GENETIC IMPROVEMENT OF WHEAT- A REVIEW

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Abstract: Bread wheat (*Triticum aestivum* L.) plays a major role among the few crop species being extensively grown as staple food sources. As the human population grows, new methods and approaches must be found to attain wheat cultivars with improved characteristics. The challenge now is to produce higher-yielding varieties with good technological quality that are resistant or tolerant to a wide range of biotic and abiotic stresses. However, because of the critical nutritional status of human population, there is an urgent need for development of such wheat varieties that would be more nutritious (with improved protein, zinc, iron, etc. value), meeting our health demands. This article summarises present status in this field.

Keywords: biotic/abiotic factors, genetic transformation, grain yield, nutritional quality, plant breeding, wheat

1. Introduction

Wheat (*Triticum* spp.) is a self-pollinating annual plant, belonging to the family *Poaceae* (grasses), tribe *Triticeae*, genus *Triticum*. According to different classifications, number of species in the genus varies from 5 to 27 (MEREZHKO, 1998). The two main groups of commercial wheats are the durums (*Triticum durum* L.) and bread wheats (*Triticum aestivum* L.) with 28 and 42 chromosomes respectively. The wild species are still a valuable source of useful agronomic traits for the continued improvement of cultivated wheats. Wide hybridization of wheat with grasses, coupled with cytogenetic manipulation of the hybrid material, has been instrumental in the genetic improvement of wheat. Chromosome engineering methodologies based on the manipulation of pairing control mechanisms and induced translocations, have been employed to transfer into wheat specific disease and pest resistance genes from annual (e.g., rye) or perennial (e.g., *Thinopyrum* spp., *Lophopyrum* spp., and *Agropyron* spp.) members of the tribe *Triticeae*. The use of DNA markers helps to identify desirable genotypes more precisely and facilitates gene transfer into wheat. The development of novel gene-transfer techniques that allow direct delivery of DNA into regenerable embryogenic calli has opened up new avenues of alien-gene transfer into wheat cultivars. Thus, transgenic bread and durum wheats have been produced. The application of transgenic technology has not only yielded herbicide-resistant wheats, but has also helped to improve grain quality by modifying the protein and starch profiles of the grain (REGINA *et al*., 2006; BICAR *et al.,* 2008). Recently, biofortification of cereal crops with micronutrients (vitamins, minerals, etc.) using plant breeding and/or transgenic strategies has become of great interest.

Approaches to gene transfer are developing rapidly, and promise to become an integral part of plant breeding efforts. However, the new biotechnological tools will complement, not replace, conventional plant breeding (JAUHAR and CHIBBAR, 2001; VASIL, 2007).

2. History, cultivation, production and green revolution

Wheat in its present-day form has gone through a long and interesting evolution. The origin of the genus *Triticum* (wheat) is found in Asia, in the area known as the Fertile Crescent, and parts of Africa, in the area that stretches from Syria to Kashmir, and southwards to Ethiopia. The genetic relationships between einkorn and emmer indicate that the most likely site of domestication is near Diyarbakir in Turkey. The cultivation of wheat began to spread beyond the Fertile Crescent during the Neolithic period. By 5,000 years ago, wheat had reached Ethiopia, India, Great Britain, Ireland and Spain. A millennium later it reached China (DUBČOVSKÝ and DVOŘÁK, 2007).

All the species belonging to the genus *Triticum* can be divided into three basic groups, each distinguished by the number of chromosomes in the generative and vegetative cells. Unfertilized egg cells contain 7, 14 or 21 chromosomes. In vegetative cells this number is doubled. Consequently, diploid, tetraploid and hexaploid wheat species carry 2x7=14; 4x7=28 and 6x7=42 chromosomes, respectively (BELDEROK *et al.,* 2000).

Hexaploid wheat is believed to have arisen, when genomes of tetraploid wheat (*T. turgidum*, 2n=28, AB-genome) and *Aegilops squarrosa* L. (also called *Triticum tauschii*) were combined via amphidiploidisation (Fig. 1). *Aegilops* is a species without any economic value that grows as a weed on the borders of wheat fields in the Near East and it has a somatic chromosome number of 14. These chromosomes belong to the D-genome. Therefore, the genome of *T. aestivum* is called the ABD-genome (DVOŘÁK, *et al.*, 1998). The bread wheats (*T. aestivum* L.) encompass a wide range of different types classified largely by their growth habit and functionality. The various classes are combinations of winter or spring growth habit with white or red and hard- or soft-textured kernels. Since only the hexaploid wheat cultivars, possessing the D set of chromosomes, have the unique milling and baking properties, these desirable quality characteristics have been attributed preponderantly to the third genomic component (BELDEROK *et al*., 2000).

An important attribute of wheat is its adaptability to varied climatic conditions. Although grown mostly in temperate climates (between latitudes 30° and 60° north and south) with an optimum growing temperature of 25°C (minimum and maximum temperatures of 3°C and 32°C), it can be grown from within the arctic circle to higher elevations near the equator, and from sea level to as much as 3000m above sea level. As such, it is one of the most widely cultivated crops with a short growing season, and a good yield per unit area. These attributes makes wheat one of the most important commodities in international trade (VASIL, 2007).

With 607 mMT (million metric tons) produced on 217 mha (million hectares) in 2007, wheat continues to be one of the largest food crops in terms of area of

cultivation as well as production (FAOSTAT, 2007; Table 1). The IGC's (International Grains Council) current estimate for production in 2008 is 683 mMT (source: IGC, http://www.igc.org.uk/; 2008).

