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# Understanding how plants cope with acid soils

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**Abstract.** Supplying food and fuel to meet the demands of a growing population is a challenge facing every society. Crop yields will need to increase significantly over the next 40 years to support an extra two billion people by 2050. Acid soils limit plant production around the world but especially in the tropical and sub-tropical latitudes where a large proportion of the population increases are expected to occur. Aluminium toxicity and phosphorus deficiency are two of the major stresses affecting plant growth on acid soils. How plants combat these stresses was a theme at the '7th International Symposium on Plant–Soil Interactions at Low pH', held in Guangzhou in 2009, and the focus of this issue of *FPB*. We provide an overview of recent progress in the area and introduce a selection of invited papers for this research front on acid soils.

**Additional keywords:** ALMT, aluminium, citrate, malate, MATE, phosphorus.

Over 30% of the world's arable soils and up to 70% of potentially arable land are acidic (pH <5.5; von Uexküll and Mutert 1995). Crop and pasture production on acid soils can be limited by an array of stresses. Aluminium toxicity and phosphorus deficiency are particularly important constraints but proton and manganese toxicity can be damaging as can deficiencies in calcium, magnesium and some micronutrients (Marschner 1995). Many soils become acidic naturally due to the normal weathering of rocks and leaching of basic minerals. Acid soils are common in the high rainfall zones around the equator where much of the food production is subsidence agriculture on small farms. However, acidification can be accelerated by certain farming practices. Rapid declines in soil pH have been associated with intensive agriculture and with the excessive use of nitrogen fertilizers (Guo *et al*. 2010). Sub-Saharan Africa and Asia are likely to accommodate unprecedented increases in population over the next 40 years and cereal production alone will have to increase by 50% to support this growth (Food and Agricultural Organisation 2006). To a large extent these gains will need to be met by increasing the yields on land currently under cultivation. However, such increases are unlikely to be sufficient by themselves and another 100 million ha or more of extra land may have to be brought into production despite their environmental or biological constraints. Enhancing crop production through resource management, agronomic practices and germplasm improvement remain important challenges for agricultural scientists and governments.

Although aluminium is the most abundant metal in the Earth's crust, it mostly occurs in forms that are harmless to plants: either locked up in minerals, as precipitates or as non-toxic ions. Under acidic conditions, however, these minerals dissolve more rapidly and the increased prevalence of the toxic $Al^{3+}$ species in the soil solution can inhibit root growth and, subsequently, the uptake of water and nutrients (Kochian *et al.* 2004; Ma 2007). Phosphorus is an essential macronutrient that is often poorly available to plants on acid soils because it becomes bound to mineral surfaces, incorporated into organic compounds or precipitated with aluminium or iron (Marschner 1995). Some plant species and even cultivars within species have evolved strategies for overcoming aluminium toxicity and for accessing the sparingly soluble phosphorus in acid soils. Encouraging progress has been made over the last few years in our understanding of these strategies. These developments are already assisting plant breeders improve the aluminium resistance and phosphorus-use efficiency of major crops. A few of these highlights are briefly described below.

Aluminium resistance in a wide range of species, monocotyledonous and dicotyledonous, relies on the release (efflux) of organic anions such as malate, citrate and oxalate from their roots (Ma *et al.* 2001; Ryan *et al.* 2001; Kochian *et al.* 2004). These anions bind with the toxic $Al^{3+}$ cations and prevent them from damaging the root apices and inhibiting growth. The genes controlling this response in many species have now been identified (Delhaize *et al.* 2007). *TaALMT1* from wheat (*Triticum aestivum* L.) was the first aluminium resistance gene cloned in plants that accounts for genotypic variation (Sasaki *et al.* 2004). It encodes a novel anion channel that controls the aluminium-activated efflux of malate from root apices. Homologous genes conferring similar functions have been isolated in *Arabidopsis* (Hoekenga *et al.* 2006), rape (*Brassica napus* L.; Ligaba *et al.* 2006) and rye (*Secale cereale* L.; Collins *et al.* 2008). Interestingly, the genes controlling citrate efflux in response to aluminium stress are members of a different family named the multi-drug and toxic compound extrusion


