

Transgenics: Fast Track to Plant Stress Amelioration

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ABSTRACT

Crop researchers are under increasing pressure to breed designer crops that are able to survive a plethora of biotic and abiotic threats while enhancing their nutritional or other inherent value. Conventional crop breeding is no longer able to meet the challenges of the 21st century. Genetic transformation is a realistic and viable means of modifying traits of economic significance in crops that ultimately provide a solution to solve the global problems of hunger and malnutrition. Genetically modified crops can now overcome biotic (pathogens and insect pests) and abiotic stresses (herbicides, drought, salinity, salt, etc.) while maintaining the same productivity. This review focuses on the significant achievements of genetic transformation in crops built to be tolerant to different biotic and abiotic stresses.

Keywords: Transgenics, insects, pathogen, salinity, drought, herbicide

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INTRODUCTION

Population growth and climate change present the biggest challenges to crop researchers in the 21st century to breed designer crops in an environment overcast by different biotic and abiotic threats in addition to nutritional enrichment (Park *et al.* 2010). Conventional crop technologies that were able to feed the growing world in the 20th century were highly input dependent with a primary emphasis on fertilizers, high-yielding varieties, management of water resources, etc., as witnessed in the era of the green revolution (Swaminathan 2006). Moreover, the availability of arable land is declining due to malfunctioning agro-practices (non-sustainable farming), natural stresses viz. droughts, storms, floods, heat waves and rises in sea-level that are predicted to occur more frequently amid soil health problems (soil salinity and other toxicities), which are likely to be much more problematic in some areas (Ashraf and Akram 2009). So, there is a need to find alternatives for environmentally safe and economically viable solutions to enhance crop production. In this context, genetic transformation has emerged as an important means for crop researchers to modify traits of economic significance in crops that

ultimately provide solutions to solve the global problem of hunger and malnutrition. Redesigning crops to ameliorate biotic (pathogen and insect pests) and abiotic stresses (herbicide, drought, salinity, salt, etc.) by using genetic transformation is a better way for tailoring the genetic architecture of plants for dramatically enhancing agricultural production under adverse conditions (Lemaux 2008). The advent of molecular genetic technologies have recently advanced our understanding of crop stress resistance mechanisms that allow us to address these emerging issues much more effectively and efficiently than in the past. Moreover, the powerful combination of biotechnological tools (genetic engineering and transgenesis) and conventional breeding permits exploration and utilization of valuable traits encoded by transgene(s) to be introduced into commercial crops within an economically viable time frame. During the last two and a half decades, improved resistance against insect pests, pathogens, drought and salinity has been observed in transgenic plants that express/overexpress genes regulating osmolytes, specific proteins, antioxidants, ion homeostasis, transcription factors and membrane composition. Transformed plant 'factories' are also being designed for high volume production of pharmaceuticals, nutraceut-

tics and other beneficial chemicals. Transgenic plants have become devices for drug-delivery, being synthesized in plants (fruits and vegetable crops) that have been engineered to produce edible vaccines. Moreover, with the establishment and expansion of the “omics” (genomics, proteomics and metabolomics) era, a much broader range of genes with potential for crop improvement are being identified and, in some cases, tailored for further enhancement of their properties within specific crops. This review focuses on the significant achievements of genetic transformation in crops to ameliorate them for tolerance to different biotic and abiotic stresses.

Conventional breeding methods alone cannot feed the extra hungry mouths as the global population is expected to reach 8.1 billion by the 2025 (PRB 2009). Despite the successes of the green revolution with substantial strides in food grains production, India is still classified by FAO as a low income, food deficit country, nearly 26% of India's population is considered food insecure, consuming less than 80% of minimum energy requirements and account for about a third of the world's population that suffers from chronic hunger (Kumar and Bhatt 2006). The biggest limitation of traditional breeding is its notoriously slow nature of transferring a desired trait which is often associated with linkage drag (undesirable traits) into an otherwise superior crop cultivar. The time needed to transfer a desired gene into a crop plant depends on the source of the gene and the evolutionary distance of that source to the recipient crop plant (Jauhar 2006). If the gene source is a landrace or a related species, forming a primary gene pool with the crop species in question, the gene transfer may take five to eight years if not longer. Less related wild species belonging to the secondary or even tertiary gene pool may be rich reservoirs of genes for agronomic traits like disease or pest resistance, but to transfer such genes into crop cultivars may take 10 to 15 years or even longer, if they are at all possible. Pre- and post-fertilization barriers may impede sexual hybridization between the donor and the crop species and compound the problem of alien gene transfers (Jauhar 2006). In some cases, it may not even be possible to incorporate a certain trait by conventional means because a suitable donor may not be available or, if available, it may not be possible to hybridize the donor species with the cultivated crop plant. Moreover, the great challenge of food security being faced these days world over, has directed plant scientists towards gene revolution after green revolution due to advances in field of plant biotechnology. The gene revolution, in fact, involves a direct modification of qualitative and quantitative traits in an organism by transferring desired genes from one species to another by using tools of biotechnology (tissue culture and genetic engineering). This strategy is referred to as the ‘transgenic approach’ or ‘genetic transformation’. In contrast to classical breeding, the genetic engineering offers an excellent tool for asexually inserting a well-characterized gene(s) of unrelated organisms into plant cells, which on regeneration produce full plants with the inserted gene(s) integrated into their genome (Sanghera *et al.* 2009). This process may take less than a year to about 18 months in some cases, thus accelerating the process of genetic improvement of crop plants. In addition, this exciting technology allows access to an unlimited gene pool without the constraint of sexual compatibility. Over the past few decades, breeding possibilities have been broadened by genetic engineering and gene transfer technologies, as well as by gene mapping and identification of the genome sequences of model plants and crops which resulted in efficient transformation and generation of transgenic lines in a number of crop species (Gosal *et al.* 2009). Further, pyramiding of desirable genes with similar effects can also be achieved by using these approaches. Genetic transformation by *Agrobacterium*-mediated and microprojectile bombardment has been the most successful approach (Sanghera *et al.* 2009) used in plant transformation and successfully demonstrated for different economically important traits including biotic resistance (insect and disease) and abiotic stress tolerance

(herbicide, drought and salt) enhancement in different crop plants. In this review, an attempt has been made to cover the most important crop improvements through transgenic technologies.

TRANSGENIC STRATEGIES TO COMBAT BIOTIC STRESSES

Tremendous loss in yield of several economically important crops occurs due to biotic stresses (insect infestation and diseases). Recently, significant research and development efforts have been made to produce plants with high degree of tolerance or resistance to insect pest and diseases following transgenic technology which are described in subsequent section. The knowledge of the molecular basis of disease caused by plant pathogens and herbivory interactions shown by insects has allowed testing different strategies to produce resistant transgenic plants.

It is well known that plant pathogens represent real threat to world agriculture (Gurr and Rushton 2005). Even now, after adoption of various agricultural practices and agrochemicals, every year plant diseases account approximately 12% yield loss at the field level, to which is added 9-20% during post-harvest stages (Agrios 2005). For some diseases, chemical control is very effective, but it is often non-specific in its effects, killing beneficial organisms as well as pathogens, and it may have undesirable health, safety, and environmental risks (Manczinger *et al.* 2002; Haggag 2008; Park *et al.* 2010). Our knowledge of molecular events occurring during plant-pathogen interactions has expanded significantly in the last few decades. Based on this knowledge, several strategies have emerged for developing crop varieties resistant to pathogens. Strategies include the manipulation of resistance by expression of PR proteins, antifungal peptides and manipulation of biosynthesis of phytoalexins (Quaim 2005; Punja 2007). The exploitation of genetic transformation technology to engineer plants in crops and against different pathogens has been elaborated in this section.

Transgenics for insect resistance

The one of the most practical way of increasing crop yield would be to preserve more of what is grown from loss to insect pests, which are estimated to consume around 14% of total global agricultural output (Oerke *et al.* 1994). Insects are not only responsible for massive direct losses of productivity as a result of their herbivory, but also cause massive indirect losses due to their role as vectors for various plant pathogens. These losses occur despite the extensive use of pesticides and fungicides. Moreover, more than 600 pests have been reported to develop resistant against chemical pesticides (Raman 1995). So, durability in the inherent resistance capacity of particular crop against insect pest is essential. This can be achieved by exploiting tools like genetic transformation to tailor insect resistance transgenic crops carrying genes that encode proteins toxic to insects. Since the first reports of transgenic plants appeared in 1984 (Horsch *et al.* 1984) there has been very rapid progress directed at using this technology for the practical ends of crop improvement (James 2008).

As an example, transgenic plants expressing the *Cry* genes from the soil bacterium *Bacillus thuringiensis* (*Bt*) has become the most prevalent method of insect control for several commercial crops. Besides the *cry* genes from *Bt*, other bacterial genes such as *choM* and *ipt* from *Actinomyces* and *Agrobacterium*, respectively, have strong insecticidal properties and have been transformed into cotton, brinjal, tobacco plants, etc. in order to determine their ability to control insect infestation (Jauhar 2006). European corn borer [ECB, *Ostrinia nubilalis* (Hübner)], for example, causes a loss of up to 2000 million US\$ annually in the USA alone (Hyde *et al.* 1999). Resistance breeding by conventional means is cumbersome and fraught with uncertainty. To breed a corn cultivar with resistance or even par-

tial resistance to ECB may well take 10 to 15 years by traditional breeding, provided a suitable resistance donor is available. Thus, through 12 years of breeding, Syngenta, a Swiss agrochemical company, was able to produce a corn cultivar with only 10% resistance to ECB. However, a gene from a soil-borne bacterium, *Bt*, when bioengineered into the corn genome, confers almost complete resistance to ECB. This is an efficient means of eliminating the pest damage and pesticide application without affecting grain yields. Thus, *Bt*-corn acquired the capacity of an efficient pesticide a biopesticide. It took Syngenta only 5 years to engineer the *Bt* gene into corn. Scientists at the University of Minnesota estimated that farmers averaged several times greater returns on their investment by using *Bt* corn for insect control, compared to the use of a chemical insecticide (Ostlie *et al.* 1997). The *Bt* corn hybrids had 4 to 8% higher grain yields than standard hybrids when infested with ECB (Lauer and Wedberg 1999). Moreover, *Bt* corn is beneficial to the environment and the *Bt*-induced insect resistance in corn is much safer to farmers and other field workers, compared with the use of a chemical insecticide. Based on safety data, the U.S. Environmental Protection Agency (EPA) authorized commercial planting of *Bt* corn varieties (Palevitz 2001). Several transgenic crops with insecticidal genes have been introduced in temperate regions of the world (Sharma *et al.* 2003). Transgenic rice varieties resistant to yellow stem borer [*Scirpophaga incertulas* (Walker)] have been produced in India (Ramesh *et al.* 2004). Because of its higher productivity and positive health effects through reduced pesticide use, *Bt* cotton has been commercialized aggressively especially in Asian countries like China (Huang *et al.* 2002a) and India (Whitfield 2003). Carrière *et al.* (2003) found long-term regional suppression of pink bollworm [*Pectinophora gossypiella* (Saunders)] by *Bt* cotton. *Bt* rice has the potential to eliminate yield losses caused by lepidopteran insects, estimated at 2 to 10% of Asia's annual rice yield of 523 million tons (High *et al.* 2004). Field trials of transgenic rice suggested high tolerance of transgenic rice against yellow stem borer (Bashir *et al.* 2004). Most recently, an insect-resistant variety GM Xianyou 63 that was produced by inserting a Chinese-created *B. thuringiensis* gene, showed resistance to rice stem borer (*S. incertulas*) and leaf roller [*Cnaphalocrocis exigua* (Butler)] and is on the threshold of being released for commercial cultivation in China. This insect-resistant variety is reported to benefit small farmers because of higher crop yields and reduced use of pesticides, which is important for health reasons (Huang *et al.* 2005).

