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## MECHANISMS OF ADAPTATION OF SMALL GRAINS TO SOIL ACIDITY\*

**ABSTRACT:** Acid soils limit crop production on 30—40% of the world's arable land and up to 70% of the world's potentially arable land. Over 60% of the total arable lands in Serbia are acid soils. Soil acidity is determined by hydrogen (H<sup>+</sup>) in soil solution and it is influenced by edaphic, climatic, and biological factors. Major constraints for plant growth on acid mineral soils are toxic concentrations of mineral elements like Al of H<sup>+</sup> and/or low mineral nutrient availability due to low solubility (e.g. P and Mo) or low reserves and impaired uptake (e.g. Mg<sup>2+</sup>) at high H<sup>+</sup> concentrations. Aluminum (Al) toxicity is primary factor limiting crop production on acid soils. This review examines our current understanding of mechanisms of Al-toxicity, as well as the physiological and genetic basis for Al-toxicity and tolerance. Inhibition of root growth by Al leads to more shallow root systems, which may affect the capacity for mineral nutrient acquisition and increase the risk of drought stress. Of the two principal strategies (tolerance and avoidance) of plants for adaptation to adverse soil conditions, the strategy of avoidance is more common for adaptation to acid mineral soils. At the same, the short view of the most important genetics tolerance mechanisms, developed and determined in some small grains genotypes, is showed as well.

**KEY WORDS:** acid soils, adaptation mechanisms, small grains

### INTRODUCTION

Acid soils currently reduce plant production on 30—40% of total and up to 70% of potentially arable land worldwide. They are distributed mainly in two distinctive geographical belts: in the cold, humid, and moderate climate of a northern belt, and the warm and humid climate of southern tropical regions (Eswaran et al., 1997).

Van Wambeke (1976) reported that acid soils cover 1,455 million hectares of land, or some 11% of total global land surface, while Von Uexkull and Mutert (1995) made estimates that acid soils (defined as soils

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\* Review paper.

with  $\text{pH} < 5.5$  in the top layer) cover 3,950 million hectares, or about 30% of arable land worldwide, with a tendency of further growth.

In the Republic of Serbia, acid soils are widespread, accounting for over 60% of total arable land (Stevanović et al., 1995). Those are mostly lowland or hillside types of pseudogley or its leached variants, acid vertisols, podzolic eutric cambisols, diluvial, brown, or leached brown soils of mountainous regions. Those soils are rather poor in bases, medium to heavily acidic, having very poor texture and poor organic content, and more or less ill suited for cultivation of most cereal crops. Most acid soils are located in the central parts of Serbia and in Kosovo and Metohija. With the exception of soils in major river valleys (formed upon alluvial deposits) and soils formed upon calcareous, marine and lake sediments and limestone, nearly all regions of central Serbia have soils with some degree of acidity.

The acidity of these soils, their high contents of  $\text{H}^+$  ions and low contents of essential plant nutrients, primarily P and Ca, are limiting factors for high and stable yields of cultivated cereal crops. Apart from acidity, those soils are also often characterized by high contents of toxic forms of Al, Fe and Mn, and by deficits caused by leaching or decreased availability of P, Ca, Mg and some other micronutrients, especially Mo, Zn and B (Narro et al., 2001; Sumner, 2004; Welcker et al., 2005; Kovačević et al., 2006; Jovanović et al., 2006; Đalović et al., 2007).

Recent investigations worldwide have shown that massive deterioration of small grains on acid soils is caused by elevated concentrations of mobile forms of some toxic elements (Al, Fe, Mn), whose contents become especially evident when no phosphorus nutrition is practiced or the Ca component is missing from nitrogen fertilizers (Jelić, 1996).

Acidity restrains root growth and, consequently, the uptake of water and mineral nutrients. The top soil layer containing more organic matter is dominated by  $\text{H}^+$  ions, while Al toxicity is more evident in layers beneath.