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(MATE) family. MATE genes also encode membrane-bound transport proteins, which transport a much wider range of substrates in microorganisms, plants and animals (Omote *et al.* 2007). Their substrates are as diverse as organic anions, secondary metabolites and even exogenous compounds such as antimicrobial drugs. The involvement of MATE genes in aluminium resistance was established after they were mapped to major aluminium-resistance QTLs in sorghum (*Sorghum bicolor* (L.) Moench; Magalhaes *et al*. 2007) and barley (*Hordeum vulgare* L.; Furukawa *et al.* 2007; Wang *et al.* 2007). Homologues of these genes have since been found to perform similar functions in *Arabidopsis* (Liu *et al.* 2009), wheat (Ryan *et al.* 2009) and maize (*Zea mays* L.; Maron *et al.* 2010). The genes controlling the release of oxalate from roots have yet to be identified.

Analyses of aluminium-sensitive mutants established that a third family of transport proteins also contributes to aluminium tolerance. The *ALS1* and *ALS3* genes from *Arabidopsis* (Larsen *et al.* 2005, 2007) and *STAR1*+*STAR2* from rice (Huang *et al.* 2009) encode ATP-binding cassette (ABC) proteins, which appear to protect plants from aluminium stress in different ways. The substrates of these transporters and exactly how they provide protection remain uncertain. Experimental evidence showing STAR1+STAR2 transports UDPglucose suggests that the efflux of sugars from root cells can help repair cell walls or avoid aluminium damage in other ways (Huang *et al.* 2009). Suggestions that ALS1 and ALS3 exclude aluminium ions from the cytoplasm by shunting them to the apoplasm or into internal compartments remain intriguing possibilities (Larsen *et al.* 2005, 2007). More recently, C2H2 zinc finger-type transcription factors have been shown to regulate the expression, not only of the *ALMTs*, *MATE*s and *ABC*s, but also of other genes conferring tolerance to low pH. The genes encoding these transcription factors are *STOP1* in *Arabidopsis* (Iuchi *et al.* 2007) and *ART1* in rice (*Oryza sativa* L.; Yamaji *et al.* 2009).

The availability of phosphorus in acid soils can also be increased by the release of organic anion from roots (Marschner 1995; Ryan *et al.* 2001). Plants have other strategies for accessing poorly soluble phosphorus as well such as the efflux of protons and phosphatases, high-affinity phosphate transporters, establishment of mycorrhizal associations, changes in root hair length, the formation of specialised roots structures such as cluster roots, and modified root architecture (Neumann *et al.* 2000; Lynch 2007). Arguably the most exciting developments in phosphorus nutrition do not target the acquisition of phosphorus from acid soils *per se* but rather the regulation of plant responses to phosphate deficiency in general (Doerner 2008). Recent studies in *Arabidopsis* show that the activity of some of the Pht1 transporters responsible for uptake of phosphate from the soil is subject to several levels of control. When phosphorus is plentiful, the expression of two *Pht1* genes is reduced by the E2 ubiquitin conjugase-related enzyme (UBC24) encoded by *PHO2* by mechanisms that remain unclear but likely involves protein degradation at some level (Aung *et al*. 2006; Bari *et al*. 2006). When phosphorus supply is restricted, *PHO2* expression is repressed by a very large increase in shoot expression of the microRNA *miR399. miR399* moves to the roots via the phloem and initiates the degradation of *PHO2* transcripts by targeting complementary regions of the 5′UTR. The reduced level of *PHO2* transcript with subsequent reduced activity of UBC24 results in increased *Pht1* expression and greater transport activity. This regulatory circuit is further modulated by non-coding RNAs, named *Induced by Phosphorus Starvation* (*IPS1*) genes, which contain sequences almost identical to those recognised by *miR399* that target the *PHO2* transcript. In effect, the *IPS1*s compete with *PHO2* for interactions with *miR399* without being degraded themselves (Shin *et al.* 2006; Franco-Zorrilla *et al.* 2007) and serve to attenuate the degradation of *PHO2* transcript. While this mechanism for regulating phosphorus uptake appears to function in a range of species it is only one component of a complex network controlling phosphorus homeostasis. The result is a set of regulation loops that allow plants to finely tune their responses to phosphorus status. These control mechanisms are being unravelled by analysing the altered expression of additional genes in mutants and transgenic plants.

