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Review

Comparative genomics of grasses tolerant to aluminum

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ABSTRACT. The family Poaceae includes over 10,000 species, among which are the most economically important cereals: maize, sorghum, rice, wheat, rye, barley, and oat. These cereals are very important components of human and animal food. Although divergence of the members of this family occurred about 40 million years ago, comparative genome analyses demonstrated that gene orders among species of this family remain largely conserved, which can be very useful for understanding their roles and evolution. Even with an intricate evolutionary history in which chromosome fragments, losses and duplications have to be considered at the ploidy level, grasses present a genetic model system for comparative genomics. The availability of mapped molecular markers, rice genome sequences and BAC and EST libraries from several grass species, such as rice, wheat, sorghum, and maize, facilitates biology and phylogeny studies of this group. The value of using information from different species in modern plant genetics is unquestionable, especially in the study of traits such as tolerance to aluminum

in soils, which affects plant growth and development. Comparative genomic approaches to aluminum tolerance can identify genomic regions and genes responsible for aluminum tolerance in grasses.

Key words: Comparative genomics, Aluminum tolerance, Grasses

INTRODUCTION

The grasses, which belong to the family Poaceae, currently include over 10,000 species (Kellogg, 2000); they share a common ancestor between 41 and 47 million years ago (Paterson et al., 2004). Among the members of this family are the cereals of highest economic relevance in the world, such as maize, sorghum, rice, wheat, barley, rye, and oats, which are responsible for a large proportion of human and animal food. These species present great diversity in the number of chromosomes (rice, 12; maize, 10; sorghum, 10; barley, rye and diploid wheat, 7; hexaploid wheat and oats, 21) and genome size (430 MPB in rice to 15,996 MPB in wheat) (Arumuganathan and Earle, 1991). Despite this variation, there is conservation in the content and gene order in the grasses (Gale and Devos, 1998), with high collinearity between the genetic maps, and in the positioning in regions corresponding to important characteristics controlled by quantitative trait loci (QTLs). For such reasons, they have been considered to be a unique genetic system (Bennetzen and Freeling, 1993).

Similarities and differences between the genomes of distinct species may be studied through comparative genomics, an area of genetics that allows the comprehension of the function of such genomes and the evolutionary processes that acted on them. Model organisms are widely employed in these studies, especially those with genomes that have already been sequenced, because the complete sequence has much of the information necessary to comprehend these organisms. Characteristics that are common to two species, from close phyla or not, provide useful information that may be explored in these studies.

Ionic aluminum is highly toxic to plant growth, and there is a wide variation in aluminum sensitivity between different species, which means there are differences in the ability to resisting the hazardous effects of Al^{3+}. Significant differences have been described, even among species of the same genus. Many studies regarding genes involved in aluminum tolerance have been conducted with grass species, and some loci of certain species have been related to this tolerance. Tolerance to aluminum is a very appropriate trait for comparative genomic studies in plants, because it is related to a complex metabolic process that remains unclear, and there are great variations in the mechanisms of action between different species. Comparative genomics will allow the identification of the best alleles to aid in the development of new cultivars in different species, either by assisted selection programs or by producing transgenic plants.

MACRO- AND MICRO-COLLINEARITY OF GRASS GENOMES

The first consensus genetic map of grasses was published by Moore et al. (1995), who described the genome alignment of six species: rice, wheat, maize, sugar cane, sorghum, and

foxtail millet. This consensus map has been updated (Gale and Devos, 1998; Devos and Gale, 2000; Devos et al., 2005), including maize, rice, foxtail millet, sorghum, pearl millet, Festusca/Lolium, oat, and Triticieae genomes in its latest version.

Ortholog markers have been widely used in the construction of genetic maps of grasses. The first sorghum genetic map used RFLP probes from maize (Hulbert et al., 1990). Cloned fragments of 14 characterized genes and 91 random maize fragments were tested in sorghum using RFLPs. Most of the probes detected polymorphisms among the seven sorghum lines tested, which allowed the construction of linkage groups and comparison of the same loci with maize. Many rearrangements were detected between these two species.

cDNA rice clones corresponding to unique loci in the rice map were evaluated in two maize lines and 85% of the clones hybridized with some region of the maize genome. These cDNAs were used for the construction of a linkage map based on ortholog rice regions (Ahn and Tanksley, 1993).