Aluminum toxicity is considered to be the most important factor limiting plant growth on acid soils (Foy, 1984; Carver and Ownby, 1995; Jayasundara et al., 1998; Arsenijević-Maksimović et al., 2001; Jelić et al., 2004). Even though Al is present in water, soil, and atmosphere, most of it is bound to aluminosilicate minerals in soil, while small, submicromolar amounts appear as soluble forms able to affect biological systems (May and Nordstrom, 1991).

When their contents and mobility are high in soil, plants become stressed, and the state of stress becomes evident from such negative symptoms as slow growth, weak tillering, thinning of crop and delay in various stages of development. High Al concentrations in plants interfere with the uptake, transport, and reutilization of calcium, magnesium, phosphorus, and potassium that coincide with water uptake and enzymatic activity in the root system, and disrupt plant homeostasis. Obstruction of development of generative organs and grain filling, and frequent deterioration and death of plants, are the other consequences of the toxic activity of Al.

A primary response to Al-induced stress occurs in the root system of plants (Taylor, 1988; Jayasundara et al., 1998). The main symptom

of Al toxicity is fast inhibition of root growth, which may be caused by changes in various physiological processes, including Al interaction with other ions in the cell wall, plasma membrane or symplast of the root system (Marschner, 1991; Horst, 1995; Kochian, 1995). Aluminum also impairs cell division in root tips, hardens cell walls, interferes with DNA replication, blocks a number of enzymes, reduces the production and transport of cytokinin, modifies the structure and functioning of plasma membrane, binds phosphorus in its less available forms in soil and on root surface, decreases root respiration, reduces water uptake and blocks the uptake and metabolism of most nutrients.

Plant species differ regarding their tolerance to soil acidity and high content of mobile Al in the nutrient media. Some of them are intrinsically more tolerant than others, for example cowpea (*Vigna unguiculata* L. Walp), peanut (*Arachis hypogea* L.), rice (*Oryza sativa* L.) or rye (*Secale cereale* L.) (Little, 1988). Rye is one of the most stress-tolerant species in Triticeae family. Hitherto research of the tolerance of cereal species has shown that rye is most tolerant, followed by triticale (*X Triticosecale* Wittmack), wheat (*Triticum aestivum* L.) and barley (*Hordeum vulgare* L.) (Aniol and Madej, 1996).

We intended to discuss mechanisms of adaptation of small grains to soil acidity, focusing on high contents of mobile Al in nutrient medium. Acid soils are in a process of world scale expansion, largely due to human activities, and this issue has scientific as well as acute economic relevance.

## MECHANISMS OF SMALL GRAINS ADAPTATION TO SOIL ACIDITY AND HIGH ALUMINIUM CONTENTS

Adaptation of small grains to elevated soil acidity and high Al contents in soil solution may be due to one or more different mechanisms (Marschner, 1991). Our present knowledge shows that various types of mechanisms, depending on their sites of activity, can be grouped into: *i*) external mechanisms that stimulate Al elimination from root tips; *ii*) internal mechanisms dependent on the capacity of Al tolerance in plant symplast, and *iii*) genetic mechanisms. One should bear in mind that soil acidity normally coincides with high Al contents, but that some plant species are sensitive to acidity and at the same time tolerant to high Al concentration, while the reverse applies to some other species.

### *External mechanisms of tolerance*

External mechanisms of tolerance act to prevent penetration of Al and its accumulation in plants. Their activity is present in the apoplast, cell wall, and rhizosphere. The activity of external mechanisms of tolerance is based on: Al immobilization in cell wall (Blamey et al., 1990; Taylor, 1991; Kochian, 1995), leaching of Al through plasma membrane (Zhang and Taylor, 1991; Taylor, 1991), formation of a pH barrier in the plant rhizosphere (Foy, 1988; Taylor, 1991; Pellet et al., 1997) and secretion of

organic acids, phosphates, chelates and the other ligands through the root to the exterior (Henderson and Ownby, 1991; Ryan et al., 1995; De la Fuente et al., 1997; Pellet et al., 1997).