This research front on plant responses to acid soil, contains five papers most of which were presented at the '7th International Symposium on Plant–Soil Interactions at Low pH (PSILPH)', held in Guangzhou, China, 17–21 May 2009. A review by Ryan and Delhaize (2010) argues that convergent evolution has shaped the emergence of aluminium resistance in plants and offers ideas for why organic anion efflux has become such a widespread mechanism in different species. Their paper is also part of the 'The Evolution of Plant Function' series of reviews initiated by *FPB* in 2009 to commemorate the publication of 'On The Origin of Species' by Charles Darwin 150 years ago. The research paper by Yokosho *et al*. (2010) characterises two MATE genes in rye, *ScFRDL1* and *ScFRDL2*, which are homologues of the aluminium resistance gene in barley *HvAACT1* (Furukawa *et al.* 2007). While both genes are predominantly expressed in the roots, *ScFRDL2* shows all the hallmarks of contributing to aluminium resistance while *ScFRDL1* behaves similarly to *FRD3* in *Arabidopsis* and *OsFRDL1* in rice (Yokosho *et al.* 2009), and is likely to be involved in long distance transport of iron to the shoots. The paper by Xu *et al*. (2010) describes how changes in mitochondrial citrate metabolism contribute to the aluminium-induced secretion of citrate from soybean (*Glycine max* L.) roots. Two final papers examine the relationship between root morphology and phosphorus acquisition in maize and soybean. Zhu *et al*. (2010) estimated the contribution of root hair length to phosphorus uptake in a set of six recombinant inbred lines of maize and concluded that the ability to vary root hair length in changing nutrient conditions could be an important for optimising plant growth in different environments. Ao *et al*. (2010) compared gross root architecture among soybean lines and showed that phosphorus-efficient genotypes had larger shallower roots. They argued that a greater distribution of roots in the upper layers of soil would enable plants to access more phosphorus.

It is clear that tolerance to acid soils involves complex interactions that are controlled by many genes. We hope that these papers provoke ongoing discussion and experimentation to improve our understanding for how plants cope with these stresses. Ultimately this knowledge will be necessary to help maintain and even increase plant production in these hostile environments.

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## References


Ao J, Fu J, Tian J, Yan X, Liao H (2010) Genetic variability for root morph-architecture traits and root growth dynamics as related to phosphorus efficiency in soybean. *Functional Plant Biology* **37**, 304–312. doi:10.1071/FP09215

Aung K, Lin SI, Wu CC, Huang YT, Su CL, Chiou TJ (2006) *pho2*, a phosphate accumulator, is caused by a nonsense mutation in a microRNA target gene. *Plant Physiology* **141**, 1000–1011. doi:10.1104/pp.106.078063

Bari R, Datt Pant B, Stitt M, Scheible WR (2006) *PHO2*, microRNA399, and *PHR1* define a phosphate-signaling pathway in plants. *Plant Physiology* **141**, 988–999. doi:10.1104/pp.106.079707

Collins NC, Shirley NJ, Saeed M, Pallotta M, Gustafson JP (2008) An *ALMT1* gene cluster controlling aluminum tolerance at the *Alt4* locus of rye (*Secale cereale* L.) *Genetics* **179**, 669–682. doi:10.1534/genetics.107.083451

Delhaize E, Gruber BD, Ryan PR (2007) The role of organic anion permeases in aluminium resistance and mineral nutrition. *FEBS Letters* **581**, 2255–2262. doi:10.1016/j.febslet.2007.03.057

Doerner P (2008) Phosphate starvation signaling: a threesome controls systemic $P_i$ homeostasis. *Current Opinions in Plant Science* **11**, 536–540. doi:10.1016/j.pbi.2008.05.006

Food and Agricultural Organisation (2006) 'Statistics division, statistical yearbook 2005–2006.' (United Nations: Rome)

Franco-Zorrilla JM, Valli A, Todesco M, Mateos I, Puga MI, Rubio-Somoza I, Leyva A, Weigel D, Garcia JA, Paz-Ares J (2007) Target mimicry provides a new mechanism for regulation of microRNA activity. *Nature Genetics* **39**, 1033–1037. doi:10.1038/ng2079