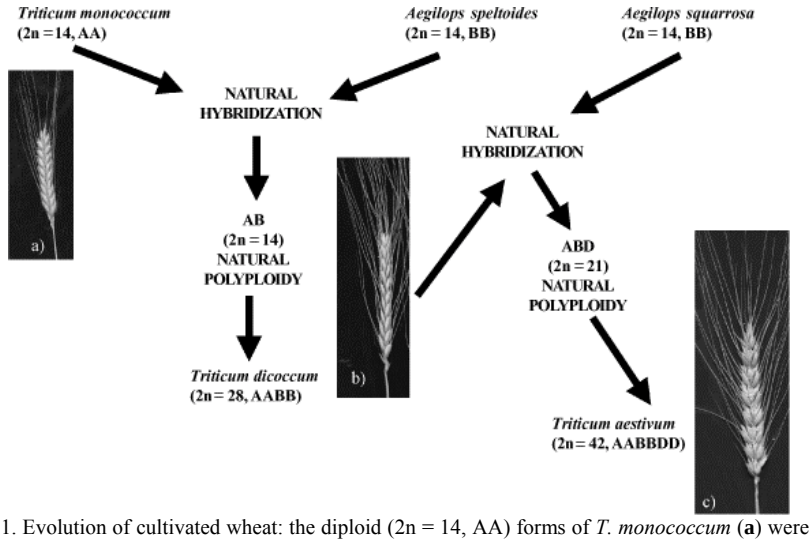

Fig. 1. Evolution of cultivated wheat: the diploid (2n = 14, AA) forms of *T. monococcum* (**a**) were naturally pollinated by weed species (2n = 14, BB). The subsequent genome duplication of hybrids by natural polyploidy gave rise to several wild and cultivated tetraploid species (2n = 28, AABB) like *T. dicoccum* (**b**) and *T. durum*; again, the natural pollination of the tetraploid *T. dicoccum* (**b**) by *Aegilops squarrosa* (2n = 14, DD) gave rise to the hexaploid (2n = 42, AABBDD) species (**c**) (from FERNANDES *et al*., 2000).

In the middle of the twentieth century, wheat breeders were faced serious problem: increases in productivity have fallen below the rate of population growth. At the request of the Mexican government and the urging of the USA, a program to develop high-yielding and disease-resistant varieties of wheat started in Mexico in 1944. Norman Borlaug and his team first developed disease-resistant varieties and then crossed these with the Japanese dwarf variety Norin 10, to produce semi-dwarf, disease-resistant and high-yielding varieties of wheat (HEDDEN, 2003). These new varieties- which made more grain and less stem- formed the basis of the "Green Revolution", which has allowed many countries (such as India, Pakistan, China, etc.) to be self-sufficient and food production to keep pace with worldwide population growth (VASIL, 2007). Before the period of the Green Revolution, the farmers in Slovakia cultivated tall historical wheat cultivars (landraces), with insufficient seed yield. Later, wheat cultivars originated in Czech Republic and Soviet Union were adopted. From the year 1967, there were no Slovak varieties grown in Slovakia. From 1945 to 1970, sixteen breeding stations were established and Slovak wheat breading began to progress rapidly. New, modern semi-dwarf wheat varieties with higher yields and improved resistance to pathogens replaced the tall traditional varieties like in almost all countries over the world. Between the years 1976 and 2008, 47 wheat cultivars of Slovak origin were included in the National List of Released Varieties (ANONYMOUS, 2008).

Wheat production will have to be doubled to 1200 mMT by the 2025 in order to meet increasing world demands and future needs. This increase must be brought about by improving productivity on land that is already under cultivation and not by bringing new land into use by destruction of forests, grasslands, etc. (VASIL, 2003). Such significant increases in yield are unlikely to be attained through only the traditional, or even the newly developed marker-assisted breeding methods, because neither the germplasm of wheat nor its close relatives is likely to contain the wide variety of genes that would be needed to meet future demands. Therefore, new methods and approaches must be found to integrate useful genes from any organism (plants, animals or microorganisms) to attain the dramatic yields that would be required to meet future demands: (1) Significantly reduce or eliminate productivity losses caused by pests, pathogens and weeds (OERKE *et al*., 1994), and the substantial additional losses attributed to abiotic factors (drought, salinity, etc.) as well as post-harvest spoilage during storage. (2) Fundamental improvement of the physiological capability or limit of the plant by increasing its photosynthetic efficiency and nutrient utilization in order to attain higher yields. Moreover, the number of micronutrient-malnourished people is raising, therefore the improvement of nutritional quality of wheat as a staple crop must also be of interest to plant breeders.

Table 1. Production quantity of the most important cereal crops.

Cereal crop	**Production quantity [million tonns]/Area harvested [million hectars]**		
	Year		
	2005	2006	2007
maize	716/ 148	699/ 147	785/ 158
rice	632/ 155	644/ 156	651/ 157
wheat	626/ 220	598/ 214	607/ 217

Source: FAOSTAT (http://www.faostat.fao.org)

These objectives require the introduction of novel- and in many instances alien and multiple- genes into commercial varieties of wheat by genetic transformation, and production of transgenic varieties with the desired attributes (VASIL, 2003). However, high costs currently limit the implementation of functional genomics in breeding programs. Genomics research will continue to enhance the efficiency and precision for crop improvement but will not totally replace conventional breeding and evaluation methods (VARSHNEY *et al*., 2007)

3. Approaches to genetic improvement

Landraces of cereal crops contain an array of genes for agronomically important traits. These landraces fall in the primary gene pool with their respective crop species with which they can be easily crossed. Complete or high pairing between chromosomes of the landrace and those of the crop plant facilitates alien gene transfer into the crop species (VASIL, 2007).

Many wild relatives of wheat carry genes that offer superior traits, some of which have been incorporated into wheat via interspecific and intergeneric hybridization

(JAUHAR and CHIBBAR, 1999). Chromosome pairing between chromosomes of the alien donor and those of cereal crops is the key to such gene introgressions. This process is relatively easy in diploid cereals. On the other hand, the hexaploid wheat has three genomes and there is genetic control of chromosome pairing so that only homologous partners pair to form bivalents. Thus, wheat (both bread wheat and durum wheat) has a homologous pairing suppressor gene, *Ph1*, which ensures diploid-like chromosome pairing and hence disomic inheritance. These characteristics are essential for the meiotic and reproductive stability of wheat. However, *Ph1* does not permit pairing between the wheat and alien chromosomes, thereby impeding alien gene transfer. Methods of suppressing the activity of *Ph1* and hence promoting wheat-alien chromosome pairing are known (JAUHAR and CHIBBAR, 1999).

Through wide hybridization coupled with manipulation of chromosome pairing, several desirable genes have been incorporated into wheat (JAUHAR and CHIBBAR, 1999). Thus, genes for resistance to leaf rust and barley yellow dwarf virus have been transferred from *Agropyron*, *Thinopyrum* and *Aegilops* into wheat. JAUHAR and PETERSON (2000) produced scrab-resistant durum wheat germplasm by transferring in it segments of chromosomes from *Thinopyrum junceiforme*.

A better understanding of the factors limiting practical exploitation of exotic germplasm promise to transform existing, and accelerate the development of new, strategies for efficient and directed germplasm utilization (FEUILLET *et al*., 2008).