Through the hybridization with the same cDNA clone collection in wheat and rice, a genetic map of rice based on ortholog regions between these two species was constructed, which showed that synteny in many loci is highly conserved (Ahn et al., 1993). By combining these data and a comparative map of rice and maize (Ahn and Tanksley, 1993) many homologies were found between chromosomes of these three species.

The high degree of conservation of position and order of ortholog markers between different grass species revealed by mapping studies is surprising, considering the size differences and the long interval since the divergence of the species in this family, 41 to 47 million years ago (Devos and Gale, 1997; Gale and Devos, 1998; Keller and Feuillet, 2000; Paterson et al., 2004). QTL and genes related to important evolutionary and agronomic characteristics, such as shattering, dwarfing, and flowering time, were also found to have collinearly between grass species (Paterson et al., 1995; Pereira and Lee, 1995), reinforcing the macro-collinearity concept.

Plants height is an example of such behavior. Three QTLs for plant height in sorghum were identified in linkage groups A, E and H, orthologs to regions of chromosomes 1, 6 and 9 of maize, respectively, which also have QTLs for plant height (Pereira and Lee, 1995).

Genes and QTLs related to aluminum tolerance are located in ortholog genomic regions between the grasses. The QTL to the characteristic, located on chromosome 1 of rice is ortholog to the Alt_{SB} sorghum gene, located on chromosome 3, and the QTL found on chromosome 3 of rice is ortholog to the Alt_{BH} wheat genes (chromosome 4DL) and to barley *Alp* (chromosome 4H) (Magalhães et al., 2004).

However, there are many exceptions to collinearity at a molecular level. The first comparative studies to evaluate genic organization were developed between genomic regions flanking two maize loci, *sh2/a1* and *Adh1*, and homologue regions in sorghum and rice. The restriction mapping and the partial sequencing of *sh2/a1* demonstrated that gene order and composition are conserved among maize, sorghum and rice (Chen et al., 1997), but the non-codifier regions, such as MITEs and SSRs, are not conserved.

A comparison of maize, sorghum and rice sequences for locus *Adh1* (Tarchini et al., 2000) showed that deletions/insertions or translocations of genes occurred during evolution. In maize, nine genes were found at this locus, distributed along 225 kb. In a 78-kb space in the sorghum genome, nine maize homologues were identified in co-linear order, along with five additional genes. The quantity of DNA conserved between maize and sorghum at this locus is 22% for maize and 57%

for sorghum. At this locus, most of the maize DNA is composed of LTRs in the intergenic spaces, while no LTR was detected in sorghum in this region (Tikhonov et al., 1999). In rice, locus *Adh1* is connected to locus *Adh2*, on chromosome 11, whereas in maize and sorghum, these loci are found on different chromosomes: *Adh1* on chromosome 1 of maize and linkage group C of sorghum; *Adh2* on chromosome 4 of maize (Paterson et al., 1995; Tarchini et al., 2000).

A similar microcollinearity loss was found between stem rust resistance gene *rgp1* locus in barley and the ortholog region in rice. In barley this locus is found on chromosome 1, with considerable synteny with chromosome 6 of rice. However, the insertion of a 10-15-kb fragment ruptured collinearity between these chromosomes at the *rgp1* gene locus (Kilian et al., 1997).

Therefore, if on one hand macrocollinearity is maintained between the grasses, on the other hand different types of rearrangements affect this microcollinearity.

Song et al. (2002) identified ortholog regions in maize, sorghum, and in two subspecies of rice that presented microcollinearity; however, the microcollinearity was interrupted between these species. Six genes were found in the rice genomic region, 15 genes in sorghum and 13 genes in maize. The microcollinearity detours were attributed to micro-rearrangements or genomic changes on a small scale, such as insertions, deletions, duplications, and inversions (Bancroft , 2000).