Furukawa J, Yamaji N, Wang H, Mitani N, Murata Y, Sato K, Katsuhara M, Takeda K, Ma JF (2007) An aluminum-activated citrate transporter in barley. *Plant & Cell Physiology* **48**, 1081–1091. doi:10.1093/pcp/pcm091

Guo JH, Liu XJ, Zhang Y, Shen JL, Han WX, Zhang WF, Christie P, Goulding KWT, Vitousek PM, Zhang FS (2010) Significant acidification in major Chinese croplands. *Science* **327**, 1008–1010. doi:10.1126/science.1182570

Hoekenga OA, Maron LG, Pineros MA, Cancado GMA, Shaff J, *et al*. (2006) *AtALMT1*, which encodes a malate transporter, is identified as one of several genes critical for aluminum tolerance in *Arabidopsis*. *Proceedings of the National Academy of Sciences of the United States of America* **103**, 9738–9743. doi:10.1073/pnas.0602868103

Huang CF, Yamaji N, Mitani N, Yano M, Nagamura Y, Ma JF (2009) A bacterial-type ABC transporter is involved in aluminum tolerance in rice. *The Plant Cell* **21**, 655–667. doi:10.1105/tpc.108.064543

Iuchi S, Koyama H, Iuchi A, Kobayashi Y, Kitabayashi S, Kobayashi Y, Ikka T, Hirayama T, Shinozaki K, Kobayashi M (2007) Zinc finger protein STOP1 is critical for proton tolerance in *Arabidopsis* and coregulates a key gene in aluminum tolerance. *Proceedings of the National Academy of Sciences of the United States of America* **104**, 9900–9905. doi:10.1073/pnas.0700117104

Kochian LV, Hoekenga OA, Piñeros MA (2004) How do crop plants tolerate acid soils? Mechanisms of aluminium tolerance and phosphorus efficiency. *Annual Review of Plant Biology* **55**, 459–493.

Larsen PB, Geisler MJB, Jones CA, Williams KM, Cancel JD (2005) *ALS3* encodes a phloem-localized ABC transporter-like protein that is required for aluminum tolerance in *Arabidopsis*. *The Plant Journal* **41**, 353–363. doi:10.1111/j.1365-313X.2004.02306.x

Larsen PB, Cancel J, Rounds M, Ochoa V (2007) *Arabidopsis ALS1* encodes a root tip and stele localized half type ABC transporter required for root growth in an aluminum toxic environment. *Planta* **225**, 1447–1458. doi:10.1007/s00425-006-0452-4

Ligaba A, Katsuhara M, Ryan PR, Shibasaka M, Matsumoto H (2006) The *BnALMT1* and *BnALMT2* genes from rape encode aluminum-activated malate transporters that enhance the aluminum resistance of plant cells. *Plant Physiology* **142**, 1294–1303. doi:10.1104/pp.106.085233

Liu J, Magalhaes JV, Shaff J, Kochian LV (2009) Aluminum-activated citrate and malate transporter from the MATE and ALMT families function independently to confer *Arabidopsis* aluminum tolerance. *The Plant Journal* **57**, 389–399. doi:10.1111/j.1365-313X.2008.03696.x

Lynch JP (2007) Roots of the second green revolution. *Australian Journal of Botany* **55**, 493–512. doi:10.1071/BT06118

Ma JF (2007) Syndrome of aluminum toxicity and diversity of aluminum resistance in higher plants. *International Review of Cytology* **264**, 225–252. doi:10.1016/S0074-7696(07)64005-4

Ma JF, Ryan PR, Delhaize E (2001) Aluminium tolerance in plants and the complexing role of organic acids. *Trends in Plant Science* **6**, 273–278. doi:10.1016/S1360-1385(01)01961-6

Magalhaes JV, Liu J, Guimaraes CT, Lana UGP, Alves VMC, *et al*. (2007) A gene in the multidrug and toxic compound extrusion (MATE) family confers aluminum tolerance in sorghum. *Nature Genetics* **39**, 1156–1161. doi:10.1038/ng2074