Cell wall is a barrier for Al ions transported from nutrient medium into the cell interior. For that reason, cell wall, together with plasma membrane, provides the most important external mechanism of plant protection from the toxic effects of Al (Takabatake and Shimmen, 1997). Complex structure of the cell wall and its chemical composition provides a protection from abiotic stress, including Al-induced stress. Evidence has been found that different wheat cultivars have different capacities to bind Al in the cell wall, consequently demonstrating different levels of Al tolerance. However, mechanisms of tolerance of some genotypes are still not clear.

Plasma membrane is the primary site where Al intoxication takes place (Takabatake and Shimmen, 1997). Primary effects of Al on the permeability of root membrane may appear several minutes or as much as several hours after exposure to Al. These effects are probably due to an ability of Al to bind carboxyl groups in the cell wall and phosphate groups in the membrane (Gunsé et al., 1997). Although the first reaction to Al is taking place at the tip of the root (Taylor, 1995; Sivaguru et al., 1999), the mechanism of growth inhibition caused by Al has still not been adequately explained and continues to provoke different opinions. Some data indicate that Al penetrates the root symplast at considerable degree, probably affecting membrane growth (Lazof et al., 1994).

As the exact target site of Al toxicity in the cell has not yet been identified, intensive research has focused on the symplast on one side, and the apoplast on the other (Marienfeld et al., 2000). The bulk of absorbed Al accumulates in the apoplast and accounts for 30–90% of total Al in tissues (Rengel, 1996). Most of Al has thus been uncritically attributed to symplast as a result either of apoplast contamination or insufficient desorption. Although various research reports have indicated that Al binds to different cell components, such as cell wall, plasma membrane or DNA (Rengel, 1996; Silva et al., 2000; Taylor et al., 2000), it seems that Al mostly accumulates in the cell wall. Rengel and Reid (1997) used giant cells of *Chara corallina* algae and found that 99.99% of total Al in those cells was accumulating in cell wall, while Chang et al. (1999) found that this applied mostly to the cell wall pectin that remains in the protoplast even after enzyme digestion of the wall. The authors went so far to assume that Al is able to bind pectin formed after Al treatment. However, in order to understand the mechanism of Al tolerance, quantitative information is required to clarify the uptake and distribution of Al inside the cell.

During contact with plasma membrane, Al acts as an ion-exchanging agent. Therefore, cation exchange capacity (CEC) is very important for its uptake, as hitherto research has confirmed that Al-tolerant genotypes have significantly lower CECs than Al-sensitive genotypes. Besides, higher Al accumulation in sensitive wheat and barley cultivars than in tolerant cultivars has also been found inside the root and on total root surface, while tolerant cultivars had higher Al accumulation only in the root cap zone (Foy, 1988).

Wagatsuma (1983) also found a positive correlation between CEC and Al content in roots of some plant species. However, other data based on Al distribution between wheat apoplast and symplast have not indicated any genotype differences regarding Al tolerance. Al immobilization in plasma membranes is also based on maintenance of its selective permeability. Specific calmodulin-type proteins have a significant role in this process as they are intensively synthesized by tolerant cultivars when plants are exposed to Al stress.

Aluminum phytotoxicity to cereals is heavily dependent on soil pH as well. The mechanism of Al tolerance by some cereal genotypes is based on their ability to maintain high rhizosphere pH. So far, it has been shown that tolerant cultivars have higher rhizosphere pH than Al-sensitive ones (Foy and Fleming, 1982). Wagatsuma and Yamasaku (1985) discovered a positive correlation between Al tolerance of barley and increased pH in its medium caused by the activity of the root system. However, in trials involving different nitrogen forms ( $\text{NH}_4\text{-N}$  and  $\text{NO}_3\text{-N}$ ), the build-up of a pH barrier in order to achieve wheat tolerance was less important than some other mechanisms and was very slow under conditions described (Taylor, 1988). On the other hand, there is information indicating that increased pH aiming at establishing a pH barrier is highly efficient despite being quite slow.