Cotton boll weevil larvae, which feeds inside young fruits (bolls) is one of the most damaging cotton pests in the United States. The *choM* gene, isolated from *Actinomyces A19249*, encodes the enzyme cholesterol oxidase (*ChoM*), which has powerful insecticidal properties against the boll weevil larvae (Corbin *et al.* 1994). This enzyme acts by oxidizing cholesterol in the insect's midgut epithelial membrane, disrupting the physical and functional properties of the membrane and causing death. Corbin *et al.* (2001) developed transgenic tobacco plants expressing the *Actinomyces ChoM* gene. The transgenic tobacco plants were produced through *Agrobacterium*-mediated transformation. The researchers observed that the mortality rate of cotton boll weevil larva feeding on these transgenic plants ranged from 54 to 87%. These data indicate that expression of bacterial *ChoM* in the tissues of transgenic plants can result in an effective and environmentally safe eradication method against cotton boll weevil.

Tobacco hornworm (caterpillars of *Manduca sexta*) is one of the most destructive insect pests of tobacco plants. The transfer of the *Agrobacterium ipt* gene, encoding cytokinin *isopentenyl transferase*, to transgenic plants has been shown to increase the levels of endogenous cytokinin and effectively enhance the resistance of plants to a number of insects. Smigocki *et al.* (1993) introduced the *ipt* gene into tobacco plants by *Agrobacterium*-mediated transformation. The transgene was placed under the control of a wound-

inducible promoter from the potato proteinase inhibitor II (PI-IIK) gene. Transgenic tobacco plants had a 25- to 35-fold increase in *ipt* mRNA following induction by wounding of the plant tissue. Exogenous application of the transgenic leaf crude extracts reduced the hatch rate of hornworm eggs by 30%. In insect feeding assays, hornworm larvae consumed up to 70% less leaf material from the transgenic tobacco plants compared to wild-type plants.

Mehlo *et al.* (2005) engineered plants with a fusion protein combining the δ -endotoxin *CryIAC* with the galactose-binding domain of the non-toxic ricin B-chain (RB). Transgenic rice and corn plants designed to express the fusion protein (*BtRB*) were significantly more toxic in insect bioassays than those containing the *Bt* gene alone, due to increased number of potential fusion protein-receptor interactions at the molecular level in target insects. Transgenic rice plants overexpressing *ASAL* under the control of phloem specific promoters at the insect feeding site were constructed by Bandyopadhyay *et al.* (2001). The transgenic plants contained high level of *ASAL* (1.01% of total soluble protein) and showed adverse effect on survival, growth and populations of brown planthopper and green leafhopper pests (Saha *et al.* 2006). Recently, Choi *et al.* (2009) isolated the *Brassica rapa* Defensin 1 (*BrD1*) gene and introduced it into rice (*Oryza sativa* L.) to produce brown planthopper (*Nilaparvata lugens*) resistant transgenic plants.

The simultaneous introduction of three genes expressing insecticidal proteins (*CryIAC*, *Cry2A*, and *Gna*) into rice to control three major pests (rice leaf folder, yellow stem borer and the brown planthopper) imparted more resistance than combinations of only two of these transgenes (Bano-Maqbool *et al.* 2001). Another study of transgene pyramiding showed that transgenic cotton containing two *Bt* genes (*CryIAC* and *Cry2Ab*) performed better than either the single gene *CryIAC* or the *Cry2Ab* transgenic cotton (Jackson *et al.* 2004). A *cry2Aa* gene with a sequence-modified open reading frame encoding an insecticidal crystal protein from *Bt* was introduced into chickpea (*Cicer arietinum* L.) by Acharjee *et al.* (2010). Insect bioassays using the progeny of selected transgenic lines showed elevated level of resistance to pod borer larvae (*Helicoverpa armigera*). The genetic transformation and pyramiding of aprotinin-expressing sugarcane with *cryIAb* was also utilized to enhance the level of resistance in sugarcane towards *C. infuscatellus* (Arvinth *et al.* 2010). As a result, transgenics sugarcane produced considerably lower percentage of dead-hearts in comparison to untransformed plants. Zheng *et al.* (2005) expressed *CryICa* in transgenic shallots under the control of a *chrysanthemum* Rubisco small subunit promoter, and the transgenic plants showed high resistance to beet armyworm. Similarly, a modified novel *cryIC** gene (Tang and Lin 2007) was driven by the rice *rbcS* promoter, when introduced into Zhonghua 11 (*Oryza sativa* L.) by *Agrobacterium*-mediated transformation. Transgenic plants were examined for both insect resistance and agronomic traits under field conditions against yellow stem borer (*Tryporyza incertulas*), striped stem borer (*Chilo suppressalis*) and leaf folder (*Cnaphalocrocis medinalis*) (Ye *et al.* 2009). Weng *et al.* (2010) synthesized a truncated insecticidal gene m-cryIAC by increasing its GC content from 37.4 to 54.8%, based on the codon usage pattern of sugarcane genes, and transferred it into two sugarcane cultivars (ROC16 and YT79-177). In a greenhouse plant assay, about 62% of the transgenic lines exhibited excellent resistance to heavy infestation by stem borers. In field trials, the m-cryIAC transgenic sugarcane lines expressing high levels of *CryIAC* were immune from insect attack.

The plant expression vectors harbouring the bivalent *Vitreoscilla haemoglobin VHb* gene and insecticidal gene insecticidal gene (GFM*cryIA*) were successfully transferred to tobacco plants by Youru and Sandui (2010). The toxicity assay indicated that most of the transgenic plants showed high resistance to *Heliothis armigera*. Among 32 transgenic tobacco plants, 46.8% of the transgenic plants showed high

Table 1 Transgenic crops engineered for enhanced resistance against different insect pests.

Transgenic plant	Gene	Insect	Reference
Tobacco	<i>VHb</i> and <i>GFMcryIA</i>	<i>Heliothis armigera</i>	Youru and Sandui 2010
Chickpea	<i>cry2Aa</i>	<i>Helicoverpa armigera</i>	Acharjee <i>et al.</i> 2010
Sugarcane	<i>Cry1Aa</i> + <i>Cry1Ab</i> + <i>Cry1Ac</i>	<i>Chilo infuscatellus</i>	Arvinth <i>et al.</i> 2010
Sugarcane	<i>m-cry1Ac</i>	<i>C. infuscatellus</i>	Weng <i>et al.</i> 2010
Rice	BrD	<i>Nilaparvata lugens</i>	Choi <i>et al.</i> 2009
Sugarcane	Aprotinin	<i>Scirpophaga excerptalis</i>	Christy <i>et al.</i> 2009
Tobacco	<i>Magi 6</i>	<i>Spodoptera frugiperda</i>	Hernández-Campuzano <i>et al.</i> 2009
Chickpea	ASAL	<i>Aphis craccivora</i>	Chakraborti <i>et al.</i> 2009
Rice	<i>pin2</i>	<i>Scirpophaga incertulas</i>	Rao <i>et al.</i> 2009
Rice	ASAL	<i>N. virescens</i> and <i>N. lugens</i>	Saha <i>et al.</i> 2006
Sorghum	<i>cry1Ac</i>	<i>Chilo partellus</i> (Swinhoe)	Girijashankar <i>et al.</i> 2005
Rice	<i>cry1Ac</i> , 2A	<i>S. incertulas</i> and <i>S. medinalis</i>	Bashir <i>et al.</i> 2005
Rice	<i>cry1Ac</i> and <i>gna</i>	<i>S. incertulas</i> and <i>N. lugens</i>	Ramesh <i>et al.</i> 2004
Rice	<i>cry1Ac</i>	<i>Scirpophaga incertulus</i>	Khanna and Raina 2002
Rice	<i>Gna</i>	<i>Nilaparvata lugens</i> (Stal)	Foissac <i>et al.</i> 2000
Rice	<i>SKTI</i>	<i>Nilaparvata lugens</i> (Stal)	Lee <i>et al.</i> 1999
Potato	<i>CpTi</i>	<i>Lacanobia oleracea</i> (Linnaeus)	Gatehouse <i>et al.</i> 1999
Rice	<i>gna</i>	<i>Nilaparvata lugens</i> (Stal)	Rao <i>et al.</i> 1998
Rice	<i>cry1Ab</i>	<i>Scirpophaga incertulus</i>	Datta <i>et al.</i> 1998
Rice	<i>PI-II</i>	<i>C. suppressalis</i> (Walker)	Daun <i>et al.</i> 1996
Rice	<i>CpTi</i>	<i>S. incertulas</i>	Xu <i>et al.</i> 1996
Tobacco	<i>PI-II</i>	<i>Spodoptera exigua</i> (Hubner)	Jongsma <i>et al.</i> 1995
Tobacco	<i>M.sexta PI</i>	<i>Bemisia tabaci</i> (Gennadius)	Thomas <i>et al.</i> 1995
Pea	<i>a-amylase</i>	<i>Callosobrunchus</i> spp.	Shade <i>et al.</i> 1994
Rice	<i>cry1Ab</i>	<i>Chilo suppressalis</i> (Walker)	Fujimoto <i>et al.</i> 1993
Potato	<i>cry3a</i>	<i>Leptinotarsa decemlineata</i> (Say)	Perlak <i>et al.</i> 1993
Corn	<i>cry1Ab</i>	<i>Ostrinia nubilalis</i> (Hubner)	Koziel <i>et al.</i> 1993
Cotton	<i>cry1Ab/1Ac</i>	<i>Pectinophora gossypiella</i> (Saunders)	Perlak <i>et al.</i> 1990
Tobacco	<i>PI-II</i>	<i>Menduca sexta</i> (Johannson)	Johnson <i>et al.</i> 1989
Tobacco	<i>CpTi</i>	<i>Heliothis virescens</i> (Fabricius)	Hilder <i>et al.</i> 1987

resistance to the insect. Taken together, the findings from these studies indicate a promising potential of engineering an insect-resistant gene to tailor its protein expression levels in transgenic sugarcane to combat insect infestations. Wang and Guo (2010) transferred synthesized *VHb* gene and insecticidal gene *GFMcryIA* to tobacco plants by *Agrobacterium*-mediated transformation. Toxicity assay indicated that insecticidal gene expressed pesticidal toxin protein. The net weight of transgenic tobacco plants exceeded that of non-transgenic ones by 8%. Compared to non-transgenic tobacco plants, transgenic plants appeared to be high-yielding, insect-resistant varieties.

Various studies have illustrated the importance of continued identification of bacterial genes and genes from other sources (**Table 1**) that have insecticidal properties for the control of important agricultural insects in a more efficient and environmentally safe manner.