Plant protoplasts were an attractive target for transformation during the 1980s as it was already known that plants could be regenerated from protoplasts and that DNA could be introduced into them by electroporation or by osmotic shock (by polyethylene glycol treatment). These methods are technically simple and inexpensive, often resulting in thousands of transformed micro-colonies in one experiment, with the possibility of producing many independent transformants. However, cell suspension cultures used for protoplast isolation are highly genotype-dependent, often prone to somaclonal variations and have a time-limited morphogenic competence. These disadvantages have restricted full use of the protoplast-based transformation technology, and the interest for the technique has declined for most cereals (REPELLIN *et al*., 2001; VASIL, 2007). Although production of stably transformed cell lines of *T. monococcum* as well as *T. aestivum* was described (Muller *et al*. 1996), none of these transformed lines were regenerated into plants. Neither the fertility of the plants, nor the transmission of the transgenes to progeny, was demonstrated on the rare occasions when plants were regenerated from transformed protoplasts (He *et al*. 1994).

During the past quarter century the unique and natural ability of the soil-borne crown gall bacterium- *Agrobacterium tumefaciens*- to transfer and integrate DNA into the genome of wounded intact plant cells has been exploited extensively for the genetic transformation of higher plants (Fig. 2). Although *Agrobacterium* as a phytopathogen is known to have an exceptionally wide host range, it does not generally infect monocots, particularly the economically important cereal crops. Its inability to infect monocots in nature was the main reason for the widely accepted wisdom of the time that *Agrobacterium* could not be used to transform cereals. This created the need to find alternative methods of transformation and led to the now

universally-held view that embryogenic cultures are the best, and perhaps the only, source of regenerable cells in the *Poaceae* (JAUHAR, 2006; LAKSHMAN, 2006).

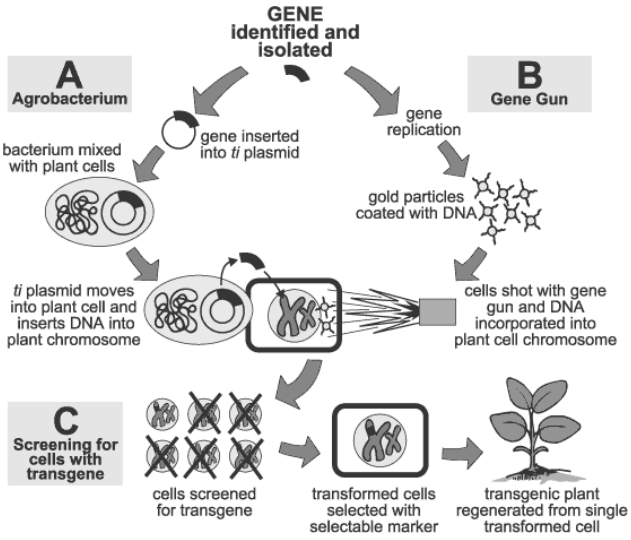

Fig. 2. Approaches usable in genetic improvement of wheat. A: *Agrobacterium*-mediated transformation, B: biolistic method (www.ag.ndsu.edu/pubs/plantsci/crops/a1219-2.gif).

One reason for the delay in cereal transformation by *Agrobacterium* was the weak, or lack of woundresponse, from injured cereal tissues. The difficulties were overcome by co-cultivation of actively dividing embryogenic cells with supervirulent strains of *Agrobacterium tumefaciens* in the presence of acetosyringone, a potent inducer of virulence genes (SHRAWAT and LORZ, 2006).

The most commonly used method to deliver DNA into plant tissues and callus is the high velocity bombardment of DNA- coated microprojectiles (biolistics) (Fig. 2). This technology of direct DNA delivery, developed by SANFORD *et al.* (2000), overcame many of the problems inherent in the use of protoplasts. It rapidly became the method of choice for the transformation of cereals, particularly wheat (VASIL and VASIL, 2006). For optimal efficiency, a balance between the penetration power of the particles and the intensity of the wounds created in the target tissues must be attained.

Transgenic plants of wheat were produced for the first time in 1992, by the bombardment of embryogenic callus tissues with the plasmid pBARGUS, in which the expression of the GUS reporter gene is driven by the maize Adh1 promoter attached to Adh 1 intron 1, and the expression of the selectable bar gene which confers resistance to the broad-spectrum herbicide Basta is driven by the CaMV35S promoter attached to the maize Adh1 intron 1 (VASIL *et al*., 1992). Further improvements in production of transgenic wheat plants were obtained by using other types of plasmids and promoters. Although the transgenes are integrated at various sites in the genome, they do not cause any detectable chromosomal rearrangements, and their expression is more a function of the promoters used rather than the site of integration (VASIL, 2007).

Agrobacterium-based systems and biolistic methods share common features. The same explant tissues can be used as targets, the transformation frequencies are comparable (STOGER *et al*., 1998), and both techniques are genotype-dependent (LEE *et al*., 1999). However, the perceived disadvantages of particle bombardment compared to *Agrobacterium*-mediated transformation, i.e., the tendency to generate large transgene arrays containing rearranged and broken transgene copies, are not borne out by the recent detailed structural analysis of transgene loci produced by each of the methods. There is also little evidence for major differences in the levels of transgene instability and silencing when these transformation methods are compared in agriculturally important cereals (ALTPETER *et al*., 2005a)

It is also important to keep in mind that one of the serious problems associated with *Agrobacterium*-based transformation is the frequent vector backbone integration in transgenic lines of wheat and other plants, which is a serious impediment to gaining regulatory approval for environmental release (WU *et al*., 2006). Irrespective of the method of transformation used, the transgenes are integrated at random sites in the host genome that may sometimes cause position effects, gene silencing, etc. Site-specific recombination has been proposed as a solution to this problem in wheat (SRIVASTAVA *et al*., 1999). This technology also allows the removal of the selectable marker gene.

4. Herbicide, pathogen and pests resistance

Weeds compete with crop plants for available nutrients and light energy, and thus reduce crop yields. Actual worldwide crop losses to wheat productivity owing to weeds are estimated to be 12.3%, but as high as 23.9% without crop protection (OERKE *et al*., 1994). With widespread and long-term herbicide use, and the fact that wheat has a single natural mechanism for degrading herbicides, many of the most noxious weeds found in wheat fields have over time developed resistances to the commonly used selective herbicides by evolving a similar mechanism (GRESSEL, 1996). In general, production of herbicide-resistant crops has involved insertion of only one or two genes that encode inactivation of the herbicide by any of the following three mechanisms: (i) overproduction of a herbicide-sensitive biochemical target, (ii) structural alteration in biochemical target resulting in altered binding to the herbicide, or (iii) detoxification or degradation of the herbicide, before it reaches its target site in the plant cell (REPELLIN *et al*., 2001).

