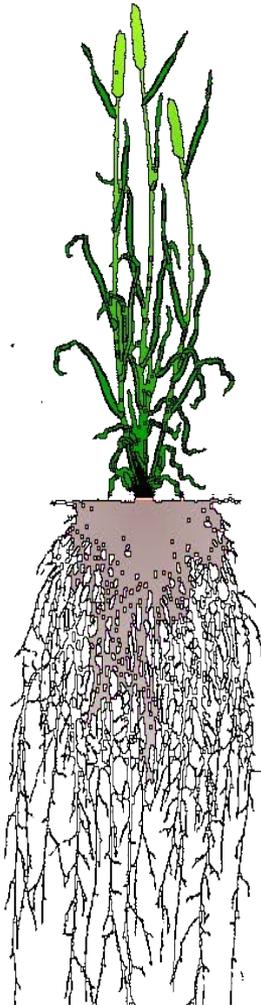


Potassium enters plant roots from the soil solution

*Supply from soil is largely governed
by diffusion and mass flow*

- Increasing early root vigour
- Increasing root biomass or root/shoot ratio
- Increasing root surface area (lateral rooting, root hairs)
- Improving root architecture for soil foraging
- Increasing root length density
- Increasing exudation of H^+ and organic compounds
- Increasing water uptake through transpiration
- Increasing K^+ uptake capacity of root cells
- Increasing affinity for K^+ of transport proteins

Plant Traits Influencing Potassium Utilisation Efficiency (KU_tE)



Increasing photosynthesis
Accelerating canopy development
Increasing canopy longevity
Increasing harvest index
Tolerating lower tissue K⁺ concentrations
Replacing K⁺ in non-essential functions
Partitioning K⁺ to metabolic cell compartments
Redistributing K from senescent to developing tissues
Redistributing K from root to shoot

Potassium is required for plant growth

Potassium is required in the cytoplasm

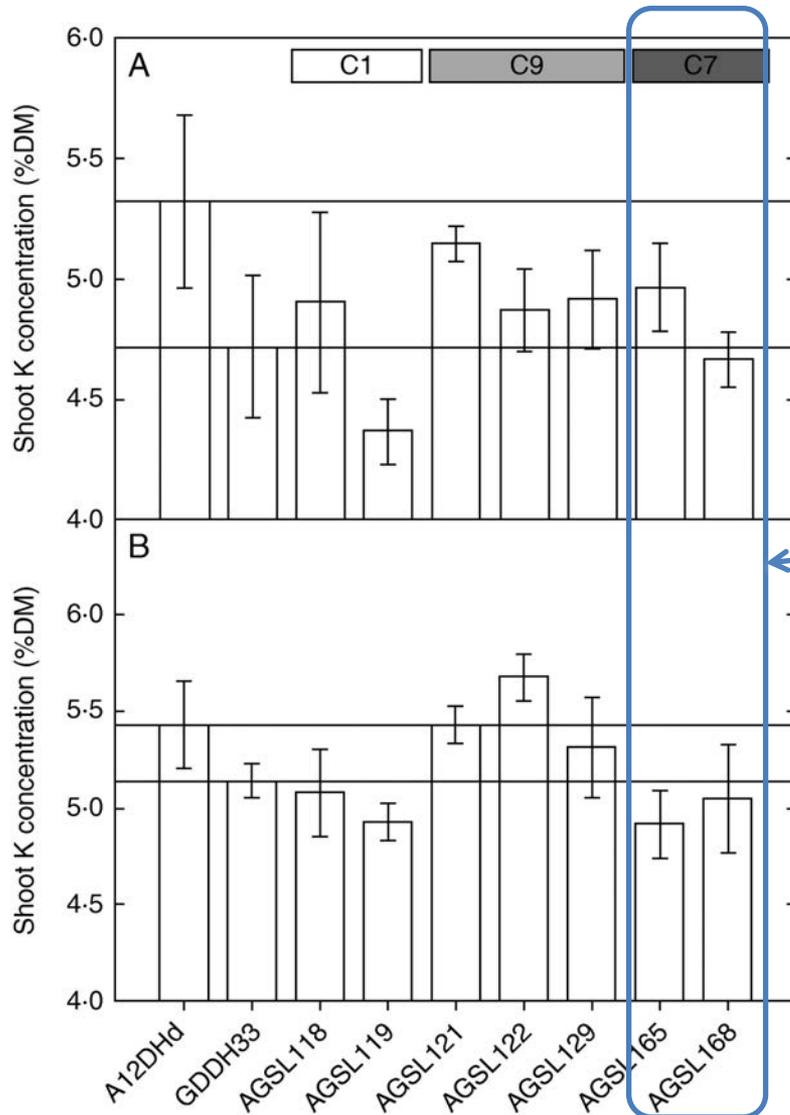
*Plant growth is largely governed
by photosynthetic capacity*