Transgenics for fungal disease resistance

With the beginning of the molecular era of plant biology in the early 1980s, many complex mechanisms that evolved in plants in response to pathogen infection have been identified. The role of multitude genes that are involved in immune responses after fungus infestation and the various pathways involved therein, have been elucidated (Melchers and Stuiver 2000). Transgenic plants have been produced with genes involved in different pathways to enhance disease resistance against fungal pathogens. The first report on developing fungus resistant transgenic plant came in 1991. Broglie *et al.* (1991) constitutively expressed bean chitinase in tobacco and *Brassica napus* to enhance resistance towards *Rhizoctonia solani*. Similarly, antifungal genes have been engineered in various crop plants to render resistance against fungal pathogens (Jauhar and Khush 2002; Sahrawat *et al.* 2003). The role of chitinases in fungal protection has been documented in rice (Datta *et al.* 2001; Itoh *et al.* 2003). Transgenic peanut expressing a tobacco chitinase gene was shown to possess enhanced resistance to the late leaf spot caused by *Phaeosariopsis personata* (Rohini and

Sankara Rao 2001; Anuradha *et al.* 2008). Genetic engineering has been employed to contain *Fusarium* head blight, a ravaging disease of wheat (Anand *et al.* 2003, 2004). Expression of genes for suitable pathogenesis related proteins and defensins offers a suitable approach for controlling diseases that affect crop productivity. Some proteins, called defensins, are small cysteine-rich peptides with antimicrobial activity. Transgenic expression of plant defensins has been reported to enhance protection in vegetative tissues against pathogen attack. Constitutive expression of *RsAFP-2* enhanced resistance of tobacco plants to *Alternaria longipes* (Terras *et al.* 1995) and tomato to *Alternaria solani* (Parashina *et al.* 2000) and rice to *M. grisea* and *R. solani* (Jha and Chattoo 2010). Canola expressing a pea defensin showed enhanced resistance against blackleg disease caused by *Leptosphaeria maculans* (Wang *et al.* 1999). The constitutive expression of an alfalfa defensin in potato provided robust resistance against the agronomically important fungus *Verticillium dahliae* under field conditions (Gao *et al.* 2000). Overexpression of *BSDI* (stamen specific defensin) in transgenic tobacco plants enhanced their tolerance against the pathogen *Phytophthora parasitica* (Park *et al.* 2002). Another alfalfa defensin was shown to inhibit the growth of the FHB pathogen *Fusarium graminearum* *in vitro* in wheat (Spelbrink *et al.* 2004). The generation of transgenic tomato plants constitutively expressing the chili defensin (*cdef1*) gene resulted in enhanced resistance against *Phytophthora infestans* and *Fusarium* spp. (Zainal *et al.* 2009). Expression of Dahlia defensin, Dm-AMP1, in rice directly inhibits the pathogen, *Magnaporthe oryzae* and *Rhizoctonia solani*. It was observed that constitutive expression of Dm-AMP1 suppresses the growth of *M. oryzae* and *R. solani* by 84 and 72%, respectively (Jha *et al.* 2009). Chenault *et al.* (2005) expressed a rice chitinase and an alfalfa glucanase in transgenic peanut and observed enhanced resistance against *Sclerotinia* blight in the transgenic plants. Expression of a barley oxalate oxidase in transgenic peanut also enhanced resistance to *Sclerotinia minor* (Livingstone *et al.* 2005). Overexpression of pepper pathogen induced genes *CAPIP2*, *CASAR82A* and *RAV1* in trans-

Table 2 Transgenic crops engineered for enhanced resistance against fungal pathogens.

Transgenic crop	Gene/gene product	Donor	Target pathogen	References
Rice	<i>Rs-AFP2</i>	<i>Raphanus sativus</i>	<i>Magnaporthe oryzae</i> and <i>Rhizoctonia solani</i>	Jha and Chattoo 2010
Cotton	<i>NPR1</i>	<i>Arabidopsis</i>	<i>Verticillium dahliae</i> , <i>Fusarium oxysporum</i> f. sp. <i>vasinfectum</i> , <i>Rhizoctonia solani</i> , and <i>Alternaria alternata</i>	Parkhi <i>et al.</i> 2010
Cotton	<i>hpa_{xoo}</i>	<i>Xanthomonas oryzae</i> pv. <i>oryzae</i>	<i>Verticillium dahliae</i>	Miao <i>et al.</i> 2010
Poplar (<i>Populus tomentosa</i> Carr.)	<i>LJAMP2</i>	<i>Leonurus japonicus</i>	<i>Alternaria alternata</i> and <i>Colletotrichum gloeosporioides</i>	Jia <i>et al.</i> 2010
Tomato	<i>cdef1</i>	<i>Capsicum annuum</i>	<i>Phytophthora infestans</i> and <i>Fusarium spp</i>	Zainal <i>et al.</i> 2009
Rice	<i>Dm-AMP1</i>	<i>Dahlia</i>	<i>Magnaporthe oryzae</i> and <i>Rhizoctonia solani</i>	Jha <i>et al.</i> 2009
Carrot	Acidic wheat class IV chitinase + acidic wheat β 1,3-glucanase + rice cationic peroxidase (<i>POC1</i>)	Wheat, rice	<i>Botrytis cinerea</i> and <i>Sclerotinia sclerotiorum</i> .	Wally <i>et al.</i> 2009
Rice	<i>hrf1</i>	<i>X. oryzae</i> pv. <i>oryzae</i>	<i>M. grisea</i>	Shao <i>et al.</i> 2008
Carrot	Microbial factor 3 (<i>MF3</i>)	<i>Pseudomonas fluorescense</i>	<i>Alternaria dauci</i> , <i>Alternaria radicina</i> and <i>Botrytis cinerea</i>	Baranski <i>et al.</i> 2007
Tobacco	<i>hrp N</i>	<i>Erwinia amylovora</i>	<i>Botrytis cinerea</i>	Sohn <i>et al.</i> 2007
Rice	PRm5	Maize	Enhanced resistance to multiple fungal pathogen	Gomez-ariza <i>et al.</i> 2007
Carrot	Lipid transfer protein gene and chitinase	Wheat, barley	Foliar fungal pathogen	Jayaraj and Punja 2007
Tobacco	Vv WRKY 1	Grape	Multiple fungal pathogen	Marchive <i>et al.</i> 2007
Rice	RCH10, RAC22, β -glucanase, β -RIP	Rice, alfalfa, barley	<i>Magnaporthe grisea</i>	Zhu <i>et al.</i> 2007
Barley	Chitinase and Thaumatin like protein	Rice	Resistance not tested	Tobias <i>et al.</i> 2007
Tobacco	PR1	<i>W. japonica</i>	<i>B. cinerea</i>	Kiba <i>et al.</i> 2007
<i>Arabidopsis</i>	SAR 8.2 gene (CASAR82A)	Pepper	<i>Fusarium</i> and <i>Botrytis</i>	Lee and Hwang 2006
Rice	Allene oxide synthase	Rice	<i>Magnaporthe grisea</i>	Mei <i>et al.</i> 2006
Wheat	Ace-AMP1	Onion	Enhanced antifungal activity	Ro-barman <i>et al.</i> 2006
Tobacco	<i>GAFP</i> (gastrodia antifungal gene)	<i>Gastrodia</i> (orchid)	<i>Rhizoctonia</i> spp., <i>Phytophthora</i> spp.	Cox <i>et al.</i> 2006
Rice	PR3	<i>T. viride</i>	<i>R. solani</i>	Balasubramaniam 2005
Tobacco	PR3	Bean	<i>R. solani</i>	Mohandas 2005
Rice	<i>Cercosporin A</i>	Giant silk moth	<i>Magnaporthe grisea</i>	Coca <i>et al.</i> 2006
Tobacco	<i>hrp N</i>	<i>Erwinia amylovora</i>	<i>Botrytis cinerea</i>	Jang <i>et al.</i> 2006
Pearl millet	<i>Afp</i>	<i>Aspergillus giganteus</i>	Rust and Downy mildew	Girgi <i>et al.</i> 2006
Wheat	<i>NPR 1</i>	<i>Arabidopsis</i>	<i>Fusarium graminearum</i>	Makandar <i>et al.</i> 2006
Rice	<i>AFP</i>	<i>Aspergillus giganteus</i>	<i>Magnaporthe grisea</i>	Moreno <i>et al.</i> 2005
Wheat	<i>Stilbene synthase</i>	Grape	<i>Puccinia recondite</i>	Serazetdinova <i>et al.</i> 2005
Tobacco	Cercopin-A-melittin peptide gene	Hybrid peptide	<i>Fusarium solani</i>	Yevtushenko <i>et al.</i> 2005
Italian rye grass	Chitinase	Rice	Crown rust disease	Takahashi <i>et al.</i> 2005
Tomato	<i>NPR1</i>	<i>Arabidopsis</i>	Resistance to fungal and bacterial disease	Lin <i>et al.</i> 2004
Rice	<i>AFP</i>	<i>Aspergillus giganteus</i>	<i>Magnaporthe grisea</i>	Coca <i>et al.</i> 2004
<i>Arabidopsis</i>	<i>Fusarium</i> specific antibody linked to antifungal peptides	Fusion proteins	Multiple fungal pathogens	Peschen <i>et al.</i> 2004
Rice	<i>ech42</i> , <i>nag 70</i> , <i>gluc 78</i>	<i>Trichoderma atroviridae</i>	<i>Magnaporthe grisea</i>	Liu <i>et al.</i> 2004
Peanut	PR2	Alfalfa	<i>S. minor</i>	Chenault <i>et al.</i> 2003
Pea nut	PR3	Rice	<i>S. minor</i>	Chenault <i>et al.</i> 2003
Rice	<i>Glucose oxidase gene</i>	<i>Aspergillus niger</i>	<i>Magnaporthe grisea</i>	Kachroo <i>et al.</i> 2003
Sunflower	<i>Oxalate oxidase gene</i>	Wheat	<i>Sclerotinia sclerotiorum</i>	Hu <i>et al.</i> 2003
Rice	<i>Chitinase C</i> (Chi C)	<i>Streptomyces griseus</i>	<i>Magnaporthe grisea</i>	Itoh <i>et al.</i> 2003
Wheat (spring)	<i>Thaumatin like protein</i> , <i>chitinase</i> , <i>glucanase</i>	Wheat (Sumai-3 cultivar)	<i>Fusarium graminearum</i>	Anand <i>et al.</i> 2003
Tomato	<i>Pn-AMPs</i> (hevein like protein)	<i>Pharbitis nil</i>	<i>Phytophthora</i> spp., <i>Fusarium</i> spp.	Lee <i>et al.</i> 2003
Tobacco and banana	MSI-99 peptide	African clawed frog	<i>Alternaria</i> , <i>Botrytis</i> , <i>Mycosphaerella musicola</i>	Chakrabarti <i>et al.</i> 2003
Tomato	PR2	Tobacco	<i>F. oxysporum</i>	Foolad <i>et al.</i> 2002
Tobacco	Mannitol dehydrogenase	Celery	<i>Alternaria alternata</i>	Jennings <i>et al.</i> 2002
Tobacco	Spi-2 (peroxidase gene)	Norway spruce	<i>Phytophthora</i> spp.	Elfstrand <i>et al.</i> 2002
Apple	Endochitinase, Exochitinase	<i>Trichoderma harzianum</i>	<i>Venturia inaequalis</i>	Bolar <i>et al.</i> 2001
Pea nut	Chitinase	Tobacco	<i>Cercospora arachidicola</i>	Rohini and Rao 2001
Rice	Puroindolines (antimicrobial peptide gene)	Wheat	<i>Magnaporthe grisea</i> , <i>Rhizoctonia solani</i>	Krishnamurthy <i>et al.</i> 2001
Tobacco	Magainin analog	<i>Xenopus laevis</i>	<i>Peronospora tabacina</i>	Li <i>et al.</i> 2001
Wheat	Chitinase	Barley	<i>Blumeria graminis</i> , <i>Puccinia recondita</i>	Oldach <i>et al.</i> 2001
Poplar	Oxalate oxidase	Wheat	<i>Septoria musiva</i>	Liang <i>et al.</i> 2001
Rice	Chitinase	Rice	<i>Rhizoctonia solani</i>	Datta <i>et al.</i> 2001
Rice	Chitinase	Rice	<i>Rhizoctonia solani</i>	Datta <i>et al.</i> 2000

Table 2 (Cont.)