GENOMIC DUPLICATION

According to Stebbins (1971) all genera and families of grasses are derivatives of lines that underwent genome duplication at some time during their evolutionary history. Ancient duplication and subsequent diploidization has shaped the genomes of all Poaceae crop species. In maize, the most recent duplication of its genome occurred about 11.4 million years ago (Gaut and Doebley, 1997). With rice, for instance, it has been found that 53-62% of the genome is duplicated (Guyot and Keller, 2004; Paterson et al., 2004) and phylogenetic studies of these duplicated genes suggest that this occurred before grass line divergence (Vandepoele et al., 2002; Paterson et al., 2004).

Gene duplication is the main source of new genes in genomes. Sequences of two paralogous genes from a duplication event will become different from each other due to evolutionary processes (Wen et al., 2005). Because they have duplicated regions, grass genomes also present inconsistency when compared to themselves, which makes studying them much more difficult. Loci that are incongruent with the most parsimonious syntenic/colinear relationships among rice and sorghum (for example), are located on the homoeologous chromosomal regions that resulted from ancient duplication (Paterson et al., 2004). Loss of some DNA sequences after polyploidy formation is rapid (Eckhardt, 2001) and the extent to which differential gene loss accounts for incongruity in comparative maps should be related to the duration of the period between the duplication event and the divergence of the respective lineages. Rapid diploidization events that occurred shortly after polyploidization would be expected to affect all Poaceae, whereas gene loss after taxon divergence would contribute to incongruities among comparative maps of the Poaceae (Paterson et al., 2004).

MONOCOT AND DICOT DATA COMPARISON

Similar to what is known for grasses, many studies also suggest common content and gene orders among evolutionarily close dicots (Lan et al., 2000; Rossberg et al., 2001; Lukens

et al., 2003). However, gene order conservation between mono- and dicots is still highly controversial. Paterson et al. (1996) suggested that the collinearity of chromosome segments between sorghum and *Arabidopsis thaliana* includes a distance smaller than 3 cM throughout the entire genome. Tikhonov et al. (1999) and Bennetzen et al. (1998) showed that the *Adh1* and *sh2/a1* gene regions between maize, sorghum and *Arabidopsis* did not present sequence collinearity. Both genes were mapped in only one region of the genome, both in sorghum and maize; that does not occur with *Arabidopsis*. In this genus, both genes bore similarity to two distinct BACs separated by at least 100 kb. Hence, there apparently is a lack of microcollinearity between *Arabidopsis* and maize, and between *Arabidopsis* and sorghum for these genes.

Though a comparative analysis of rice and *Arabidopsis*, model species for monocots and dicots, respectively, identified homologue segments between the genomes, only 5 of 24 genes were conserved between these two genomes (van Dodeweerd et al., 1999). There has been considerable controversy regarding the collinearity between these two species. Comparison of the *Arabidopsis* sequence to selected fully sequenced rice BACs or contigs has led to conclusions ranging from 'scant collinearity' (Gaut and Doebley, 1997; Ming et al., 1998) to 'frameworks of conserved genes' (Kellogg, 2003).

However, as a result of the sequencing of rice and *Arabidopsis* genomes, more precise studies have been developed. Goff et al. (2002) compared all annotated *Arabidopsis* proteins to mapped rice contigs, forming syntenic groups. They found 137 *Arabidopsis*-rice syntenic groups at 75 rice chromosomal locations throughout the genome with 99.9% confidence. However, within these syntenic groups, several rice blocks map to more than one site in the *Arabidopsis* genome, supporting previous hypotheses that detectable synteny exists between monocots and dicots even after 200 million years of divergence, although the conservation is less extensive than previously predicted (Paterson et al., 1996). The rice and *Arabidopsis* genomes are rearranged to such an extent that constructing a monocot-dicot comparative framework based on these two genomes would be difficult (Goff et al., 2002).