Genetics of KUE in Plant Species

Plant Species	Quantitative Trait Loci (QTL)
<i>Arabidopsis thaliana</i>	Harada & Leigh, 2006; Ghandilyan et al. 2009; Kanter et al. 2010; Prinzenberg et al. 2010
<i>Brassica oleracea</i>	White et al. 2010
Rice (<i>Oryza sativa</i>)	Wu et al. 1998; Koyama et al. 2001; Lin et al. 2004; Cheng et al. 2012; Wang et al. 2012; Miyamoto et al. 2012, Fang et al. 2015
Wheat (<i>Triticum aestivum</i>)	Genc et al. 2010, 2013; Guo et al. 2012; Kong et al. 2013; Zhao et al. 2014; Gong et al. 2015
Barley (<i>Hordeum vulgare</i>)	Nguyen et al. 2013ab
Maize (<i>Zea mays</i>)	Zdunić et al. 2014
<i>Miscanthus sinensis</i>	Atienza et al. 2003
Barrel medic (<i>Medicago truncatula</i>)	Arrauadi et al. 2012
Tomato (<i>Solanum lycopersicum</i>)	Villalta et al. 2008
Cotton (<i>Gossypium hirsutum</i>)	Liu et al. 2015

Few genes underlying QTL affecting shoot K concentration have been validated

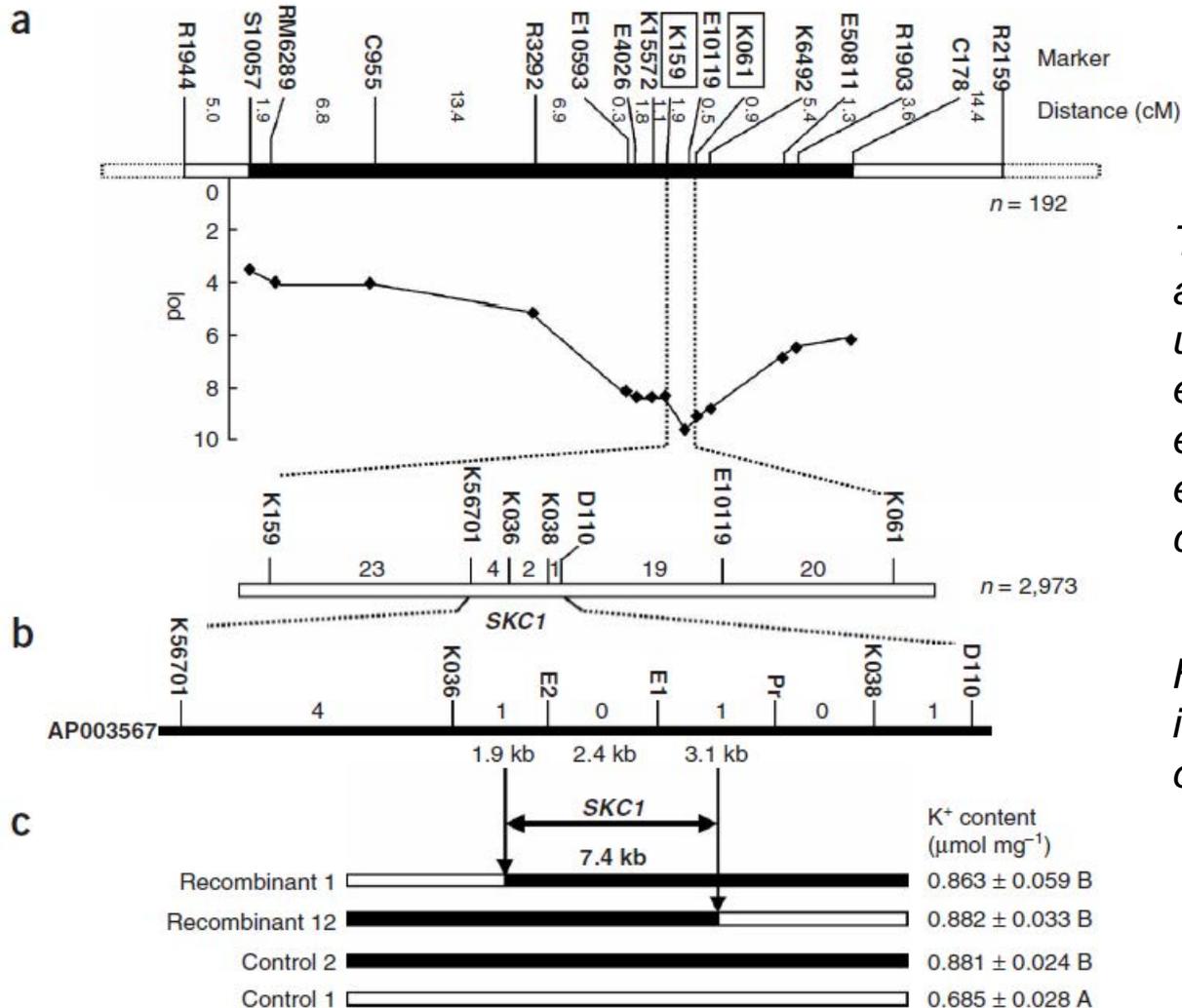
Chromosomal Loci (QTL) Impacting Shoot K Concentration in *B. oleracea*