Transgenic crop	Gene/gene product	Donor	Target pathogen	References
Grape	Endochitinase	<i>Trichoderma harzianum</i>	<i>Botrytis cinerea</i>	Kikkert <i>et al.</i> 2000
Tobacco	Chitinase	<i>Baculovirus</i>	<i>Alternaria alternata</i>	Shi <i>et al.</i> 2000
Potato	Defensins (alfAFP)	Alfalfa	<i>Verticillium dahliae</i>	Gao <i>et al.</i> 2000
Potato	Cercosporin-melittin cationic peptide	Synthetic gene	Multiple pathogens	Osusky <i>et al.</i> 2000
Tomato	Gene1-2	Tomato	<i>Fusarium</i> spp.	Mes <i>et al.</i> 2000
Tobacco	Sarcotoxin peptide gene	Sarcophaga peregrine	<i>Rhizoctonia solani</i> , <i>Pythium aphanidermatum</i> , <i>Phytophthora nicotianae</i>	Mitsuhashi <i>et al.</i> 2000
Tobacco	Chloroperoxidase	<i>Pseudomonas</i>	<i>Colletotrichum destructivum</i>	Rajsekaran <i>et al.</i> 2000
Wheat	RIP	Barley	<i>Blumeria graminis</i>	Bieri <i>et al.</i> 2000
Alfalfa	Resveratrol synthase	Peanut	<i>Phoma medicaginis</i>	Hipsking and Paiva 2000
Tomato	Defensin	Raddish	<i>Alternaria solani</i>	Parashina <i>et al.</i> 2000
Carrot	Human lysozyme	Human	<i>Erysiphe heraclei</i> , <i>Alternaria dauci</i>	Takaichi and Oeda 2000
Grape	Chitinase	Rice	<i>Uncinulla necatar</i> , <i>Elsinoe ampelina</i>	Yamamoto <i>et al.</i> 2000
Grape	Polygalacturoase inhibiting protein	Pear	<i>Botrytis cinerea</i>	Powell <i>et al.</i> 2000
Tobacco	Salicylic acid synthase	Bacterial origin	<i>Oidium lycopersicon</i>	Verberne <i>et al.</i> 2000
Carrot	Chitinase	Tobacco	<i>Alternaria dauci</i> , <i>A. radicina</i> , <i>Colletotrichum corotae</i>	Melchers and Stuvier 2000
Potato	Lactoferrin	Human	Not tested	Chong and Langridge 2000
Tobacco	Antimicrobial peptide	Synthetic	<i>Colletotrichum destructivum</i>	Cary <i>et al.</i> 2000
Tomato	Oxalate decarboxylase	<i>Collybia velutipes</i>	<i>Sclerotinia sclerotiorum</i>	Kesarwani <i>et al.</i> 2000
Wheat	TL protein	Rice	<i>Fusarium graminearum</i>	Chen <i>et al.</i> 1999
Rice	TL protein	Rice	<i>Rhizoctonia solani</i>	Datta <i>et al.</i> 1999
Rice	RIP	Maize	No effect on <i>M. grisea</i> or <i>R. solani</i>	Kim <i>et al.</i> 1999
Potato	Osmotin gene	Tobacco	<i>Phytophthora infestans</i>	Li <i>et al.</i> 1999
Chrysanthemum	Chitinase	Rice	<i>Botrytis cinerea</i>	Takatsu <i>et al.</i> 1999
Geranium	Antimicrobial protein	Onion	<i>Botrytis cinerea</i>	Bi <i>et al.</i> 1999
Wheat	PR5	Barley	<i>E. graminis</i>	Bliffeld <i>et al.</i> 1999
Tobacco	β -cryptogein elicitor	<i>Phytophthora cryptogea</i>	<i>Phytophthora parasitica</i>	Tepfer <i>et al.</i> 1998
Tobacco	PAPII	<i>Phytolacca americana</i>	Broad spectrum resistance to viral and fungal pathogens	Wang <i>et al.</i> 1998
Potato	Endochitinase	<i>Trichoderma harzianum</i>	Foliar and soil borne fungal pathogen	Lorito <i>et al.</i> 1998

genic plants resulted in disease resistance (Lee and Hwang 2006; Sohn *et al.* 2006). The *chit1* gene from the entomopathogenic fungus *Metarhizium anisopliae*, encoding the endochitinase *CHIT42*, showed enhanced resistance in tobacco plants against *Rhizoctonia solani* (Kern *et al.* 2010). Three genes, *ech42*, *nag70* and *gluc78*, encoding hydrolytic enzymes, from a biocontrol fungus *Trichoderma atroviride*, were introduced in single or in combinations into rice. *Gluc78*-overexpressing transgenic plants showed enhanced resistance to *Magnaporthe grisea*, while transgenic plants over expressing the *ech42* gene encoding for an endochitinase increased resistance to *R. solani*, resulting in a reduction of 62% in the sheath blight disease index (Liu *et al.* 2004; Shah *et al.* 2008).

Shao *et al.* (2008) introduced a harpin-encoding gene *hrf1*, derived from *X. oryzae* pv. *oryzae*, into rice and generated transgenic rice lines with overexpression of the *hrf1* gene. Disease assays revealed that the *hrf1*-overexpressing transgenic rice plants and were highly resistant to all major *M. grisea* races in rice-growing areas. Jhang *et al.* (2010) introduced antifungal puroindoline proteins, *PINA* and *PINB* into corn under the control of a corn *Ubiquitin* promoter. Two *Pina/Pinb* expression-positive transgenic events were evaluated for resistance to *Cochliobolus heterostrophus*, the corn southern leaf blight (SLB) pathogen. Transgenic corn expressing Pins showed significantly increased tolerance to *C. heterostrophus*, averaging 42.1% reduction in symptoms.

It is evidenced from the aforementioned reports that genetic transformation approach is an example of environmentally friendly biotechnology that could save threatened agricultural landscapes and ecosystems worldwide (Gartland *et al.* 2002, 2003). Several examples where this technology have been applied to different crops to combat fungal diseases (Table 2).

Transgenics for bacterial disease resistance

Many bacterial genes involved in pathogenicity have been identified and expressed in transgenic plants. The genetically transformed plants carrying these genes showed spontaneous activation of different defense mechanisms, leaving the plant in a elevated state of defense. This 'defense mode' greatly enhances the plant's ability to quickly react to a pathogen invasion and more successfully overcome the infection. This has been made possible by genetic engineering by using genes found in fungi, insects, animals and other plants. Antimicrobial proteins, peptides, and lysozymes that naturally occur in insects (Jaynes *et al.* 1987), plants (Broekaert *et al.* 1997), animals (Vunnam *et al.* 1997), and humans (Mitra and Zhang 1994; Nakajima *et al.* 1997) are now a potential source of plant resistance.

Antibacterial lytic peptides like cecropins are found in the hemolymph of the giant silk moth (*Hyalophora cecropia*) (Durell *et al.* 1992; Tripathi *et al.* 2004). Transgenic tobacco plants expressing cecropins have increased resistance to *P. syringae* pv. *tabaci*, causing wildfire of tobacco (Huang *et al.* 1997). Synthetic lytic peptide analogs, *Shiva-1* and *SB-37*, produced from transgenes in potato plants reduce bacterial infection caused by *Erwinia carotovora* subsp. *atroseptica* in transgenic potato plants (Arce *et al.* 1999). Similarly, transgenic rice plants overexpressing *cecropin B* gene showed a significant reduction in development of lesions caused by *X. oryzae* pv. *oryzae* (Coca *et al.* 2004). Moreover, expression of *SB-37* lytic peptide analog in transgenic apple plants showed increased resistance to *E. amylovora* under field tests (Norelli *et al.* 1998). Further, the expression of the *D4E1* in poplar has resulted resistance to *Agrobacterium tumefaciens* and *Xanthomonas populi* (Mentag *et al.* 2003; Montesinos 2007).

Similarly, attacins are another group of antibacterial proteins produced by *Hyalophora cecropia* pupae (Hult-

Table 3 Transgenic crops engineered for enhanced resistance against bacterial pathogens.

Transgenic plant	Gene/gene product	Source	Target pathogen	Reference
Rice	<i>Np3</i> and <i>Np5</i>	Chinese shrimp	<i>Xanthomonas oryzae</i> pv. <i>oryzae</i>	Wei <i>et al.</i> 2011
Tomato	Cationic lytic peptide cecropin B	<i>Hyalophora cecropia</i>	<i>Ralstonia solanacearum</i> and <i>Xanthomonas campestris</i> pv. <i>vesicatoria</i>	Jan <i>et al.</i> 2010
Potato	magainin II	Synthetic peptide	<i>Erwinia carotovora</i>	Barrell and Conner 2009
Tomato	ferredoxin-I protein	Sweet pepper	<i>Ralstonia solanacearum</i>	Huang <i>et al.</i> 2007
Poplar hybrid (<i>Populus tremula</i> L. x <i>Populus alba</i> L)	<i>D4E1</i>	Synthetic peptide	<i>Agrobacterium tumefaciens</i> and <i>Xanthomonas populi</i>	Mentag <i>et al.</i> 2007
Rice	<i>Rxo1</i>	Maize	<i>Xanthomonas oryzae</i> pv. <i>oryzae</i>	Zhao <i>et al.</i> 2005
Rice	<i>NPR1</i> orthologue (<i>NH1</i>)	Rice	<i>Xanthomonas oryzae</i> pv. <i>oryzae</i>	Chern <i>et al.</i> 2005
<i>Arabidopsis</i>	<i>hrap</i>	Sweet pepper	<i>E. carotovora</i> subsp. <i>carotovora</i>	Pandey <i>et al.</i> 2005
Potato (cv. cv. Irish Cobbler)	<i>shiva-1</i>	Synthetic peptide	<i>Erwinia carotovora</i>	Yi <i>et al.</i> 2004
Rice	<i>cecropin B</i>		<i>X. oryzae</i> pv. <i>oryzae</i>	Coca <i>et al.</i> 2004
Rice	<i>GOX/</i> Glucose oxidase	<i>Aspergillus niger</i>	<i>X. oryzae</i> pv. <i>oryzae</i>	Kachroo <i>et al.</i> 2003
Tobacco	<i>M28L</i> /mutated esculentin gene	Bean	<i>Pseudomonas aeruginosa</i> , <i>P. syringae</i> pv. <i>tabaci</i>	Ponti <i>et al.</i> 2003
Poplar hybrid (<i>Populus tremula</i> L. x <i>Populus alba</i> L)	<i>D4E1</i>	Synthetic peptide	<i>Agrobacterium tumefaciens</i> and <i>Xanthomonas populi</i>	Mentag <i>et al.</i> 2003
Tomato	Lactoferrin gene	Tomato	<i>Ralstonia solanacearum</i>	Lee <i>et al.</i> 2002
Rice	ferredoxin-like protein (AP1)	Sweet pepper	<i>Xanthomonas oryzae</i> pv. <i>oryzae</i>	Tang <i>et al.</i> 2001
Tobacco	<i>bo/</i> Bacterio-opsin (BO)	<i>Halobacterium halobium</i>	<i>Pseudomonas syringae</i> pv. <i>tabaci</i>	Rizhsky and Mittler 2001
Tobacco	<i>expI</i> /N-oxoacyl-homoserine lactone (OHL)	<i>Erwinia carotovora</i>	<i>Erwinia carotovora</i>	Mae <i>et al.</i> 2001
Tobacco	<i>aiiA</i> /Acyl-homoserine lactonase	<i>Bacillus</i> sp. 240B1	<i>Erwinia carotovora</i>	Dong <i>et al.</i> 2001
Rice	cecropin B	<i>Bombyx mori</i>	<i>Xanthomonas oryzae</i> pv. <i>oryzae</i>	Sharma <i>et al.</i> 2000
Apple/Pear	<i>attacin E</i> gene (<i>attE</i>)	<i>Sarcophaga peregrina</i>	<i>E. amylovora</i>	Ko <i>et al.</i> 2000
Potato	34-aa chimaeric peptide MsrA1+ melittin	Bee venom	<i>E. carotovora</i> ssp. <i>atroseptica</i>	Osusky <i>et al.</i> 2000
Potato	cecropin SB-37		<i>Erwinia carotovora</i> subsp. <i>atroseptica</i>	Arce <i>et al.</i> 1999
Tomato	<i>Bs2</i>	Pepper	<i>X. campestris</i> pv. <i>vesicatoria</i>	Tai <i>et al.</i> 1999
Apple	<i>attacin E</i> gene (<i>attE</i>)	<i>Sarcophaga peregrina</i>	<i>E. amylovora</i>	Norelli <i>et al.</i> 1998
Potato	<i>sarco</i> gene coding for sarcotoxin IA	<i>Sarcophaga peregrina</i>	<i>E. carotovora</i> , <i>P. syringae</i> pv. <i>lachrymans</i> and <i>R. solanacearum</i>	Galun <i>et al.</i> 1996
Apple	<i>attacin E</i> gene (<i>attE</i>)	<i>Sarcophaga peregrina</i>	<i>E. amylovora</i>	Norelli <i>et al.</i> 1994
Tobacco	<i>argK/</i> ROCT ornithine carbamoyltransferase	<i>Pseudomonas syringae</i>	<i>Pseudomonas syringae</i> pv. <i>phaseolicola</i>	Hatziloukas and Panopoulos 1992

mark *et al.* 1983). Attacin expressed in transgenic potato enhanced its resistance to bacterial infection by *E. carotovora* subsp. *atroseptica* (Arce *et al.* 1999). Transgenic pear and apple expressing attacin genes have significantly enhanced resistance to *E. amylovora* in *in vitro* and greenhouse (Ko *et al.* 2000). In field tests, reduction of fire blight disease has been observed in transgenic apples expressing attacin genes (Norelli *et al.* 1999).