Glyphosate is the active ingredient of herbicide Roundup®. Glyphosate-tolerant wheat plants were obtained showing in field trials neither any vegetative nor reproductive damage, nor any reduction in yield (ZHOU *et al*., 2003). Recent advances have focused on development of highly efficient detoxifying enzyme that allows plants to resist glyphosate and provide improved protection against weeds when incorporated into wheat (JOHANNES and ZHAO, 2006). Metabolic inactivation has been used as a powerful and effective tool in engineering tolerance to the non-selective, broad-spectrum, post-emergent, contact herbicides commonly known as a Basta, Bialaphos, Herbiace and Glufosinate (VASIL, 1996). They provide a high degree of human and environmental safety because they are non-toxic and are rapidly

biodegraded, resulting in minimal residue persistence in soil. Their herbicidal activity is due to L-phosphinothricin (PPT), a potent inhibitor of the biosynthetic enzyme glutamine synthetase (GS), which is involved in general nitrogen metabolism in plants. PPT is inactivated by the acetylating enzyme phosphinothricin- N-acetyltransferase (PAT). Two similar genes, *bar* and *pat*, that encode PAT, have been identified, cloned and used to transform wheat, thus making the transgenic wheat immune to PPT and making it possible to use Basta for effective weed control in wheat fields. The transgene is transmitted to progeny in a Mendelian fashion and has been shown to be stable under field conditions (VASIL, 2007).

A large number of fungal (such as rust caused by *Puccinia* spp., smut and bunt caused by *Tilletia* and *Ustilago* spp., blotch caused by *Septoria* spp., *Fusarium* blight/scab, *Helminthosporium* leaf blight, powdery mildew caused by *Blumeria graminis*, etc.), bacterial (such as leaf streak caused by *Xanthomonas translucens*) and more than 50 viral diseases are known to cause considerable worldwide damage to wheat production (CURTIS *et al*., 2002). Losses of wheat production owing to pathogens are estimated to be 12,4%, but as high as 16.7% without crop protection (OERKE *et al.*, 1994). Only limited protection against pathogens can be achieved by chemical treatments or cultural practices (CURTIS *et al*., 2002). Resistance breeding is a continuing and difficult process as resistance in most cases appears to be under polygenic control, and even when resistant cultivars are developed, they do not provide long-term relief due to ever-evolving or mutating pathogens (FRIESEN *et al*., 2006).

Only modest progress has been made in engineering resistance to major fungal and viral pathogens of wheat. In an early study, the coat protein gene of barley yellow mosaic virus was introduced into wheat but no information was provided about its effect on protection from any pathogens (KARUNARATNE *et al*., 1996.). However, transgenic plants expressing the *rnc70* gene expressing a mutant bacterial ribonuclease III showed a high level of resistance to barley stripe mosaic virus (ZHANG *et al*., 2001). Wheat plants transformed with the viral replicase gene *Nib* or the coat protein gene of wheat streak mosaic virus showed a high level of resistance to inoculations with two strains of the virus, had milder symptoms and lower virus titer than the control plants but did not provide field resistance to the virus and yielded less than their parent cultivars (SHARP *et al*., 2002).

The *pinA* gene could be considered as a potential and effective for the control of a wide range of plant pathogens by genetic engineering. LUO *et al*. (2008) produced transformed durum wheat cultivars expressing the PINA protein (puroindoline protein), which has been shown to have antimicrobial and antifungal activity. Transgenic plants showed enhanced response to leaf rust in greenhouse and field.

Transgenic wheat plants stably expressing an antifungal barley seed class II chitinase gene (*pr3)* showed increased resistance to powdery mildew, but even more significant protection was obtained with the introduction of the gene for an apoplastic ribosome-inactivation protein (RIP) from barley (YAHIAOUI *et al*., 2006). The expression of genes for an antifungal protein from *Aspergilus giganteum* and a barley class II chitinase were shown to significantly reduce the formation of powdery mildew and leaf rust (OLDACH *et al*., 2001). ALTPETER *et al*. (2005b) found enhanced

resistance against powdery mildew in wheat plants over-expressing the defence-related *TaPERO* peroxidase gene in shoot epidermis.

Expression of the antifungal protein KP4 from *Ustilago maydis*-infecting virus resulted in increased endogenous resistance against stinking smut. Partial protection against *Fusarium* head blight has been reported in wheat plants expressing the *F. sporotrichioides* gene *FsTRI101* (VASIL, 2007).

Much work still needs to be done to produce wheat lines that are resistant to various pathogens that cause major losses in productivity. The mapping of the leaf rust resistance gene *Lr10*, of *Fhb1*, a major gene controlling *Fussarium* head blight resistance (CUTHBERT *et al*., 2006; CHEN *et al*., 2007), and the identification and characterization of the stripe rust resistance gene *Yr34* should help in the isolation and sequencing of the relevant genes that can be of much use in the development of resistant varieties through marker-assisted breeding as well as genetic transformation (CUTHBERT *et al*., 2006; LIN and CHEN, 2008; ŠLIKOVÁ *et al.,* 2009).

Actual worldwide crop losses to wheat productivity owing to a variety of pests (aphids, Hessian fly, locusts, beetles, moths, etc.) are estimated to be 9,3%, but as high as 11,3% without crop protection (OERKE *et al*., 1994). Pests-resistant crops are expected to increase crop yields and also to reduce the amount of agrochemicals used for crop protection. Pests cause additional losses during post-harvest storage. Unfortunately, research on introduction of pest resistance genes into wheat has so far been very limited, because breeding for these traits is time consuming and does not provide long-term protection as the pests develop biotypes which are able to overcome the resistance genes. Future work should explore the possible benefits of introducing resistance genes from related as well as unrelated species, such as the recent characterization and expression study of a novel wheat gene (*Hfr-3*) encoding a putative chitin-binding lectin that is associated with resistance against Hessian fly, a major pest that causes considerable damage (GIOVANINI *et al*., 2007).