	LG	Position (cM)	LOD	R ²
Glass	C1	91.2	7.06	0.216
	C3	81.7	3.05	0.092
	C4	10.0	5.13	0.156
	C4	31.5	4.23	0.114
	C7	62.2	2.08	0.051
	C9	33.5	6.60	0.204
Field	C2	43.8	2.36	0.107
	C2	117.5	2.16	0.098
	C9	55.1	4.99	0.230

QTL on C7 impacting $[K]_{\text{shoot}}$ in glasshouse confirmed using substitution lines. QTL corresponds to Arabidopsis C4 (AtKUP9, AtAKT2, AtKAT2, AtTPK3) and *B. rapa* sequence (BrKUP9).

Gene Responsible for a QTL Impacting Shoot K Concentration in Rice



The locus SKC1, which affects shoot K concentration under saline conditions, encodes OsHKT8, a gene encoding a Na^+ transporter expressed in parenchyma cells surrounding the xylem.

Homologues of this gene are implicated in salt tolerance in other plant species.

HKT Subfamily I Genes

Impact Shoot Na and K Concentrations

Plant Species	Genes	Reference
Rice	OsHKT1;5 (OsHKT8)	Ren et al. (2005)
Wheat	TmHKT1;5-A TaHKT1;5D	Munns et al. (2012)
Barley	HvHKT1;5	Nguyen et al. (2013a)
Tomato	SlHKT1;1 SlHKT1;2	Asins et al. (2013)