The lysozyme genes have been used to confer resistance against plant pathogenic bacteria in transgenic plants (Trudel *et al.* 1995). T4L, from the T4-bacteriophage has been reported to enhance resistance of transgenic potato against *E. carotovora*, which causes bacterial soft rot (Düring *et al.* 1993). Transgenic apple plants with the T4L gene showed significant resistance to fire blight infection (Ko 1999).

Thionins are plant antimicrobial proteins which are able to inhibit a broad range of pathogenic bacteria *in vitro* (Molina *et al.* 1993). Carmona *et al.* (1993) reported the expression of alpha-thionin gene from barley in transgenic tobacco confers enhanced resistance to *P. syringae*.

Pathosystem-specific plant resistance (*R*) genes have been cloned from several plant species (Bent 1996). The *Bs2* resistance gene of pepper specifically recognizes and confers resistance to strains of *X. campestris* pv. *vesicatoria* that contain the corresponding bacterial avirulence gene, *avrBs2* (Tai *et al.* 1999). Transgenic tomato plants expressing the pepper *Bs2* gene suppress the growth of *X. campestris* pv. *vesicatoria*.

Hatziloukas and Panopoulos (1992) used *Agrobacterium*-mediated transformation to produce tobacco plants carrying the *argK* gene, which encodes ROCT. Since in plant cells OCT is produced in the chloroplast, *argK* was

fused to the chloroplast transit sequence of the pea Rubisco small subunit (*rbcS*) gene for localized expression of the enzyme. The ROCT enzyme produced by the transgenic tobacco showed greater resistance to phaseolotoxin. In a different approach, Rizhsky and Mittler (2001) used the *Halobacterium halobium* bacterio-opsin (*bo*) gene under the control of the wound-inducible promoter *Pin2*, to develop transgenic tobacco plants resistant to *Pseudomonas syringae* pv. *tabaci* via *Agrobacterium*-mediated transformation. Bacterio-opsin activates the self-defense mechanisms in plants by enhancing proton pumping across the cell membrane (Mittler *et al.* 1995). Transgenic tobacco plants expressing the *bo* gene produced hypersensitive response (HR), and showed enhanced expression of different types of defense-related proteins such as chitinase, glucanase, and salicylic acid. The resulting transgenic tobacco plants expressing the *bo* gene, when challenged with *P. syringae* pv. *tabaci*, slowed down the growth of the pathogen. Tang *et al.* (2001) showed that transgenic rice plants expressing ferredoxin like protein (PFLP) from sweet pepper enhanced resistance to pathogenic Gram-negative bacteria. Along the same line, the expression of *hrap* gene in transgenic potatoes may enhance their resistance to pathogenic Gram-negative bacteria. Haung *et al.* (2007) demonstrated that expressing sweet pepper ferredoxin-I protein (PFLP) in transgenic plants can enhance disease resistance to *E. carotovora* subsp. *carotovora* that attack tomato plants. Similarly, Pandey *et al.* (2005) also showed that constitutive expression of the *hrap* gene in *Arabidopsis* enhanced the level of disease resistance towards *E. carotovora* subsp. *carotovora*.

An interesting example concerns the *NPR1* (or *NIMI*)

gene, a key defence regulator first identified in *Arabidopsis* (Durrant and Dong 2005). Transgenic rice plants over-expressing the rice NPR1 orthologue (NH1) acquire high levels of resistance to *Xanthomonas oryzae* pv. *oryzae* (Chern *et al.* 2005). In addition, *Rxo1*, an R-gene derived from maize (*Zea mays*), a non-host of the rice bacterial pathogen, *Xanthomonas oryzae* pv. *oryzicola* was successfully transformed into rice (*Oryza sativa*) and shown to confer resistance against *X. oryzae* pv. *oryzae* (Zhao *et al.* 2005).

Besides genetic transformation, a new approach to protect plants against bacterial diseases is based on interference with the communication system, quorum-sensing, used by several phytopathogenic bacteria to regulate expression of virulence genes according to population density (Cui and Harling 2005). The enzyme, *AiiA*, isolated from bacterial strain, *Bacillus* sp. 240B1, was found to degrade the quorum-sensing signalling molecule of the soft rot pathogen, *Erwinia carotovora*, and thereby rendering the bacteria incapable of infecting the host (Dong *et al.* 2000). Transgenic expression of *AiiA* in planta was subsequently demonstrated to provide significant enhancement of resistance against soft rot in potato (Dong *et al.* 2001). Recently, Tripathi *et al.* (2010) reported that the constitutive expression of the sweet pepper *Hrap* gene in banana results in enhanced resistance to BXW (Banana *Xanthomonas* wilt) caused by the bacterium *Xanthomonas campestris* pv. *musacearum*. The majority of transgenic lines (six of eight) expressing *Hrap* did not show any symptoms of infection after artificial inoculation of potted plants in the screen house, whereas control non-transgenic plants showed severe symptoms resulting in complete wilting. Transgenic tomato plant transformed with cationic lytic peptide cecropin B (CB), isolated from the giant silk moth (*Hyalophora cecropia*) demonstrated significant resistance to bacterial wilt and bacterial spot diseases Jan *et al.* (2010). The levels of CB expressed in transgenic tomato plants were ~0.05 µg in 50 mg of leaves. Integration of the CB gene into the tomato genome was confirmed by PCR, and its expression was confirmed by Western blot analyses. Comprehensive information on quorum quenching has been recently documented by Kashyap *et al.* (2010), wherein authors have given a deep insight of this approach operating in various systems of phytopathogenic bacteria. **Table 3** represents a detailed account on various crops engineered through genetic transformation, showing promise to reduce the harmful effects of bacterial pathogens.

Transgenics for viral disease resistance

Transgenic technology also offers an excellent option to protect crop plants against devastating viral pathogens (Wani and Sanghera 2010). Transformation of plants with nucleotide sequences derived from viral genomes has been shown to provide protection against the virus from which the sequences were derived. The evidence for such a pathogen-derived resistance (PDR) was provided by Powell-Abel *et al.* (1986), who demonstrated that transgenic tobacco plants expressing *Tobacco mosaic virus* (TMV) coat protein were resistant to the virus. Beachy *et al.* (1990) suggested that expression of a virus coat protein as a transgene in a plant confers resistance to the virus in direct proportion to the quantity of coat protein produced by the transformed plant. This novel technique opened up new avenues of controlling viral diseases (Lomonossoff 1995; Bendahmane *et al.* 2007) in crop plants and fruit trees. *Rice yellow mottle virus* (RYMV) is a serious viral disease causing enormous losses in rice yields. Because of lack of a conventional solution to this problem, a transgenic approach based on PDR was successfully employed to produce an RYMV-resistant rice variety (Pinto *et al.* 1999). Similarly, transgenic wheat plants, engineered with the coat-protein gene of *Wheat streak mosaic virus* (WSMV) conferred protection against some WSMV strains (Sivamani *et al.* 2002). The PDR technology offers a promising means for inducing

virus resistance in a variety of plants (Wesseler 2003) including potato (Schubert *et al.* 2004). Coat-protein-mediated resistance has helped to control *Papaya ring spot virus* (PRSV) in papaya (*Carica papaya* L.) in Hawaii (Gonsalves 1998; Ferreira *et al.* 2002) and the papaya industry was spared from disaster posed by *Papaya ring spot virus* (PRSV) (Gonsalves 2003).

Engineering virus resistance by using genes encoding viral RNA dependent RNA-polymerases (RdRps) was first reported for TMV (Golemboski *et al.* 1990). Biotechnological approaches expressing sense and antisense RNA in transgenic plants have been employed successfully against *Tomato golden mosaic virus* (TGMV) (Day *et al.* 1991), *TYLCSV* (Bendahmane and Gronenborn 1997) and *TYLCV* (Yang *et al.* 2004), confirming the suggestion that RNA silencing can be harnessed for antiviral defence (Lapidot and Friedman 2002). In attempts to improve transgenic resistance further, Pooggin *et al.* (2003) obtained recovery from virus infection in a transient assay using IR constructs containing the common region of the begomovirus *Vigna mungo yellow mosaic virus* (VMYMV). Gafni and colleagues obtained plants resistant to *TYLCV* by targeting the CP gene with an IR construct (Zrachya *et al.* 2007). Similarly, Noris *et al.* (2004) and Ribeiro *et al.* (2007) produced transgenic plants expressing siRNAs against *TYLCSV* and *Tomato chlorotic mottle virus* (ToCMoV), respectively. More recent attempt to confer resistance to *CMV* using a small RNA pathway focused on transgenic artificial microRNAs (miRNA) that targeted a 21-nucleotide sequence within the 2b gene by using an inverted-repeat construct (Qu *et al.* 2007). When expressed in *Arabidopsis*, 64% of the plants were resistant to the target strain. A transformation system of pepper was set up using *Agrobacterium* that had been transfected with the coat protein gene, CMVP0-CP, with the aim of developing a new CMVP1-resistant pepper line. A large number of transgenic peppers (T1, T2 and T3) were screened for CMVP1 tolerance using CMVP1 inoculation. Transgenic peppers tolerant to CMVP1 were selected in a plastic house as well as in the field. Three independent T3 pepper lines highly tolerant to the CMVP1 pathogen were found to also be tolerant to the CMVP0 pathogen. These selected T3 pepper lines were phenotypically identical or close to the nontransformed lines. However, after CMVP1 infection, the height and fruit size of the non-transformed lines became shorter and smaller, respectively, while the T3 pepper lines maintained a normal phenotype (Lee *et al.* 2009). In a number of crops, transgenics resistant to an infective virus have been developed by introducing a sequence of the viral genome in the target crop by genetic transformation (**Table 4**). For the effective control of *Papaya ringspot virus* (PRSV) and *Papaya leaf-distortion mosaic virus* (PLDMV), an untranslatable chimeric construct containing truncated PRSV YK CP and PLDMV P-TW-WF CP genes has been transferred into papaya (*Carica papaya* cv. 'Thailand') by *Agrobacterium*-mediated transformation via embryonic tissues derived from immature zygotic embryos of papaya (Kung *et al.* 2009). Based on sequence profile of silencing suppressor protein, HcPro, it was that PRSV-HcPro, acts as a suppressor of RNA silencing through micro RNA binding in a dose-dependent manner. In planta expression of PRSV-HcPro affects developmental biology of plants, suggesting the interference of suppressor protein in micro RNA-directed regulatory pathways of plants. Besides facilitating the establishment of PRSV, it showed strong positive synergism with other heterologous viruses as well (Mangrauthia *et al.* 2010). Therefore, resistance in transgenic papaya can be overcome by PRSV with distant homology to the transgene, or by PRSV strains with HcPro that can sufficiently suppress the silencing mechanism of transgenic papaya. It would therefore be important to develop transgenic papaya that could avoid the impact of these PRSV strains (Tripathi *et al.* 2008).

Table 4 Transgenic crops engineered for enhanced resistance against viral pathogens.