Despite the fact that there are many monocot- and dicot-specific genes, roughly 30% of *Arabidopsis* genes are found in rice ssp *japonica*, but not in *Drosophila*, *Caenorhabditis elegans*, *Saccharomyces* or sequenced bacterial genomes (Goff et al., 2002), which suggests that information regarding a group (mono- or dicots) could be used to isolate ortholog genes in the other group, just as was done in 2006 by Hoekenga et al., who described the isolation of the *AtALMT1* gene in *Arabidopsis thaliana* from the sequence of their correlate in wheat; aluminum-activated malate transporter (*ALMT1*), described by Sasaki et al. (2004), and by Ligaba et al. (2006), who described the isolation of genes *BnALMT1* and *BnALMT2* in *Brassica napus*, involved in the aluminum tolerance mechanism of all three species, also from the *ALMT1* sequence.

ALUMINUM TOXICITY IN PLANTS

Many abiotic factors affect plant development and growth, the level of free aluminum present in acid soils being one of them; aluminum toxicity is the main soil constraint for food and biomass production throughout the world. Because of its pH-dependent solubility, aluminum toxicity occurs only at soil pH values below 5.5. It is estimated that 40% of the arable soils of the world are acidic and therefore present aluminum toxicity hazards (von Uexküll and Mutert, 1995).

Soil correction, by neutralizing acidity may be applied to minimize the negative effect of aluminum on plants. However, in many agricultural systems its cost is high, especially in subsuperficial layers of the soil.

The ionic aluminum seems to interfere with many biochemical and physiological processes (Kochian, 1995). Aluminum's first toxicity symptom is inhibition of root growth, resulting in a damaged and reduced radicular system that results in limited absorption of water and mineral nutrients (Zheng et al., 2005), with a loss in the quality of the grains (Foy, 1992). Nevertheless, the mechanisms of this inhibition are not well comprehended. Roots affected by aluminum become stubby and frequently are darkened. Fine branching and root hairs are reduced. At the root apex, cracks can easily be observed in the epidermis. Uneven and radial expansion of cells of the cortex cause root thickening and mechanical stress in the epidermis (Ciamprova, 2002).

The primary aluminum toxicity site is the root apex (Ryan et al., 1993; Sivaguru and Horst, 1998; Sivaguru et al., 1999), the cell wall being affected, as well as the plasmatic membrane, the cytoskeleton and the cells' nucleus. Though most of the aluminum associated with the root is located in the apoplast, a small fraction rapidly penetrates the symplast and interacts with symplast targets (Lazof et al., 1996; Sivaguru and Horst, 1998; Silva et al., 2000), rupturing the cytoskeleton dynamics and interacting with both microtubules and actin filaments, important structures for the inhibition of root elongation (Grabski and Schindler, 1995; Blancaflor et al., 1998; Sivaguru et al., 2003).

Recently, evidence that the aluminum causes oxidative stress in the cells of plants by promoting lipid peroxidation has emerged (Yamamoto et al., 2001), along with expression of oxidative-stress genes (Milla et al., 2002). Boscolo et al. (2003) demonstrated that aluminum induces the formation of oxygen-reactive species and subsequent protein oxidation in a maize line sensitive to aluminum, and not in a tolerant line. However, protein oxidation occurred after decreases in relative root growth observed in the sensitive line, indicating that oxidative stress is not the main cause of root growth inhibition.

ALUMINUM TOLERANCE

Plants possess distinct tolerance mechanisms against aluminum in the soil, which may be divided into two categories. One is based on the external detoxification of aluminum, which protects the root apex against aluminum penetration, and the other one is based on compartmentalization of aluminum ions, once they are in the cytosol.

The mechanisms of exclusion are yet to be elucidated. The exudation of phenolic compounds (Ofei-Manu et al., 2001), phosphate efflux (Pellet et al., 1996; Zheng et al., 2005), proteins connected to aluminum ion secretion (Basu et al., 1999), selective permeability of the plasmatic membrane to reduce capture of aluminum to the cytosol (Archambault et al., 1997), and pH control of the rhyzosphere mediated by the roots (Degenhardt et al., 1998) have been found to be involved in aluminum tolerance.