Breeding for KUE

Direct and Indirect Strategies

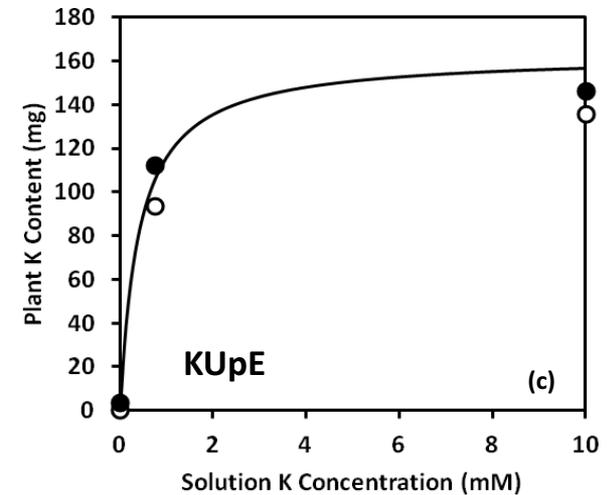
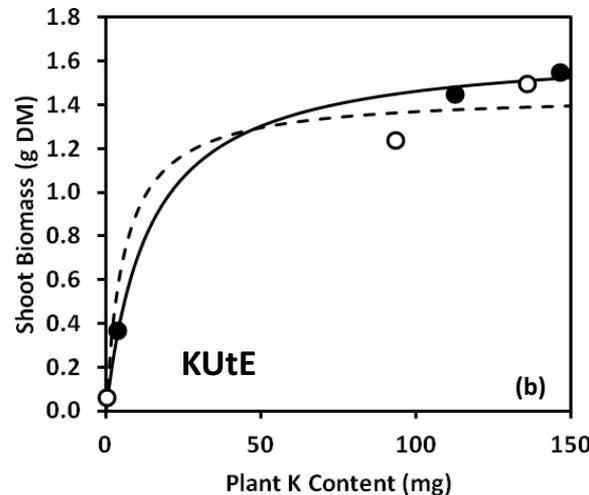
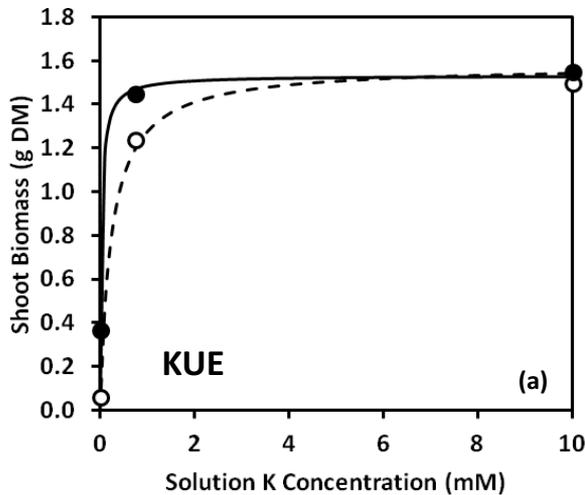


Genetic Studies Require Many Genotypes Need to Minimise Treatments / Replicates

Michaelis-Menten (M-M) Relationships

Barley Genotype

- Prisma
- Volla



White (2013) *J. Plant Nutr. Soil Sci.* 176: 305-316.

White et al. (2016) *Comm. Soil Sci. Plant Anal.* 47(S1): 104-111.