Mechanism/Strategies employed	Transgenic plant	Source/gene product	Virus	Reference
RNA interference	Tobacco	Pns10	<i>Rice dwarf virus</i> (RDV)	Zhou <i>et al.</i> 2010
	Rice	Viroplasm matrix protein/ <i>Pns12</i>	<i>Rice dwarf virus</i> (RDV)	Shimizu <i>et al.</i> 2010
	Common bean	replication initiator protein (<i>rep</i> ; <i>AC1</i>), transactivator protein (<i>TrAP</i> ; <i>AC2</i>), replication enhancer protein (<i>REN</i> ; <i>AC3</i>) and movement protein (<i>BC1</i>)	<i>Bean golden mosaic virus</i> (BGMV)	Aragão and Faira 2009
Coat protein-mediated resistance	Tobacco	Coat protein (CP)	<i>Cowpea aphid-borne mosaic virus</i> (CABMV)	Mundembe <i>et al.</i> 2009
	Tobacco	CP	<i>Cucumber mosaic virus</i> (CMV) sub group IB	Srivastava and Raj 2008
	Tomato	<i>N</i> gene	<i>Tomato spotted wilt virus</i> (TSWV)	Goldbach <i>et al.</i> 2003
	Tobacco	<i>N</i> gene	TSWV, <i>Impatiens necrotic spot virus</i> (INSV), <i>Groundnut ringspot virus</i> (GRSV)	Vaira <i>et al.</i> 1995
	Tobacco	CP	CMV	Cuozzo <i>et al.</i> 1988
	Papaya	CP	<i>Papaya ringpost virus</i> (PRSV)	Gonsalves 1998
	Tobacco	CP	<i>Tobacco mosaic virus</i> (TMV)	Powell Abel <i>et al.</i> 1986
	Tobacco	CP	<i>Tobamoviruses</i> (TMV)	Nejdat and Beachy 1990
	Tobacco	CP	<i>Cucumber mosaic virus</i> (CMV)	Namba <i>et al.</i> 1991
	Tobacco	CP	<i>Cucumber mosaic virus</i> (CMV)	Quemada <i>et al.</i> 1991
	Cucumber	CP	<i>Cucumber mosaic virus</i> (CMV)	Gonsalves <i>et al.</i> 1992
	Tobacco	CP	<i>Cucumber mosaic virus</i> (CMV)	Yie <i>et al.</i> 1992
	Melon	CP	<i>Cucumber mosaic virus</i> (CMV)	Gonsalves <i>et al.</i> 1994
	Tomato	CP	<i>Cucumber mosaic virus</i> (CMV)	Xue <i>et al.</i> 1994
	Squash	CP	<i>Cucumber mosaic virus</i> (CMV)	Tricoli <i>et al.</i> 1995
	Tomato	CP	<i>Cucumber mosaic virus</i> (CMV)	Gielen <i>et al.</i> 1996
	Tomato	CP	<i>Cucumber mosaic virus</i> (CMV)	Fuchs and Provvidenti 1996
	Tobacco	CP	<i>Cucumber mosaic virus</i> (CMV)	Rizos <i>et al.</i> 1996
	Tobacco	CP	<i>Cucumber mosaic virus</i> (CMV)	Singh <i>et al.</i> 1998
	Tomato	CP	<i>Cucumber mosaic virus</i> (CMV)	Kaniewski <i>et al.</i> 1999
	Tomato	CP	<i>Cucumber mosaic virus</i> (CMV)	Tomassoli <i>et al.</i> 1999
	Tobacco	CP	<i>Cucumber mosaic virus</i> (CMV)	Jacquemond <i>et al.</i> 2001
	Pepper	CP	<i>Cucumber mosaic virus</i> (CMV)	Shin <i>et al.</i> 2002a
Tobacco	CP	<i>Alfalfa mosaic virus</i> (AMV)	Tumer <i>et al.</i> 1987a	
RNA dependent RNA polymerase-mediated resistance	Tobacco	Gene encoding viral RNA dependent RNA-polymerases (RdRps)	<i>Tobacco mosaic virus</i> (TMV)	Golemboski <i>et al.</i> 1990
Replicase-mediated resistance	Tobacco	Modified tobacco mosaic virus replicase transgene	Broad spectrum resistance to Tobamoviruses (TMV)	Donson <i>et al.</i> 1993
	Tobacco	replicase gene (<i>rep</i>)	Pea early browning virus RNA1	MacFarlane and Davies 1992
	Tobacco	<i>rep</i>	Potato virus X (PVX)	Braun and Hemenway 1992
	Tobacco	<i>rep</i>	Potato virus Y (PVY)	Audy <i>et al.</i> 1994
	Tobacco	<i>rep</i>	<i>Alfalfa mosaic virus</i> (AMV)	Brederode <i>et al.</i> 1995
	Tobacco	<i>rep</i>	<i>Cucumber mosaic virus</i> (CMV)	Anderson <i>et al.</i> 1992
	Tobacco	<i>rep</i>	<i>Cucumber mosaic virus</i> (CMV)	Zaitlin <i>et al.</i> 1994
	Tobacco	<i>rep</i>	<i>Cucumber mosaic virus</i> (CMV)	Hellwald and Palukaitis 1994
	Tobacco	<i>rep</i>	<i>Cucumber mosaic virus</i> (CMV)	Suzuki <i>et al.</i> 1996
	Tomato	<i>rep</i>	<i>Cucumber mosaic virus</i> (CMV)	Gal-On <i>et al.</i> 1998
	Tobacco	<i>rep</i>	<i>Cucumber mosaic virus</i> (CMV)	Canto and Palukaitis 1998
	Tobacco	<i>rep</i>	<i>Cucumber mosaic virus</i> (CMV)	Wintermantel and Zaitlin 2000
	RNA satellites	Tobacco	<i>Sat-II7N</i>	<i>Cucumber mosaic virus</i> (CMV)
Tobacco		<i>Sat-II7N</i>	<i>Cucumber mosaic virus</i> (CMV)	Jacquemond <i>et al.</i> 1988
Tobacco		Sat-RNA1, Sat-RNA1 + CP (CMV-O)	<i>Cucumber mosaic virus</i> (CMV)	Yie <i>et al.</i> 1992
Tobacco		Sat-S	<i>Cucumber mosaic virus</i> (CMV)	Peña <i>et al.</i> 1994
Pepper		<i>Sat-II7N</i>	<i>Cucumber mosaic virus</i> (CMV)	Kim <i>et al.</i> 1997
Tomato		Sat-S	<i>Cucumber mosaic virus</i> (CMV)	Stommel <i>et al.</i> 1998
Antisense RNAs	Tobacco	CMV-D	<i>Cucumber mosaic virus</i> (CMV)	Tumer <i>et al.</i> 1987a
	Tobacco	CMV-Q	<i>Cucumber mosaic virus</i> (CMV)	Ali <i>et al.</i> 1988
	Tobacco	CMV-D	<i>Cucumber mosaic virus</i> (CMV)	Cuozzo <i>et al.</i> 1988
RIP	Tobacco, potato	PAP (<i>Phytolacca americana</i>)	<i>Cucumber mosaic virus</i> (CMV)	Lodge <i>et al.</i> 1993
Ribonucleases	Tobacco	TCS (<i>Trichosanthes kirilowii</i>)	<i>Cucumber mosaic virus</i> (CMV)	Krishnan <i>et al.</i> 2002
	Tobacco	<i>pac1</i> (Yeast)	<i>Cucumber mosaic virus</i> (CMV)	Watanabe <i>et al.</i> 1995
	Tobacco	2-5Aase + RNaseL	<i>Cucumber mosaic virus</i> (CMV)	Ogawa <i>et al.</i> 1996
Enhancement of HR/SAR	Tobacco	2-5Aase + RNaseL	<i>Cucumber mosaic virus</i> (CMV)	Honda <i>et al.</i> 2003
	Pepper	<i>Tsi1</i> (Tobacco)	<i>Cucumber mosaic virus</i> (CMV)	Ogawa <i>et al.</i> 1996
	Tobacco	2-5Aase + RNaseL	<i>Cucumber mosaic virus</i> (CMV)	Shin <i>et al.</i> 2002b
Hammerhead ribozyme	Tobacco	Conserved sequences of RNA1 and 2 of CMV-Y	<i>Cucumber mosaic virus</i> (CMV)	Honda <i>et al.</i> 2003
				Kwon <i>et al.</i> 1997

Table 4 (Cont.)

Mechanism/Strategies employed	Transgenic plant	Source/gene product	Virus	Reference
Plantibodies	Tomato	ScFv antibodies	<i>Cucumber mosaic virus</i> (CMV)	Villani <i>et al.</i> 2005
	Tobacco	ScFv antibodies	<i>Cucumber mosaic virus</i> (CMV)	Aebig <i>et al.</i> 2006
	Potato	ScFv antibodies	<i>Potato virus Y</i> (PVY)	Gargouri-Bouزيد <i>et al.</i> 2006
	Tobacco	ScFv antibodies	<i>Tomato bushy stunt virus</i> (TBSV)	Boonrod <i>et al.</i> 2004

Transgenics to combat nematode pathogens

Nematodes are the principal obligate parasites of plants causing >\$100 billion each year in global agriculture (Chitwood 2003). Improved plant resistance to parasitic nematodes is highly desirable to reduce the need for nematicides, some of which belong to the most unacceptable pesticides used in agriculture. Of the several possible approaches based on anti-invasion and migration, feeding-cell attenuation and anti-nematode feeding, developing transgenic plants with improved nematode resistance is a promising one (Atkinson *et al.* 1995).

Multiple studies have demonstrated that transgenic expression of a modified version of oryzacystatin, *Oc-1ΔD86*, can interfere with nematode replication (Urwin *et al.* 1995). In *Arabidopsis thaliana*, expression of *Oc-1ΔD86* using the cauliflower mosaic virus (CaMV35S) promoter and infection with the beet cyst nematode (*Heterodera schachtii*) resulted in adult females that were greatly diminished in size relative to controls (Urwin *et al.* 1997). Similarly, infection of transgenic plants with root-knot nematode (*Meloidogyne incognita*) resulted in fewer full size adults (Urwin *et al.* 1997). However, using same genes in transformation of potato plants and challenged with potato cyst nematode (*Globodera pallida*) in a field trial resulted in a 55-70% decrease in cyst number. Though, cysts formed were of normal size with a similar number of eggs to control, suggesting the potential for escape from digestive disruption. Transgenic banana plants expressing *Oc-1ΔD86* from the maize *ubiquitin* gene promoter and challenged with burrowing nematode (*Radopholus similis*) in greenhouse trials identified eight of 115 lines that expressed the protein and showed substantial control (Atkinson *et al.* 2004).

Bacillus thuringiensis bacteria produce specific toxins (*Cry* proteins) which have shown nematicidal properties (Schnepf *et al.* 2003) and testing of a *Bt* panel against free-living nematodes demonstrated the nematicidal activity of *Cry5B*, *Cry6A*, *Cry14A*, and *Cry21A* against various plant parasitic nematodes (Wei *et al.* 2003). Griffiths *et al.* (2005) reported that *Cry5B* interacts with the luminal surface of the *C. elegans* intestine via an invertebrate-specific glycolipid, loss of which conveys resistance, while expression of codon-optimized *Cry6A* in transgenic tomato roots by the CaMV35S promoter reduced 56-76% egg production in

Meloidogyne incognita (Li *et al.* 2007).

Plant resistance (*R*) genes have been the underlying basis for successes in breeding efforts generating nematode-resistant tomato, soybeans, tobacco and other crops with pronounced economic benefits (Starr *et al.* 2002). One classical example is the tomato *Mi 1.2* gene (Milligan *et al.* 1998; Vos *et al.* 1998), which encodes a leucine-rich repeat protein and confers resistance to three *Meloidogyne* species as well as aphids and white flies. *Mi 1.2* can be transgenically expressed and provide *Meloidogyne* resistance in some tomato-related plant species (such as eggplant) but not in others (Goggin *et al.* 2006). *Mi 1.2* is likely part of a surveillance cascade that detects a specific nematode factor and triggers localized host cell death where giant-cells would normally form near the head of the invading J₂ worm.