Secretion of organic acids, phosphates and other substances by the root system is another crucial mechanism of tolerance to Al. The activity of this mechanism is based on complexation of Al with mucilage, organic acid ligands, and other substances forming chelate complexes. Al complexation reduces its uptake from the rhizosphere of the root system. At low soil pH and high Al concentration, tolerant genotypes increase secretion of mucilage, i.e. substances characterized by a high capacity of binding Al. Those substances are able to bind cations (primarily  $\text{Ca}^{2+}$ ) and are secreted mostly by the root cap and the root tip zone (Puthota et al., 1991). Under high Al content in a soil solution, the tolerant wheat cultivar Atlas 66 was found to have three times the volume of mucilage synthesis that the sensitive cultivar Victor had (Johnson and Bennett, 1991).

Aluminum complexation with organic acids reduces Al phytotoxicity in the rhizosphere or the root system. Organic acids extracted from roots have different capacities for precipitating Al, namely: oxalic acid > citric acid > malic acid > succinic acid. Delhaize et al. (1993) reported that the release of apple acid from the root tip zone of tolerant genotypes was 5–10 times higher than that of Al-sensitive genotypes. Simultaneously, accumulation of Al in the root tip zone decreased.

Tolerant plants also counter toxic activity of Al by secreting chelates by the root system. Chelators on root surface or in cell walls bind Al ions and so reduce their mobility and uptake. Ohman (1988) emphasized citrates as powerful Al-chelators. The binding of citrate carboxyl groups with the Al-hydrated ion is a basis for reducing their diffusion through the lipid layer of plasmalemma (Akeson and Munns, 1989). Al also forms complexes with fatty acids. It is assumed that chelates of Al with free fatty acids (at concentrations > 200 mM) intensify Al uptake, unlike chelates with esterified fatty

acids. However, the mechanism of activity of this type of tolerance is limited by the fact that chelates are constantly being broken down by microorganisms. Their stable renewal requires a great deal of energy from the plant, which is why this mechanism is less efficient.

Root colonization with mycorrhizal fungi is also an important mechanism of plant adaptation to acid soils with high Al contents and smaller amounts of available phosphorus in warm climatic regions. Ectomycorrhizal fungi bind Al in cell walls, thus reducing its uptake. A crucial role of ectomycorrhizal fungi has been partially proved for individual genotypes cultivated on tropical soils with phosphorus deficits, and in cases where plant root systems were not secreting significant amounts of organic acids (G o e d e r t et al., 1997). Apart from their protective role against Al-induced stress, ectomycorrhizal fungi also increase phosphorus availability to some mycorrhizal plants (e.g. Norwegian spruce).

#### *Internal mechanisms of tolerance*

Internal mechanisms of tolerance to Al in Al-tolerant genotypes of cereals become activated after a large amount of Al has penetrated plant cells through the plasma membrane. The activity of this mechanism is based on Al complexation with proteins, organic acids and enzymes, and chelation in cytosols.

An important part in Al detoxication in the plant symplast is played by organic acids that form complexes with Al by accumulating them in specific cell organelles, especially the vacuoles. Al complexation with organic acids, primarily with citric and malic acids, is an important internal mechanism of tolerance to high concentrations of Al. Al detoxication in plant cell cytoplasm is based on Al complexation with proteins, especially with the enzymatic protein calmodulin. Besides calmodulin, other proteins of the metalloprotein group form complexes with Al in cells; they bind Al via the SH group, forming relatively stable complexes. The formed complexes are then transferred into the vacuole by the enzyme tonoplast transferase (Al-ATPase) (A n i o l, 1984). The activity of protein kinase in Al-tolerant cultivars has also been found to reduce the toxic levels of Al, compared to sensitive cultivars (M o u s t a k a s et al., 1992).

A decrease in cellular Al toxicity may also occur by its complexation with phytochelatins. In small grains, especially in tolerant genotypes, a large number of substances have been found that are able to form chelates with Al.

#### *Genetic mechanisms of tolerance*

Plants have genetically controlled mechanisms (present in most phenotypes) and adaptive mechanisms (present in tolerant phenotypes) of overcoming high concentrations of various elements in their nutrient medium.