ALTPETER *et al*. (1999) introduced the barley trypsin inhibitor CMe (BTI-CMe) into wheat. Expression and functional integrity of BTI-CMe in transgenic seed were demonstrated, along with a significant reduction in the survival of the Angoumois grain moth (*Sitotroga ceralella*), a major pest of stored wheat grain, reared on transgenic seed expressing BTI-CMe. Similarly, wheat plants expressing the gene encoding snowdrop lectin (*Galanthus nivalis* agglutinin: GNA) have been shown to decrease the fecundity, but not the survival, of the grain aphid *Sitobion avenae* (REPELLIN *et al*., 2001). AKHTAR *et al*. (2008) conducted experimental trials to evaluate the resistance of host wheat plants against *Rhopalosiphum padi* L. (aphid) and only one variety V-9021 was found to show the highest level of resistance.

5. Abiotic stress tolerance

Abiotic stresses (drought, salinity, flooding, excessively high or low temperatures, high levels of minerals such as salt, heavy metals, etc.) cause adverse affects on plant growth that can reduce crop productivity in wheat by more than 80% (BRAY *et al*., 2000). So far the most successful approach to these problems has been to exploit natural variation present either in the crop itself or in wild relatives (for example, salt

tolerance in *Laphopyrum elongatum,* aluminium tolerance in *Aegilops uniarisfata).* Recent advances in understanding the genetic control of abiotic stress tolerance, including the identification and coning of related genes, has encouraged research in engineering plants that can tolerate these stresses without any negative impact on their yield (SEKI *et al*., 2003). Although drought and salt tolerant genes that are present in germplasm of wheat and other crops have been successfully used to obtain stress-tolerant varieties, breeding for stress tolerance is time labor-intensive and complicated by the multigenic nature of stress tolerance and the need for the simultaneous selection of the related genes as the elimination of the undesirable genes (VASIL, 2007).

Plants are known to respond to biotic as well as abiotic stresses by inducing stress-responsive genes. Several stress-inducible genes and their products have been identified (YAMAGUCHI and BLUMWALD, 2005). Manipulation of the transcription of stress responsive genes is increasingly being used to enhance stress tolerance, such as drought resistance and salt tolerance in rice (HU *et al*., 2006). KAWAURA *et al*. (2008) found out, that approximately 19% of wheat genes are salt responsive. Although salt-responsive genes of wheat were grouped into 12 groups based on expression patterns, their functions in salt tolerance remain to be clarified.

Introduction of the ABA-responsive barley gene *HVA1* into wheat improved growth under soil-water deficit conditions. Further field evaluations of some of the transgenic lines showed greater plant biomass and grain yield in plants expressing the *HVA1* gene in comparison to the non-transformed controls (BAHIELDIN *et al*., 2005). Improved tolerance to salinity has been also reported in wheat plants expressing a vacuolar Na^+/H^+ antiporter gene (HUANG *et al*., 2006).

Much more attention needs to be paid now to the development of wheat varieties that can provide high yields under drought and at higher temperatures in saline soils (UMEZAWA *et al*., 2006). PELEG *et al*. (2008a) performed a comprehensive survey of wild emmer populations from across aridity gradient in Israel and revealed a wide phenotypic and allelic diversity for drought response, demonstrating the potential of the wild genepool for wheat improvement. These results exemplify the unique opportunities to exploit favourable alleles that were excluded from the domesticated genepool and may serve as a start point for introgression of promising QTLs into elite cultivated materials via marker-assisted selection.

Improvement of frost tolerance (winter hardiness) is an important aim of wheat breeding programs (DÖRFFLING *et al.,* 2009). MILLER *et al.* (2006) have identified several C-repeat-binding factors (CBF) located at the frost tolerance locus *Fr-A'''2* in *Triticum monococcum*. These can be useful in heat improvement programs in regions where considerable yield losses occur during severe winters.

In many parts of world, excessive deforestation causes frequent devastating floods resulting in significant crop losses when plants are submerged in water for long periods of time. Recently, *Sub1A* gene has been identified in rice and its overexpression in a submergence-intolerant variety conferred enhanced submergence tolerance to the plants (XU *et al*., 2006). It would be worthwhile to transfer this gene, that is responsible for submergence tolerance in rice, into wheat by genetic transformation to test if it will have a similar effect in wheat varieties that are grown in flood-prone areas.

Natural genetic variability has been exploited to standing of aluminium tolerance in wheat. However, further understanding of the genetic and physiological factors that regulate aluminium tolerance is needed in order to develop a wider range of wheat varieties with a high level of aluminium tolerance. Transgenic plants over-expressing citrate synthase or malate dehydrogenase genes have been shown to enhance aluminium tolerance (MAGALHAES, 2006). The gene (*ALTM1*) that regulates aluminium tolerance in wheat has been identified (ZHOU *et al*., 2007).

6. Yield increasing

Yield of wheat can be improved by increasing seed number and/or weight, the latter by increasing the amount of starch, which is the most abundant component (more than 70% of seed weight) of wheat endosperm, or by regulation of endosperm development. Starch synthesis in cereals is regulated by ADP-glucose pyrophosphorylase (AGP), that is likely involved in determination of seed sink strength (HANNAH and JAMES, 2008). SMIDANSKY *et al*. (2002) found that transgenic lines expressing a modified maize Sh2 gene (Sh2r6hs), which encoded an altered AGP large subunit, showed a 38% increase in seed weight/plant and a 31% increase in total biomass. Seed weight of inferior spikelets can be improved in rice panicle by increasing activities of starch synthesizing enzymes (MOHAPATRA *et al*., 2009)

The number of tillers formed on each plant is among many factors that determine yield in wheat (and in rice), by influencing the number and size of panicles and seeds produced. MONOCULM1 (MOC1), a gene that controls tillering in rice, has been identified (LI *et al*., 2003). Changing the architecture of the plant by the formation of more tillers and leaves which are spread out (SAKAMOTO *et al*., 2006; KURAPARTHY *et al*., 2007) would expose a larger leaf surface for the capture of sunlight for increased photosynthesis, leading to improved productivity.

Genes that regulate the activity of the major plant hormones (gibberellins, auxins, cytokinins and brassinosteroids) have been shown to be involved in dwarfing and grain production (ASHIKARI *et al*., 2005; SAKAMOTO, 2006). The increasing understanding of the genetic control of plant architecture (shoot branching, plant height, inflorescence morphology, etc.), and the effect of phytohormones on yield is expected to play a major role in the development of high yielding crops (SAKAMOTO, 2006; WANG and LI, 2006).