Maron LG, Pineros MA, Guimaraes CT, Magalhaes JV, Pleiman JK, Mao C, Shaff JE, Belicuas SNJ, Kochian LV (2010) Two functionally distinct members of the MATE (multi-drug and toxic compound extrusion) family of transporters potentially underlie two major aluminum tolerance QTLs in maize. *The Plant Journal* **61**, 728–740. doi:10.1111/j.1365-313X.2009.04103.x

Marschner H (1995) 'Mineral nutrition of higher plants. 2nd edition.' (Academic Press: San Diego)

Neumann G, Massonneau A, Langlade N, Dinkelaker B, Hengeler C, Romheld V, Martinoia E (2000) Physiological aspects of cluster root function and development in phosphorus-deficient white lupin (*Lupinus albus* L.). *Annals of Botany* **85**, 909–919. doi:10.1006/anbo.2000.1135

Omote H, Hiasa M, Matsumoto H, Osuka M, Moriyama Y (2007) The MATE proteins as fundamental transporters of metabolic and xenobiotic organic cations. *Trends in Pharmacological Sciences* **11**, 587–593.

Ryan PR, Delhaize E (2010) The convergent evolution of aluminium resistance in plants exploits a convenient currency. *Functional Plant Biology* **37**, 275–284. doi:10.1071/FP09261

Ryan PR, Delhaize E, Jones DL (2001) Function and mechanism of organic anion exudation from plant roots. *Annual Review of Plant Physiology and Plant Molecular Biology* **52**, 527–560.

Ryan PR, Raman H, Gupta S, Horst WJ, Delhaize E (2009) A second mechanism for aluminum resistance in wheat relies on the constitutive efflux of citrate from roots. *Plant Physiology* **149**, 340–351. doi:10.1104/pp.108.129155

Sasaki T, Yamamoto Y, Ezaki B, Katsuhara M, Ahn SJ, Ryan PR, Delhaize E, Matsumoto H (2004) A wheat gene encoding an aluminum-activated malate transporter. *The Plant Journal* **37**, 645–653. doi:10.1111/j.1365-313X.2003.01991.x

Shin H, Shin H-S, Chen R, Harrison MJ (2006) Loss of At4 function impacts phosphate distribution between the roots and the shoots during phosphate starvation. *The Plant Journal* **45**, 712–726. doi:10.1111/j.1365-313X.2005.02629.x

von Uexküll HR, Mutert E (1995) Global extent, development and economic impact of acid soils. *Plant and Soil* **171**, 1–15. doi:10.1007/BF00009558

Wang JP, Raman H, Zhou MX, Ryan PR, Delhaize E, *et al*. (2007) High resolution mapping of the *Alp* locus and identification of a candidate gene *HvMATE* controlling aluminium tolerance in barley (*Hordeum vulgare* L.). *Theoretical and Applied Genetics* **115**, 265–276. doi:10.1007/s00122-007-0562-9

Xu M, You J, Hou N, Zhang H, Chen G, Yang Z (2010) Tricarboxylic acid cycle metabolic network in mitochondria leads to enhanced citrate efflux in soybean exposed to aluminum. *Functional Plant Biology* **37**, 285–295. doi:10.1071/FP09223

Yamaji N, Huang CF, Nagao S, Yano M, Sato Y, Nagamura Y, Ma JF (2009) A zinc finger transcription factor ART1 regulates multiple genes implicated in aluminum tolerance in rice. *The Plant Cell* **21**, 3339–3349. doi:10.1105/tpc.109.070771

Yokosho K, Yamaji N, Ueno D, Mitani N, Ma JF (2009) OsFRDL1 is a citrate transporter required for efficient translocation of iron in rice. *Plant Physiology* **149**, 297–305. doi:10.1104/pp.108.128132

Yokosho K, Yamaji N, Ma JF (2010) Isolation and characterization of two MATE genes in rye. *Functional Plant Biology* **37**, 296–303. doi:10.1071/FP09265

Zhu J, Zhang C, Lynch JP (2010) The utility of phenotypic plasticity of root hair length for phosphorus acquisition. *Functional Plant Biology* **37**, 313–322. doi:10.1071/FP09197