However, the most widely studied means of external detoxification is the exudation of organic acids by the root, such as citrate, malate and oxalate acids (Ma et al., 1998; Ma, 2000; Ryan et al., 2001; Kochian et al., 2004). Di- and tricarboxylic acids form stable complexes with the Al^{3+} present in the rhyzosphere, reducing, or even annulling its toxic effects, since such complexes are incapable of passing the plasmatic membrane (Kochian et al., 2004).

Internal aluminum detoxification has been less studied. Both sensitive and tolerant plants are capable of accumulating aluminum when they grow in aluminum-rich acid soils (Foy, 1992; Watanabe and Osaki, 2002). In the internal mechanism, the aluminum is associated with organic binders, such as catequins, phenolic acids, and organic acids, and these complexes remain stored in specialized cells, such as the foliar epidermis (Watanabe and Osaki, 2002), thus preventing effects on plant metabolic processes. That strategy is used by moorish wheat, green tea (*Camellia sinensis*) and by hydrangea (*Hydrangea macrophylla*) (Takeda et al., 1985; Nagata et al., 1992; Ma et al., 1997a,b). In a tolerant maize variety, aluminum accumulates in the root cell vacuoles (Vazquez et al., 1999).

Though exudation of organic acids by the roots is considered the most important tolerance strategy, very little is known about the mechanism that unchains organic acid secretion. Alteration of organic acid metabolism and ionic channel activation have been investigated in the secretion of organic acids induced by aluminum. The organic acids are believed to chelate and detoxify the harmful aluminum cations near the root apex, which is the most sensitive region for aluminum stress (Ryan et al., 1993). However, Parker and Pedler (1998) emphasized that in wheat, a multifaceted, more integrative mode of resistance was probably occurring. Wenzl et al. (2001) demonstrated that organic acid secretion does not account for the high level of aluminum resistance in signal grass (*Brachiaria* sp), which indicates that organic acid secretion is not the only mechanism for aluminum resistance in plants. Recently, Piñeros et al. (2005) also reported that citrate efflux could not explain the difference in aluminum resistance in some maize cultivars, and Zheng et al. (2005) demonstrated that while aluminum-dependent oxalic acid secretion might contribute to the overall high resistance to aluminum stress of buckwheat, this response cannot explain the variation in tolerance between sensitive and tolerant cultivars; the greater aluminum resistance in buckwheat is related to immobilization and detoxification of aluminum by phosphorus in the root tissues.

ALUMINUM TOLERANCE IN GRASSES

Different species vary widely in their ability to tolerate the hazardous effects of aluminum and the significant contrasts have been described within a species. Genetic control of aluminum tolerance has been widely studied in grasses, especially members of the Triticeae tribe. In some wheat cultivars (*Triticum aestivum* L.), many genes with addition effects seem to be involved (Aniol and Gustafson, 1984; Aniol, 1990), being controlled by a single dominant gene in other cultivars (Kerridge and Kronstad, 1968; Aniol and Gustafson, 1984; Fisher and Scott, 1987; Larkin, 1987). Delhaize et al. (1993) demonstrated that locus *Alt1* explains most of the differences in aluminum tolerance between isogenic wheat lines. *Alt1* seems to be the same locus identified as *Alt2* 4D in chromosome of wheat by Luo and Dvorak (1996), using physical mapping. In this same 4D chromosome, tolerance gene Alt_{BH} was associated by Riede and Anderson (1996) with RFLP markers, being the bcd1230 drill, distant 1.1 cM from this gene. Alt_{BH} explains 85% of phenotypic variation for aluminum tolerance in the RILs generated by BH1146 and Anahuac wheat cultivars.

Recently, the *ALMT1* gene, which codes a malate transporter activated by aluminum, was cloned by Sasaki et al. (2004); it was found to be related to aluminum tolerance in wheat. This gene probably corresponds to the previously described *Alt1* locus (Sasaki et al., 2004).