The element silicon is present in significant but variable amounts in all plants. It has many useful functions, including enhancing resistance to lodging, pests and pathogens. The varied roles of the silicon transporter gene provide ‘‘a new strategy for producing crops with high resistance to multiple stresses by genetic modification of the root’s silicon uptake capacity’’ (MA *et al*., 2006).

The other possible approaches for yield improvement include: changing C3 wheat into a C4 plant (which is much more efficient because of greatly reduced loss of carbon by photorespiration) or the production of wheat hybrids (heterosis or hybrid vigor has been used to obtain dramatic increases in crop yields for nearly 75 years, most prominently in maize and recently also in rice) (WANG *et al*., 2005)

Regulation of flowering and its manipulation must remain an important part of the overall strategy to improve wheat productivity. Several genes (VRN1, VRN2 and VRN3) that have been shown to be involved in the vernalization response (the requirement for a long period of exposure to low temperatures for flowering) in wheat can be manipulated by RNA interference and other means to affect flowering time, or to convert winter wheats to spring wheats (YAN *et al*. 2006).

7. Improvement of grain quality

For most traditional uses, wheat quality derives mainly from two interrelated characteristics: grain hardness and protein content. Grain hardness is a heritable trait but it can be strongly affected by abnormal weather conditions such as excessive rainfall during the harvest period. Protein content is weakly heritable and strongly dependent on environmental factors such as available soil nitrogen and moisture during the growing season (BELDEROK *et al*., 2000). In addition, each end-use requires a specific 'quality' in the protein. Durum wheat cultivars have the hardest grain texture and are usually high in protein content. They are especially suited to the production of pasta because of their highly vitreous grain (high milling yield of semolina), unique combination of storage proteins for good cooking quality of pasta, and high yellow pigment content required for attractive appearance of cooked product. All three characteristics are highly heritable and can be readily improved by conventional breeding. Recent research has shown that the presence of γ-gliadin 45 is a reliable marker of good cooking quality. This marker is now used for screening early generation material in many durum wheat breeding programs. Bread (also common or hexaploid) wheats cover a wide range of grain hardness and protein content. The hardest wheats of this class, generally highest in protein, are used for pan bread. Common wheats of medium hardness and lower protein content are used for other types of bread and noodles. Wheats with softest texture and lowest protein are used for cakes and cookies. In some end-uses, e.g., Chinese-type noodles, starch quality is important together with protein quality; this feature should be taken into consideration in developing a screening strategy for wheats for this application. Screening tests that reflect end-use requirements for most of the known products are available, and should be applied in testing wheats according to intended use (BUSHUK, 1998).

An important factor, which affects negatively the grain quality, is sprouting. The germination causes an increase in alpha amylase, an enzyme that breaks down starch. Sprouting can affect food made from wheat in many ways. It can reduce mixing strength, cause sticky dough, and affect loaf volume and shelf life. In pasta, sprouting can reduce shelf life, increase cooking loss, and produce softer cooked pasta. Flour damaged by alpha-amylase holds less water when mixed and the dough absorbs less water during baking. “Falling number” gives an indication of the amount of sprout damage that has occurred within a wheat sample. As the amount of enzyme activity increases, the falling number decreases. Generally, a falling number value of 350 seconds or longer indicates a low enzyme activity and very sound wheat quality. As the pre-harvest sprouting (PHS) of wheat greatly reduces the quality and economic value of grain, PHS tolerance is one of the most important traits in wheat breeding. Viviparous 1 (Vp1) gene of maize is known to encode a transcription factor VP1 that

controls seed germination. Hexaploid wheat possesses three Vp1 homoeologues (TaVp1): TaVp-A1, TaVp-B1 and TaVp-D1. The sequence analyses of cDNAs revealed that some of TaVp-A1 transcripts and TaVp-D1 transcripts are spliced incorrectly, resulting in production of truncated or deleted proteins. Most TaVp-B1 transcripts are spliced correctly. The dual function of TaVP-B1 was confirmed: the activation of Em expression (required for ABA-inducible expression) and the repression of α-amylase expression (UTSUGI *et al.,* 2008). Recently, a co-dominant STS marker of Vp-B1 gene was developed and designated as Vp1B3. Statistical analysis indicated that Vp1B3 was strongly associated with PHS tolerance in the set of Chinese wheat germplasm, suggesting that Vp1B3 could be used as an efficient and reliable co-dominant marker in the evaluation of wheat germplasm for PHS tolerance and marker-assisted breeding for PHS tolerant cultivars (YANG *et al.,* 2008; XIA *et al.,* 2009).

Among all the cereals, only the flour of hexaploid wheat (*Triticum aestivum*) is able to form dough that exhibits the rheological properties required for the production of leavened bread. This property results from the ability of wheat storage proteins, gliadins and glutenins, to form special protein complex known as gluten. Biochemical and genetic evidence has demonstrated that high molecular weight glutenin subunit (HMW-GS) plays a major role in determining the viscoelastic properties thereby determining bread making qualities. The HMW glutenins are necessary to create strong dough, which is essential for making high quality, yeast-raised breads.

The HMW-GS are further subdivided into high Mr, x-type and low Mr, y-type subunits. Two HMW-GS alleles, which are inherited as tightly linked pairs encoding an x-type and a y-type subunit, are present at the Glu-1 locus on the long arms of the homoeologous chromosomes 1A, 1B and 1D of all hexaploid bread wheat cultivars (PAYNE, 1987). All cultivars of wheat, therefore, contain six HMW-GS genes, but only three, four or five subunits, because some of the genes are silent; the 1Ay gene is silent in all cultivars. HMW-GS may represent up to 10% of the total seed protein, as each HMW-GS accounts for about 2% of the total extractable protein. The HMW-GS alleles 1Ax1, 1Ax2* and the 1Dx5 + 1Dy10 subunit pair are said to be associated with stronger doughs and better baking properties, and 1Dx2 + 1Dy12 pair with weaker doughs (VASIL and ANDERSON, 1997). The number and composition of HMW-GS present in a cultivar are closely related to the quality of its gluten or dough (PAYNE, 1987). Considerable progress has been achieved in research of the molecular properties of flour proteins that are required for highest bread quality. Segregating breeding populations can be screened by electrophoresis or high performance liquid chromatography for the presence of desirable glutenin subunits. However, because of the tight linkage of the HMW-GS alleles, it is quite difficult to manipulate them by traditional breeding methods. Determination of technological quality of wheat cultivars according to analysis of HMW-GS reveals a successful progress in Slovak wheat breeding and its successes in creating cultivars with high bread-making quality. This can be seen particularly by allele distribution at *Glu-B1* and *Glu-D1* loci where HMW-GS having a negative impact on quality, mainly alleles at the *Glu-B1* 6+8 locus and *Glu-D1* 2+12 locus, occur at a substantially lower rate than in West European cultivars (GREGOVÁ *et al*., 2007; ŠRAMKOVÁ *et al.,* 2008).