The environment with all of its factors influence plant organisms, causing high variability in plants of the same inherited background. In addition, genetic sources of tolerance can be very different and scattered in different indivi-



duals of wild populations. Knowing the genetic background of tolerance is greatly important for creating genotypes tolerant to acid medium, and to the presence of high concentrations of Al.

Small grains show different levels of tolerance to acid soils and high contents of Al in soil solution. Barley (*Hordeum vulgare* L.) is the most sensitive of them, followed by wheat (*Triticum aestivum* L.), while oats (*Avena sativa* L.) and rye (*Secale cereale* L.) show higher tolerance. However, differences that have been detected in the tolerance of some genotypes within a species are often greater than those between species.

Genetic characters and gene localization on chromosomes that are responsible for tolerance to acidity and high Al content have been extensively studied in cereals, especially in wheat.

Slootmaker (1974) was one of the first researchers in the world to localize roughly wheat genes for tolerance to soil acidity, specifying the importance of genome D, as well as genomes A and B. Aniol and Gustafson (1984) found the genes responsible for wheat tolerance to Al on the following chromosome arms: 6AL, 7AS, 4BL, 2DL, 3DL, 4DL and 7D, confirming that indeed the genes for Al tolerance exist predominantly in the A and D genomes. In hexaploid wheat, the major genes that affect Al tolerance are localized on the short arm of chromosome 5A and the long arms of chromosomes 2D and 4D (Aniol, 1995).

According to Kerridge and Kronstad (1968), only one dominant gene was responsible for Al tolerance in cross-breeding of the wheat cultivars Duchamp and Brevor, but additional genes were present in the cultivar Atlas 66. This is consistent with findings reported by Campbell and Laffever (1981), who found that Al tolerance to wheat was not merely inherited, but that expression of Al tolerance was additive and highly inheritable. Camargo (1981) showed that the Al tolerance displayed by Atlas 66 was determined by a complex genetic mechanism involving at least two dominant major genes, and possibly some other minor genes. A gene on chromosome 5D had been identified previously, but Berzonsky (1992) found that Al tolerance in Atlas 66 was determined not only by the dominant genes located in genome D, but genomes A and/or B as well. In their studies of different crossbreeding, Rajaram et al. (1991) identified the presence of two complementary dominant genes in one parent, and one recessive gene in two other parents. Other studies have indicated that tolerance to Al is simply an inherited characteristic based on one dominant major gene (Delhaize et al., 1993; Somers and Gustafson, 1995; Somers et al., 1996; Basu et al., 1997). Recently, a connection has been revealed between the restriction fragment length polymorphism (RFLP) marker on chromosome 4DL and a gene for Al tolerance in the wheat cultivar BH 1146 originating from Brazil (Riede and Anderson, 1996). Ramana et al. (2005) determined the genomic structure of the Al tolerance gene (ALMT1) coding for Al-induced malate transporter. The gene was mapped on chromosome 4DL and cosegregates with Al tolerance. Tolerance to Al cosegregates with increased capacity for Al-induced malate efflux. The authors believe that Al tolerance is connected in most wheat genotypes with the function of this gene. Cai et al. (2008) disco-

vered three quantitative trait alleles (QTAs) that are related to Al tolerance. One of them cosegregates with the marker for ALMT1 gene promoter and is situated on chromosome 4DL, while the other two are on chromosomes 3BL and 2A. The two main quantitative trait loci (QTLs) on chromosomes 4DL and 3BL have an additive effect and the SSR markers linked to them can be used in marker-assisted selection aimed to increase wheat tolerance to Al.

Rye is one of the species with the highest tolerance to stress in the family *Triticeae* (Little, 1988; Aniol and Madej, 1996). Its genes for Al tolerance have been localized on chromosomes 3R, 4R, and 6RS (Aniol and Gustafson, 1984). Gallego and Benito (1997) studied gene segregation for Al tolerance and the positions of several isoenzymes in a segregating population and found that Al tolerance in rye was controlled by at least two major dominant and independent loci. The genes coding for isoenzymes Acol and Ndh2 relate to the segregating gene for tolerance to Al on chromosome 6R. Comparing segregation in several rye populations, Hede et al. (2001) discovered that Al tolerance in rye was controlled by several dominant alleles that have different effects on two or three independent loci.