Winter *et al.* (2002) demonstrated that the acetylcholinesterase-blocking nematicide aldicarb interferes with *H. glycines* chemosensation at a 1,000,000-fold lower dose (1 picomolar) than was required for inhibition of locomotion, indicating that disruption of chemosensation is likely a key feature of aldicarb's efficacy. Expression of the aldicarb-like peptides as secretory products in transgenic potato resulted in root exudates with acetylcholinesterase-blocking activity, which in greenhouse trials reduced *Globodera pallida* infection with cyst number declining 36-48% relative to vector controls (Liu *et al.* 2005). Peptide mimics of levamisole also reduced *Globodera* infection in a potato hairy root system. Similar results were obtained by Marra *et al.* (2009) who introduced a cysteine proteinase prodomain, obtained from *Heterodera glycines* (HGCP prodomain), into soybean cotyledons; there was a significant reduction in the soybean cyst nematode population.

Besides conventional transgenic technology, Mann *et al.* (2008) described the potential application of RNA interference as an eco-friendly tool for the management of plant parasitic nematodes. Though, the first published demonstration of transgenic plants with RNAi-based resistance to plant-parasitic nematode infection was reported by Yadav *et al.* (2006) for tobacco challenged with *Meloidogyne incognita*. Expression of dsRNA for a *Meloidogyne* splicing factor protein decreased gall formation and nematode reproduction almost entirely. Subsequent demonstration of RNAi-based resistance has come from work by Huang *et al.* (2006) for *Arabidopsis* challenged with *M. incognita*, *M.*

Table 5 Transgenic crops engineered for enhanced resistance against nematodes.

Transgenic crop	Gene/gene product	Donor	Target nematode	References
Tomato	Cysteine proteinase inhibitor (<i>CeCPI</i>)	<i>Colocasia esculenta</i>	<i>Meloidogyne incognita</i>	Chan <i>et al.</i> 2010
Brinjal	<i>cry1Ab</i>	<i>Bacillus thuringiensis</i> (Berliner)	<i>M. incognita</i>	Phap <i>et al.</i> 2010
Soybean	cysteine proteinase (CPs) propeptide	<i>Heterodera glycines</i>	<i>H. glycines</i>	Marra <i>et al.</i> 2009
Tomato	<i>chi 11</i>	<i>Oryza sativa</i>	<i>M. incognita</i>	Kalaiarasan <i>et al.</i> 2008
Tomato	<i>Cry6A</i>	<i>Bacillus thuringiensis</i> (Berliner)	Root knot nematode	Li <i>et al.</i> 2007
Tomato	<i>CaMi</i>	Hot pepper (<i>Capsium annuum</i> L.)	<i>Meloidogyne</i> spp.	Chen <i>et al.</i> 2007
<i>Arabidopsis thaliana</i>	<i>16D10</i>	<i>Arabidopsis thaliana</i>	<i>M. incognita</i> , <i>M. javanica</i> , <i>M. arenaria</i> , and <i>M. hapla</i>	Huang <i>et al.</i> 2006
<i>Triticum durum</i> (cv. PDW215)	<i>pin2</i>	Potato	<i>Heterodera avenae</i>	Vishnudasan <i>et al.</i> 2005
Banana	Oc-1ΔD86	Maize	<i>Radopholus similis</i>	Atkinson <i>et al.</i> 2004
Pine apple	Oc-1ΔD86	Maize	<i>M. incognita</i>	Urwin <i>et al.</i> 2000
<i>A. thaliana</i>	protease inhibitors	-	<i>Rotylenchulus reniformis</i>	Urwin <i>et al.</i> 2000
Rice	Oc-1ΔD86	Maize	<i>M. incognita</i>	Vain <i>et al.</i> 1998
Tomato	<i>Mi-1</i>	<i>S. peruvianum</i>	<i>M. incognita</i>	Milligan <i>et al.</i> 1998
<i>A. thaliana</i>	Cystatin, <i>Oc-I delta D86</i>	Rice	<i>Heterodera schachtii</i> and <i>M. incognita</i>	Urwin <i>et al.</i> 1997

javanica, *M. arenaria*, and *M. hapla*. Expression of dsRNA for a secreted *Meloidogyne* parasitism gene *16D10* decreased eggs per gram of root by 69–93%. Sanghera *et al.* (2010) reviewed the potential exploitation of RNAi in commercial nematode control through transgenic plant-delivered dsRNA. Some examples showing the utilization of transgenic technology to develop nematode-tolerant lines in different crops are listed in **Table 5**.

TRANSGENICS FOR AMELIORATION TO ABIOTIC STRESS TOLERANCE

Abiotic stresses present a major challenge in our quest for sustainable food production, as these may reduce the potential yields by 70% in crop plants (Katiyar-Agarwal *et al.* 2006). Drought and salinity stresses also limit crop production even under irrigated conditions (Chinnusamy *et al.* 2006). Many bacterial genes involved in different environmental stresses have been identified and engineered. The expression of certain bacterial stress-related proteins in plants may directly or indirectly protect plants against specific environmental stresses such as drought, high salinity, high UV radiation and low temperature. As the role of different bacterial genes in stress adaptation becomes known, genetic transformations strategies have been devised to improve abiotic stress tolerance in economically important crops and are detailed below.

Transgenics for drought tolerance

Drought is the most significant environmental stress in agriculture worldwide and improving yield under drought is a major goal of plant breeding (Cattivelli *et al.* 2008). Nevertheless, direct selection for grain yield under water-stressed conditions has been hampered by low heritability, polygenic control, epistasis, significant genotype by-environment (G × E) interaction and quantitative trait loci (QTLs)-by-environment (QTL × E) interaction (Gosal *et al.* 2009; Ashraf 2010; Sanghera *et al.* 2010). In recent years, crop physiology and genomics have led to new insights in drought tolerance providing plant engineers with new knowledge and tools for crop improvement (Tuberosa and Salvi 2006). Efforts have been made during the last few decades to generate transgenic lines of different crops, showing enhanced tolerance to drought stress (**Table 6**). The major emphasis of agricultural scientists has been on engineering genes that encode compatible organic osmolytes, plant growth regulators, antioxidants, heat-shock and late embryogenesis abundant proteins, and transcription factors involved in gene expression (Gosal *et al.* 2009; Ashraf 2010).

Compatible organic solutes play a central role in plant drought tolerance (Ashraf and Foolad 2007). Overproduction of such compatible organic osmolytes (glycine betaine, proline, trehalose, etc.) is one of the prominent responses of plants exposed to osmotic stress (Serraj and Sinclair 2002) and the genes encoding the synthesis of such organic solutes can be engineered to enhance the production of these solutes in transgenic plants. Glycine betaine (GB) is a quaternary ammonium compound, known to play a substantial role in stress tolerance and accumulated in response to dehydration stress within a plant system (Mansour 2000; Mohanty *et al.* 2002; Yang *et al.* 2003). The biosynthesis of GB in higher plants is controlled by two enzymes viz. choline monooxygenase (CMO) and betaine aldehyde dehydrogenase (BADH).

Multiple studies showed genes encoding CMO enzymes have been engineered. These transgenic lines showed higher accumulation of GB under water limited conditions and hence enhanced drought tolerance (Shen *et al.* 2002; Zhang *et al.* 2008). A potential maize inbred line DH4866 was transformed with the *E. coli betaA* gene encoding choline dehydrogenase (Quan *et al.* 2004). The transformed maize plants contained higher levels of GB and showed higher tolerance to drought as compared to wild-type plants when tested at the initial growth stages.

Like GB, proline is also an important compatible organic osmolyte that plays a key role in stress tolerance. Pyrroline-5-carboxylate synthetase (*P5CR*) is the key enzyme for proline biosynthesis. The gene for this enzyme has been engineered in soybean (Ronde *et al.* 2004), petunia (Yamada *et al.* 2005) and tobacco (Gubis *et al.* 2007). All these transgenic lines showed enhanced accumulation of proline as well as high drought tolerance.

Trehalose, a non-reducing sugar, is also a potential organic osmolyte which has a substantial role in the protection of plants against stresses. However, transgenic lines of different crops have been generated using the genes of some key enzymes involved in trehalose biosynthesis. For example, enhanced drought tolerance has been achieved by transforming the gene *TPS1* for trehalose-6-phosphate synthase in tobacco (Romero *et al.* 1997; Karim *et al.* 2007). Enhanced drought tolerance has also been observed in transformed rice plants expressing chimeric gene *Ubi1::TPSP* due to increased accumulation of trehalose (Jang *et al.* 2003). In these studies and some other reported in the literature, engineering constitutive over-expression of genes encoding TPS and/or TPP (trehalose-6-phosphate phosphatase) resulted in enhanced trehalose accumulation as well as drought tolerance. However, the main problem with such transformation had been that it led to abnormal plant development under normal growth conditions, because the gene transformed remained turned on all the time. To resolve this problem, Wu and Garg (2003) alternatively adopted another way to engineer enhanced trehalose accumulation in such a manner that trehalose biosynthesis took place only when the plant encountered abiotic stress. They employed a stress-inducible promoter for the over-expression of *E. coli* trehalose biosynthesis genes (*otsA* and *otsB*) as fusion gene (*TPSP*, trehalose-6-phosphate synthase phosphatase) for developing abiotic stress tolerance in rice. It is pertinent to note here that the *TPSP* fusion gene transformation resulted in normal growth under non-stress conditions, but the expression of the fusion gene occurred only under stress conditions. In another study, a *TPS1-TPS2* fusion gene construct was incorporated into *Arabidopsis thaliana* through *Agrobacterium* using either the 35S or the stress regulated *rd29A* promoter (Miranda *et al.* 2007). The lines over-expressing the *TPS1-TPS2* construct showed normal growth as well as enhanced tolerance to multiple stresses such as salinity, drought, freezing, and high temperature. Mannitol is another important osmo-protectant that plays a vital role in plant stress tolerance. However, attempts have been made to achieve improved drought tolerance by the over-expression of mannitol in plants by engineering genes involved in the biosynthesis of mannitol. Tobacco plants transformed with a mannitol-1-phosphate dehydrogenase gene resulted in enhanced mannitol accumulation, but enhanced mannitol accumulation did not affect osmotic adjustment or drought tolerance in the transformed plants as compared to those in the untransformed plants (Karakas *et al.* 1997).

Drought stress also leads to increased accumulation of reactive oxygen species (ROS) in plants thus causing an oxidative stress. To counteract these ROS, plants can intrinsically develop different types of antioxidants (Pastori and Foyer 2002; Sunkar *et al.* 2006). Genes encoding different types of antioxidants have been engineered in different plants for achieving enhanced drought tolerance. For example, engineering of the gene SOD encoding superoxide dismutase caused enhanced drought tolerance in potato (Perl *et al.* 1993), alfalfa (McKersie *et al.* 1997) and rice (Wang *et al.* 2005). Transgenic lines of tobacco produced by over-expressing the *monodehydroascorbate reductase* (*MDAR*) gene from *Arabidopsis* showed a 2.1-fold higher *MDAR* activity and 2.2-fold higher level of reduced ascorbic acid than that in non-transformed plants (Eltayeb *et al.* 2007). Further, Liu *et al.* (2008) generated transgenic tobacco plants over-expressing *VTE1* gene encoding tocopherol cyclase (*VTE1*), a key enzyme of tocopherol biosynthesis. The transformed plants exhibited enhanced drought tolerance which was associated with decreased electrolyte leakage,

Table 6 Drought tolerance transgenic plants expressing genes involved organic osmolytes, transcription factors, late embryogenesis proteins and hormones.