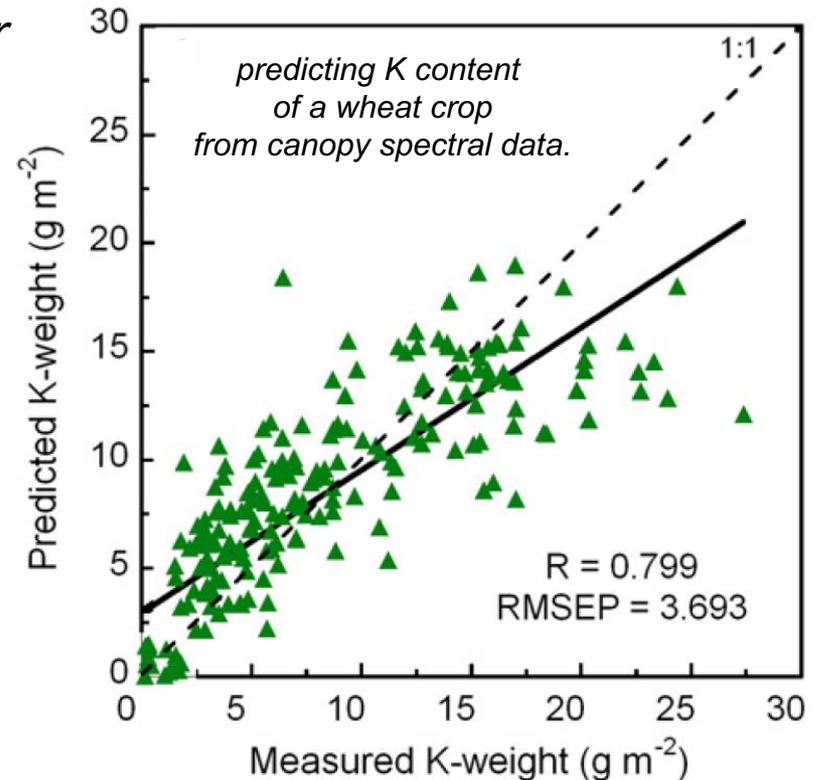
Breeding for KUE Directly

Need to Reduce the Cost of Assays

Develop techniques to estimate crop K content that are less costly and labour intensive than conventional mineral analyses .

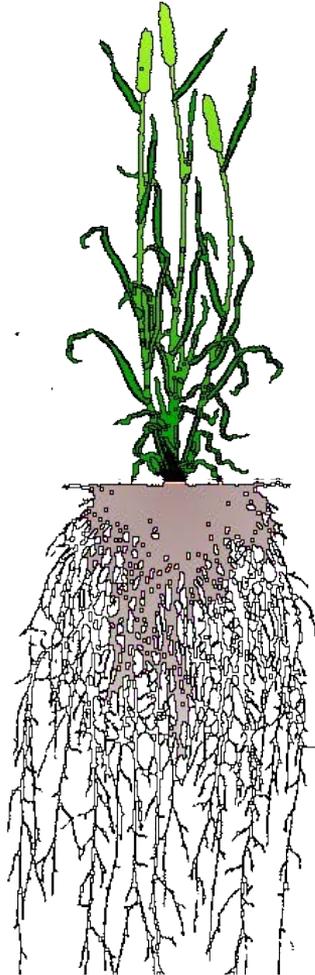
*Estimates of biomass.
Estimates of plant K concentration.*

Remote imaging techniques.



Pimstein et al. (2011) *Field Crops Research* 121: 25-135.

Breeding for Component Traits Improving Potassium Acquisition & Utilisation



Potassium Utilization Efficiency (KUtE)

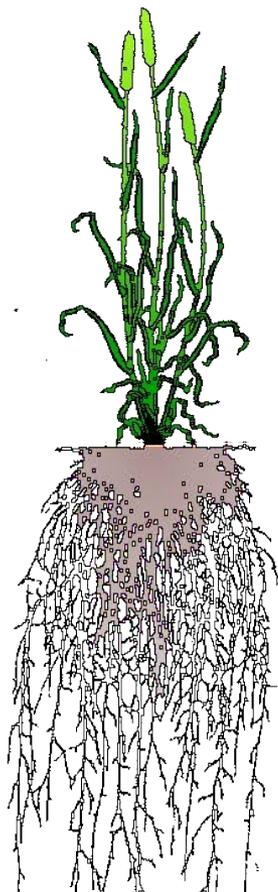
- Increasing photosynthesis
- Accelerating canopy development
- Increasing canopy longevity
- Increasing harvest index
- Tolerating lower tissue K^+ concentrations
- Replacing K^+ in non-essential functions
- Partitioning K^+ to metabolic cell compartments
- Redistributing K from senescent to developing tissues
- Redistributing K from root to shoot

Potassium Acquisition Efficiency (KU_pE)

- Increasing early root vigour
- Increasing root biomass or root/shoot ratio
- Increasing root surface area (lateral rooting, root hairs)
- Increasing root length density
- Improving root architecture for soil foraging
- Increasing exudation of H^+ and organic compounds
- Increasing K^+ uptake capacity of root cells
- Increasing affinity for K^+ of transport proteins
- Increasing water uptake through transpiration

White (2013) *J. Plant Nutr. Soil Sci.* 176: 305-316

Summary - The Genetics of Potassium Acquisition and Utilisation by Crop Plants



Potassium Uptake & Movement in Plants

Molecular Biology of Potassium Transporters

Definitions of Potassium Use Efficiency (KUE)

Variation Between and Within Plant Species

Plant Traits for Improving KUE

Genes Implicated in KUE