The same markers connected to the Alt_{BH} gene were connected to the *Alp* gene of aluminum tolerance in barley (*Hordeum vulgare* L.). In this species, aluminum tolerance inheritance is monogenic, as described by Minella and Sorrells (1992, 2002). The *Alp* gene is located on the 4H chromosome flanked at 2.1 cM by bcd1117, wg464 and cdo1395 markers, the last one being also connected to the Alt_{BH} wheat gene of tolerance. The bcd1230 marker, strongly connected to the Alt_{BH} wheat was mapped at 33 cM from the *Alp* gene, which suggests that a collinearity break by structural rearrangement between the chromosomes 4H of barley and 4D of wheat may have occurred (Tang et al., 2000).

Four QTLs for tolerance to aluminum were described in oat (*Avena strigosa* Schreb.), explaining 55% of phenotypic tolerance variation (Wight et al., 2006). The QTL of greatest effect, responsible for 39% of variation, was associated with the bcd1250 marker, connected to the Alt_{BH} wheat tolerance gene. Therefore, it is likely that this genomic region contains the gene ortholog to the main aluminum tolerance gene found in the Triticeae.

As for rye (*Secale cereale* L.), four loci related to aluminum tolerance were described: *Alt1*, located on chromosome 6RS; *Alt2*, located on chromosome 3RS; *Alt3*, located on chromosome 4RL, and *Alt4*, located on chromosome 7RS (Aniol and Gustafson, 1984; Gallego et al., 1998; Miftahudin et al., 2002, 2005; Matos et al., 2005). Fontecha et al. (2007) cloned the rye *ScALMT1* gene, homologue to wheat *TaALMT1* and mapped it on chromosome 7RS, the same position as the previously identified *Alt4* locus. The *ScALMT1* gene co-segregates with the aluminum tolerance phenotype in rye. Using the same initiators used to clone gene *ScALMT1* DNA sequences in *Triticum urartu*, *Aegilops speltoides*, *Avena sativa*, *Saccharum officinarum*, *Zea mays*, and *Phaseolus vulgaris*, all bore at least 72.3% similarity with the *TaALMT1* sequences.

In rice, aluminum tolerance is a quantitative trait and QTL studies identified aluminum tolerance loci in all 12 rice chromosomes (Wu et al., 2000; Nguyen et al., 2001, 2002, 2003). Forty QTL were identified in four different populations, and epistasis was found between some of them. Despite the large number of QTLs, some were consistently identified in the four populations, one of them with a strong effect was located on chromosome 1 (Wu et al., 2000; Nguyen et al., 2001, 2002), and another on chromosome 3 (Nguyen et al., 2003).

In sorghum (*Sorghum bicolor* L.), tolerance to aluminum is also controlled by a large gene located on chromosome 3, Alt_{SB}, whose position is not ortholog to Triticeae chromosomal group 4, the region of the Alt_{BH} wheat gene. However, sorghum chromosome 3 is homologue to chromosome 1 of rice, a region in which QTLs for aluminum tolerance were identified in different rice populations (Magalhães et al., 2004).

Tolerance to aluminum in maize also seems to be of quantitative inheritance, although it is controlled by a smaller number of genomic regions. Sibov et al. (1999) identified two QTLs associated with these characteristics on chromosomes 6 and 10 of maize, while Ninamango-Cárdenas et al. (2003) mapped 5 QTLs on chromosomes 2, 6, 8. Both groups utilized tropical maize populations and only one QTL, located on bin 6.00, a coincidence between the studies.

CONCLUSIONS

Despite the large amount of information available, comparative genomics is complicated by evolutionary history, which includes changes in ploidy level, gene loss, and gene du-

plication. Because grasses comprise a very cohesive genetic system, they are good candidates for comparative genomic studies. The current availability of mapped molecular markers and rice genome sequences, as well as BAC and EST for many species of the group, including rice, wheat, sorghum, and maize, will permit advances in the biological and phylogenic study of this group. Comparative genomic approaches to aluminum tolerance can now identify and appropriately utilize genomic regions and genes responsible for aluminum tolerance in grasses, regardless of source, for crop improvement.

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