A number of HMW-GS as well as low-molecular-weight glutenin subunit (LMW-GS) genes have been introduced into bread and pasta wheat by genetic transformation (TOSI *et al.,* 2005; BREGITZER *et al.,* 2006; BLECHL *et al*., 2007). The HMW-GS *1Ax1* gene which is known to be associated with superior bread making quality was introduced into the cultivar Bobwhite lacking this gene (ALTPETER *et al*., 1996). The transgenic plants expressing the introduced HMW-GS were normal, fertile and showed Mendelian segregation of the transgene. The effect of HMW glutenin subunits 1Ax1 and/or 1Dx5 on dough elasticity was demonstrated by introducing the corresponding genes into durum wheat and *Triticale*; cereals with poor bread making properties. Transgenic durum wheat producing one additional HMW glutenin, 1Ax1 or 1Dx5, gave an increased dough strength and stability, thus changing the properties of durum flour for both bread and pasta making (HE *et al*., 1999). ALVAREZ *et al*. (2000) introduced the HMW-GS genes 1Ax1 and 1Dx5 into a commercial cultivar of *T. aestivum* that already expresses five subunits. The overexpression of 1Dx5 gene increases the contribution of the HMW-GS to a level of 22% of the total protein content. However, the overexpression of the 1Dx5 gene was found to be associated with a dramatic increase in dough strength by making it too strong, and, therefore, unsuitable for use in conventional breadmaking (BLECHL *et al*., 2007).

Wheat landraces represent interesting biological material because of their genetic variability. Some of them possess genes, not occurring in modern cultivars, although these genes can be valuable for improvement of their quality. Thus, screening landraces for the novel HMW-GS alleles for further utilization has become a part of some breeding programs (GREGOVÁ *et al*., 1999; GREGOVÁ *et al*., 2004; GREGOVÁ *et al*., 2006).

TOSI *et al.* (2005) reported the production of transgenic wheats expressing additional LMW subunits in the commercial durum wheat varieties. The gene constructs used in this work were derived from Glu-A3 and Glu-B3 loci. Expression levels ranged up to those of the major endogenous LMW subunits. Their incorporation into polymers was demonstrated. However, co-suppression of the major endogenous HMW subunit was observed, leading to reduced dough strength in comparison with line, which did not exhibit co-suppression, having increased strength.

Identification and characterisation of novel LMW-GS suggests that there is intensive research in this area and improvement of wheat quality is in progress (AN *et al*. 2006; ZHAO *et al*. 2006; ZHAO *et al.* 2007).

In near future, molecular approaches including genetic transformation and marker-assisted selection will provide an opportunity for improving further the wheat processing qualities by introduction of genes associated with good bread-making qualities into a cultivar which is agronomically desirable but which has poor bread-making qualities. This would avoid or minimize the necessity of blending flour from different cultivars in milling operations.

8. Increasing of healthful components

Hunger and malnutrition are among the most devastating problems affecting a large part of the world's population. The nutritional value of wheat is extremely

important as it takes an important place among the few crop species being extensively grown as staple food sources. The importance of wheat is mainly due to the fact that its seed can be ground into flour, semolina, etc., which form the basic ingredients of bread and other bakery products, as well as pastas, and thus it presents the main source of nutrients such as proteins, carbohydrates, lipids, fibre and vitamins, to the most of the world population. However, the total content or absolute concentration, of a given nutrient in a food is not always a reliable indicator of its useful nutritional quality, because not all of the nutrients is absorbed (PAREDES-LÓPEZ and OSUNA-CASTRO, 2007). One of the continuing criticisms of modern crop varieties, that have been commercialized thus far, is that although they do have many desirable attributes, none of them offer any direct, tangible benefits to the consumer. This situation is changing rapidly with increasing understanding of the molecular and genetic control of various aspects of plant growth and development, which has made it possible to enhance the quality as well as the quantity of proteins/starches/oils, and the content of vitamins, essential amino acids, minerals and other healthful components of plants. Although not much work of this nature has been carried out in wheat, there is no reason why the success which has been achieved in crops such as rice, maize and soybean, or demonstrated in model species such as *Arabidopsis*, cannot be extended to wheat (VASIL, 2007).

Protein quality is based on their amino acid composition (particularly their relative content of essential amino acids) and their digestibility. Therefore, high quality proteins are those that are easily digested and contain the essential amino acids in quantities that correspond to human requirements. Deficiency in certain amino acids reduces the availability of others present in abundance. In general, cereal proteins are low in lysine (1.5–4.5% vs. 5.5% of WHO recommendation), tryptophan (Trp, 0.8–2.0% vs. 1.0%), and threonine (Thr, 2.7–3.9% vs. 4.0%). Because of this deficiency, these essential amino acids (EAAs) become the limiting amino acids in cereals. It is thus of economic and nutritional significance to enhance the EAAs in plant proteins. In the past, plant geneticists and breeders have made much effort to improve the quality of plant proteins. Natural mutations such as high-lysine corn and barley have been identified and developed into elite genotypes (BRIGHT and SHEWRY, 1983). Unfortunately, undesirable traits such as greater susceptibility to diseases and pests and lower yields were associated with these mutations. The correlation between nutritional quality and yield has been a serious issue over the years, since the two factors appear to be negatively correlated. This problem appears to have been overcome since the introduction of modifier genes (*mo2* genes) that changed the opaque-2 phenotype of the maize seed, thus allowing wild-type-like seed characteristics to be maintained, resulting in normal yield but conserving the high lysine and high tryptophan concentrations (GAZIOLA *et al*., 1999). These new maize lines have been designated QPM (Quality Protein Maize) and several hybrids were produced and introduced into the market. However, the widespread use of these varieties has not been as fast as initially expected. Apart from the QPM lines, it would appear that very little else in the way of high-lysine crops is available. Perhaps recent legislation and general concern about the use of modified genetic organisms have been the major setback regarding the release of such crops (FERREIRA *et al.,* 2005).