Many triticale cultivars are characterized by high tolerance to Al, but not as high as rye (Hede et al., 2001). Evidently, some wheat genes block the expression of Al tolerance genes from rye, while others enable the expression of rye's tolerance to Al. Aniol and Gustafson (1984) showed that expression of the 6R tolerance to Al depends on which wheat chromosome has been replaced. Gustafson and Ross (1990) found suppressors of rye tolerance to Al on chromosome arms 4AL, 5AL, 6AL, 7BS, 7BL, and 3DS. Similarly, activators of rye tolerance to Al were present on arms 2AL, 5AS, 6BS, 1DS, 1DL, 2DL, 4DL, 5DS, 5DL, 6DL, 7DS, and 7DL.

Barley is the most sensitive of all small grains to the activity of Al. Genetic analyses have shown that barley tolerance to acid soils was inherited by one dominant gene (Stølen and Andersen, 1978) and by multiple alleles (Minella and Sorrells, 1992). Stølen and Andersen (1978) found that tolerance to high soil acidity is regulated by one dominant gene, marked as Pht, on chromosome 4. According to Reid (1971), Al tolerance of the barley cultivars Dayton and Smooth Awn 86 is regulated by one dominant gene, marked as Alp. Echart et al. (2006) reported that barley tolerance to Al depended on one gene and found the RFLP marker Xwg464 on the long arm of chromosome 4H at 21.6 cM distance from the gene.

Examining sweet sorghum (*Sorghum bicolor* L.), Jurandir et al. (2007) identified a gene coding for Al-induced citrate transporter on the locus *Alt<sub>SB</sub>*, which is believed to be responsible for Al tolerance. It is one of the proteins of the MATE gene family considered to increase Al tolerance by stimulating secretion of citrates from the root.

In rice, 9 QTLs have been identified, including one responsible for root length under non-stress conditions (CRL), three for root length under Al-induced stress (SRL) and five for relative root length (RRL) (Nguyen et al., 2003). Complementary genetic analysis has revealed that QTLs for RRL, mapped on chromosomes 1 and 9, are conserved among different rice populations. Major QTL for RRL, which accounts for 24.9% of the phenotypic variability,



has been found on chromosome 3 of rice that is conserved in all cereals. These results are valuable to breeders, and further studies of these QTLs could make a significant contribution to clarifying the mechanisms of adaptation of different cereals to acid soils.

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## МЕХАНИЗМИ АДАПТАЦИЈЕ СТРНИХ ЖИТА НА КИСЕЛОСТ ЗЕМЉИШТА

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### Резиме

Кисела земљишта ограничавају биљну производњу на 30—40% укупних, као и до 70% потенцијално обрадивих светских површина. Кисела реакција ових земљишта и низак садржај најважнијих биљних хранива, пре свега Р и Са су ограничавајући фактори постизања високих и стабилних приноса гајених биљака. Поред киселе реакције, ова земљишта карактерише веома често и повећан садржај токсичних облика Аl, Fe и Mn, као и недостатак или смањена приступачност Р, Са, Mg и неких микроелемената, посебно Мо, Zn и В. Токсичност Аl се сматра најважнијим фактором који ограничава раст биљака на киселим земљиштима. Механизми адаптације стрних жита на кисела земљишта могу се поделити на: спољашње, унутрашње (физиолошке) и генетичке. Дејство спољашњих механизма толерантности заснива се на имобилизацији Аl у ћелијском зиду, истицању Аl кроз плазма мембрану, успостављању рН баријере у ризосфери и лучењу органских киселина, фосфата, хелата и других лиганата кореном у спољашњу средину. Унутрашњи механизми толерантности заснивају се на комплексирању Аl са протеинима, органским киселинама и ензимима, као и хелатизирању у цитоплазми. Стрна жита испољавају различиту толерантност према киселости земљишта и повећаном садржају Аl у земљишном раствору. Најосетљивији је јечам, затим пшеница, док већу толерантност испољавају овас, тритикале и раж.