For a long time there has been much interest in developing high-amylose wheat as a source of resistant starch (RS), which is one of the major sources of dietary fiber and its many related benefits (e.g., prevention of coronary heart disease, cancers of the colon and rectum, diabetes) to humans. Suppression of starch branching enzyme II (SBEIIa and SBEIIb) expression by RNA interference was used to produce high-amylose wheat which was shown to be healthful for rats (REGINA *et al*., 2006).

The (1→3;1→4)-*β*-D-glucans, found exclusively in the cell walls of cereal and grass species, are important components of dietary fiber and highly beneficial in the prevention and treatment of serious human health conditions, including colorectal cancer, high serum cholesterol and cardiovascular diseases, obesity and non-insulin-dependent diabetes. *β*-D-Glucans were shown to have immunostimulating activity (DALMO and BØGWALD, 2008). Genes responsible for (1→3;1→4)-*β*-D-glucan synthesis in grasses have been identified and provide an excellent opportunity to enhance the dietary fiber content of cereal and other food crops through transformation (BURTON *et al*., 2006).

In attempting to enhance micronutrient levels in wheat through conventional plant breeding, it is important to identify genetic resources with high levels of the targeted compound, to consider the heritability of the targeted traits, to explore the availability of high throughput screening tools and to gain a better understanding of genotype by environment interactions (ORTIZ-MONASTERIO *et al*., 2007).

A well-known success of genetic transformation in cereals represents the development of the golden rice. It was first engineered with the insertion of the PSY gene from daffodil (*Narcissus pseudonarcissus*) and the bacterial phytoene desaturase (CrtI) gene from *Erwinia uredovora* (YE *et al*., 2000). Bacterial CrtI can catalyze three enzymatic steps from phytoene to all-trans-lycopene. The PSY gene is under the control of an endosperm-specific glutelin promoter. To localize the product in plastids, CrtI was designed as a fusion with the ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) small subunit. An alternative construct was made by co-transformation with constructs carrying the PSY/CrtI gene as described above and the LCY gene under the control of a glutelin promoter. By the latter approach, the carotenoid content of edible rice endosperm was 1.6 μg/g dry weight (YE *et al*., 2000). However, in 2005, Golden Rice2 was developed and the carotenoid content was increased up to 23- fold (37 μg/g of dry weight) compared to the original Golden Rice. This content is close to a realistic level for palliating VAD (vitamin A deficiency) in children (PAINE *et al.,* 2005). Expression of carotenoid biosynthetic genes in other cereals, such as wheat, requires further scientific investigation.

EHRENBERGEROVÁ *et al.* (2006) presented data indicating significant effects of cropping system, genotype, and year grown on the tocol levels in barley. The results suggest that a selective breeding program using the best genotypes would be beneficial to produce food barleys with higher levels of total tocols and tocotrienols.

The International Maize and Wheat Improvement Center, along with its many partners, has identified several maize and wheat varieties with 25% to 30% higher grain iron and zinc concentrations. Wild relatives of wheat have been found to contain some of the highest iron and zinc concentrations in the grains. Backcrossing to bread

wheat could result in highly nutritious cultivars (OZTURK *et al*., 2006; PELEG *et al*., 2008b).

UAUY *et al.* (2006) have characterized and cloned *Gpc-B1*, a quantitative trait locus from wild emmer wheat that is associated with increased levels of grain protein, zinc and iron as a consequence of accelerated senescence and increased nutrient mobilization from leaves to the developing grains. In ancestral wild wheat the allele encodes a NAC transcription factor (NAM-B1), while only a non-functional NAM-B1 allele is present in modern cultivated wheat varieties. Silencing of the multiple NAM homologues by RNA interference in transgenic plants caused delayed maturation and reduced grain protein, iron and zinc content by more than 30%. The cloning of *Gpc-B1* provides a direct link between the regulation of senescence and nutrient remobilization and an entry point to characterize the genes regulating these two processes. This may contribute to their more efficient manipulation in crops and translate into food with enhanced nutritional value.

Phosphate, which is stored in the form of phytic acid in plant seeds (including wheat), is indigestible in monogastric animals including humans due to the fact that they lack phytases which degrade phytic acid in the digestive tract. Transgenic wheat plants expressing the *Aspergillus niger* phytase encoding gene *phyA* accumulate phytase in their seed (BRINCH-PEDERSEN *et al.,* 2003; BRINCH-PEDERSEN *et al.,* 2006). Further improvement in the expression and thermostability of phytases in transgenic wheat plants has the potential to increase the bioavailability of Zn^{2+}, Ca^{2+} and Fe^{2+} by breaking down their otherwise indigestible complexes with phytic acid. GUTTIERI *et al.* (2007) identified a wheat mutant (*Lpa1-1*) with reduced phytic acid phosphorus and increased inorganic phosphorus (Pi). During germination there is a large decrease in phytine, which can make up to 80% of the total phosphate found in seeds (REDDY *et al.,* 1982) and a concomitant increase of Pi suggesting that phytin acts as a storage pool of phosphate during germination. Thus, it can be disputable whether the phytine decrease could result in growth disorders of the wheat plant and negatively affect all the metabolic reactions where phosphorus is a limiting factor (biosynthesis of nucleic acids, phospholipids, proteins and other energy-generating processes). However, genetically modified, low-phytic acid strains of maize having approximately 35% of the phytic acid content of wilde-type maize (WTM), did not exhibit substantial differences in growth as well as micronutrient and mineral concentrations when compared to WTM. Moreover, absorption of iron from tortillas prepared from transgenic maize was nearly 50% greater than from normal tortillas (MENDOZA *et al.,* 1998; SHI *et al*., 2005).

The world's agricultural community should adopt plant breeding and other genetic technologies to improve human health, and the world's nutrition and health communities should support these efforts. Sustainable solutions to the enormous global problem of 'hidden hunger' will not come without employing agricultural approaches (WELCH and GRAHAM, 2004.). Biofortification has the potential to contribute to increased micronutrient intakes and improved micronutrient status. The success of this strategy will require the collaboration between health and agriculture sectors (HOTZ and McCLAFFERTY, 2007; CAKMAK, 2008).

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