Transgenic crop	Gene	Gene product	Donor	Remarks	Reference
Cotton	<i>AVP1</i>	Vacuolar pyrophosphatase	<i>Arabidopsis</i>	20% higher fibre yield of AVP1-expressing cotton plants, improved tolerance to both drought and salt stresses	Pasapula <i>et al.</i> 2010
Tomato (<i>Lycopersicon esculentum</i> L.)	<i>SINAGS1</i>	<i>N</i> -acetyl-glutamate synthase	<i>Arabidopsis thaliana</i> L.	Improved germination ability and higher accumulation of ornithine	Kalamaki <i>et al.</i> 2009
Tobacco (<i>Nicotiana tabacum</i> L.)	BhLEA1 and BhLEA2	<i>Boea hygrometrica</i> late embryogenesis abundant proteins	<i>Boea hygrometrica</i>	The relative water content of leaves and activities of photosystem II, superoxide dismutase and peroxidase increased, while membrane permeability decreased in transgenic plants	Liu <i>et al.</i> 2009
Rice (<i>Oryza sativa</i> L.)	<i>OsRACK1</i>	Receptor for activated C-kinase 1	Rice (<i>Oryza sativa</i> L. subsp. Japonica cv. Nipponbare	Reduced membrane peroxidation and production of malondialdehyde, while enhanced activity of superoxide dismutase in transgenic rice plants, RACK1 negatively regulated the redox system-related tolerance to drought stress	Li <i>et al.</i> 2009
Rice (<i>Oryza sativa</i> L.)	<i>TaSTRG</i>	<i>Triticum aestivum</i> salt tolerance gene	<i>Triticum aestivum</i> L.	Improved plant survival rate, fresh weight, chlorophyll content, higher praline, and soluble sugar contents, and significantly higher expression of putative praline synthetase and transporter genes than the non-transgenic plants	Zhou <i>et al.</i> 2009
Rice (<i>Oryza sativa</i> L.)	<i>AP37</i> and <i>OsCc1</i>	Transcription factor (encoding <i>Oryza sativa</i> cytochrome c gene	Rice (<i>Oryza sativa</i> L.)	Improved grain filling rate and grain yield (16-57%) and drought tolerance of transgenic plants	Oh <i>et al.</i> 2009
<i>Arabidopsis thaliana</i> L.	<i>MYB15</i>	R2R3 MYB transcription factor	<i>Arabidopsis thaliana</i> L.	Transgenic lines were hypersensitive to ABA in germination assays, more susceptible to ABA-elicited inhibition of root elongation, and more sensitive to ABA-induced stomatal closure. The transcript levels of ABA biosynthesis, signaling and responsive genes were generally higher in the seedlings of transgenic plants than those in wild types	Ding <i>et al.</i> 2009
Peanut (<i>Arachis hypogaea</i> L.)	<i>AtDREB1A</i>	<i>Arabidopsis thaliana</i> dehydration-responsive element-binding protein	<i>Arabidopsis thaliana</i> L.	Enhanced activities of superoxide dismutase, ascorbate peroxidase, and glutathione reductase and enhanced praline level in the transgenic plants, while a dramatic increase in the lipid peroxidation was observed in the untransformed controls under water limited conditions	Bhatnagar-Mathur <i>et al.</i> 2009
Tobacco (<i>Nicotiana tabacum</i> L.)	<i>BvCMO</i>	Choline monoxygenase	Beet (<i>Beta vulgaris</i>)	Higher accumulation of glycinebetaine in leaves, roots and seeds. Transgenic line exhibited improved tolerance to toxic level of choline and drought and stress	Zhang <i>et al.</i> 2008
Tobacco (<i>Nicotiana tabacum</i> L.)	<i>VTE1</i>	Tocopherol cyclase	<i>Arabidopsis thaliana</i> L.	Lower lipid peroxidation, electrolyte leakage and H ₂ O ₂ content, while higher chlorophyll and tocopherol contents in transgenic plants as compared to wild type	Liu <i>et al.</i> 2008
Mulberry (<i>Morus indica</i>)	<i>HVA1</i>	Late embryogenesis abundant protein	Barley (<i>Hordeum vulgare</i> L.)	The transgenic plants showed better membrane stability (CMS), photosynthetic yield, less photo-oxidative damage and better water use efficiency under drought stress	Lal <i>et al.</i> 2008
Tobacco (<i>Nicotiana tabacum</i> L.)	Ta-Ub2	<i>Triticum aestivum</i> ubiquitin 2	Wheat (<i>Triticum aestivum</i> L.)	Faster germination, seedlings grew vigorously under water deficit conditions, improved CO ₂ assimilation rate of transgenic plants both under drought and non-drought conditions	Guo <i>et al.</i> 2008
Tobacco (<i>Nicotiana tabacum</i> L.)	<i>P5CSF129A</i> and <i>nptII</i>	??-pyrroline-5-carboxylate synthetase and neomycine phosphotransferase	<i>Vigna acontifolia</i>	Transgenic plants accumulated high levels of praline and chlorophyll content and were better adapted to water stress	Gubis <i>et al.</i> 2007
Tobacco (<i>Nicotiana tabacum</i> L.)	<i>TPS1</i> and <i>TPS2</i>	Trehalose-6-phosphate synthase 1 and 2	<i>Saccharomyces cerevisiae</i>	Enhanced drought tolerance by water retention and root development	Karim <i>et al.</i> 2007
<i>Triticum aestivum</i> L. cv. CD200126	<i>P5CS</i>	Pyrroline-5-carboxylate synthetase	<i>Vigna acontifolia</i>	Improved drought tolerance was mainly due to protection against oxidative stress; praline accumulation was high in transgenic plants	Vendruscolo <i>et al.</i> 2007
Tall fescue (<i>Festuca arundinacea</i> Schreb.)	<i>DREB1A/CBF3</i>	Dehydration-responsive element-binding protein	<i>Arabidopsis thaliana</i> L.	Transgenic plants showed increased resistance to drought and high praline accumulation	Zhao <i>et al.</i> 2007
<i>Arabidopsis thaliana</i> L.	<i>CaXTH3</i>	<i>Capsicum annuum</i> xyloglucan endotransglucosylase/hydrolase	Pepper (<i>Capsicum annuum</i> L. cv. Pukang)	Transgenic plants exhibited abnormal leaf morphology, showed variable twisting and bending along the edges, resulting in a severely wrinkled leaf shape resulting in a marked improvement in tolerance to severe water deficit conditions	Cho and Hong 2006
Rice (<i>Oryza sativa</i> L.)	<i>Mn-SOD</i>	Manganese superoxide dismutase	Pea (<i>Pisum sativum</i> L.)	Reduced electrolyte leakage, injury, oxidative damage, while improved photosynthetic rate, SOD activity and drought tolerance	Wang <i>et al.</i> 2005
<i>Arabidopsis thaliana</i> L. and <i>Oryza sativa</i> L.	<i>AtP5CS</i> or <i>OsP5CS</i>	Pyrroline-5-carboxylate synthetase	Petunia (<i>Petunia hybrida</i> cv. Mitchell	Transgenic plants accumulated 1.5-2.6 times greater praline and showed better growth than wild type plants under drought stress	Yamada <i>et al.</i> 2005
Tobacco (<i>Nicotiana tabacum</i> L.)	PsTP	<i>Pleurotus sajor-caju</i> trehalose phosphorylase	<i>Pleurotus sajor-caju</i>	Transgenic plants showed normal growth, and better capacity to retain water, while the wild type and the only empty vector-transformed control withered severely	Han <i>et al.</i> 2005

Table 6 (Cont.)

Transgenic crop	Gene	Gene product	Donor	Remarks	Reference
<i>Arabidopsis thaliana</i> L.	<i>AREB1</i>	Abscisic acid-responsive element-binding protein 1	<i>Escherichia coli</i>	AREB1 regulated novel ABRE-dependent ABA signaling that enhanced drought tolerance in vegetative tissues	Fujita <i>et al.</i> 2005
Soybean (<i>Glycine max</i> cv. Ibis)	P5CR	Pyrraline-5-carboxylate reductase	<i>Arabidopsis thaliana</i> L.	NADP ⁺ levels decreased in wild type/ antisense, while increased in transgenic/sense plants. Sense plants accumulated highest amount of praline	Ronde <i>et al.</i> 2004
<i>Zea mays</i> L. inbred line DH4866	<i>betA</i>	Choline dehydrogenase	<i>Escherichia coli</i>	Higher accumulation of glycinebetaine, more tolerant to drought stress at germination stage and the young seedling stage. Most importantly, improved grain yield, integrity of the cell membrane and activities of enzymes under drought stress	Quan <i>et al.</i> 2004
<i>Nicotiana tabacum</i> L. cv. SR-1	<i>APX5</i>	Ascorbate peroxidase	<i>Arabidopsis thaliana</i> L.	Enhanced net photosynthetic rate, 3.8 fold higher level of APX activity, while reduced toxicity of H ₂ O ₂ in transgenic plants	Badawi <i>et al.</i> 2004
Rice (<i>Oryza sativa</i> L.)	<i>TPSP</i> (fusion gene of <i>otsA</i> and <i>otsB</i>)	Trehalose-6-phosphate synthase or phosphatase	<i>Escherichia coli</i>	The genetically-engineered rice plants produced higher amounts of trehalose, exhibited sustained plant growth, less photo-oxidative damage, and more favorable mineral balance under drought stress conditions	Wu and Garg 2003
Wheat (<i>Triticum aestivum</i> L.)	<i>mt1D</i>	Mannitol-1-phosphate dehydrogenase	<i>Escherichia coli</i>	Improved fresh and dry weights, plant height, and flag leaf length in transgenic plants	Abebe <i>et al.</i> 2003
Tobacco (<i>Nicotiana tabacum</i> L.)	AhCMO	Choline monoxygenase	<i>Atriplex hortensis</i>	Improved drought tolerance by accumulating higher amount of glycinebetaine	Shen <i>et al.</i> 2002
<i>Zea mays</i>	<i>zm-Asr1</i>	<i>Zea mays</i> ABA/ water stress/ ripening induced protein	Sorghum (<i>Sorghum bicolor</i>)	Transgenic plants showed increased intrinsic water use efficiency accompanied by a dry weight increase under drought conditions	Jeanneau <i>et al.</i> 2002
Ryegrass (<i>Lolium multiflorum</i> Lam.)	<i>sacB</i>	<i>Bacillus subtilis</i> chimeric gene	<i>Bacillus subtilis</i>	Transgenic plants had a lower level of total fructose, unchanged sucrose levels and a slight reduction in hexose levels. However, growth of the levan-accumulating <i>sacB</i> -transgenic plants was decreased with the onset of reproductive phase	Ye <i>et al.</i> 2001
<i>Arabidopsis thaliana</i> L.		Ssuperoxide dismutase and Ascorbate peroxidase	Alfalfa (<i>Medicago sativa</i> L.)	Improved seed germination, plant growth, osmotic adjustment, and activities of superoxide dismutase and ascorbate peroxidase	Luo <i>et al.</i> 2000
Tobacco (<i>Nicotiana tabacum</i> L.)	<i>mt1D</i>	Mannitol-1-phosphate dehydrogenase	<i>Escherichia coli</i>		Karakas <i>et al.</i> 1997
Tobacco (<i>Nicotiana tabacum</i> L.)	<i>TPSI</i>	Trehalose-6-phosphate synthase	<i>Escherichia coli</i>	Trehalose accumulating plants exhibited multiple phenotypic alterations including stunted growth, lancet-shaped leaves, reduced sucrose content and improved drought tolerance	Romero <i>et al.</i> 1997

lipid peroxidation and H₂O₂ content, but increased chlorophyll content compared with the non-transformed plants.

Late embryogenesis abundant (LEA) proteins play a vital role in plant protection against the adverse effects caused by drought stress (Hong *et al.* 2005; Gosal *et al.* 2009). Efforts have been made during the last two decades to engineer LEA genes for enhanced plant drought tolerance. For example, engineering the LEA genes *PMA1959* and *PMA80* from wheat and transformed in rice resulted in enhanced drought tolerance (Cheng *et al.* 2002). Similarly, a LEA gene *HVA1* from barley was engineered in rice (Xu *et al.* 1996), and wheat (Sivamani *et al.* 2000). Both rice and wheat transformed lines so produced showed enhanced tolerance to drought stress. In two independent studies, a LEA protein gene *ME-lea N4* from *Brassica napus* was transferred through *Agrobacterium* to lettuce (*Lactuca sativa* L.) (Park *et al.* 2005a) and Chinese cabbage (*Brassica campestris* Pekinensis) (Park *et al.* 2005b) using the CaMV 35S promoter. The transgenic lines of both crops showed enhanced tolerance to drought. Another LEA protein gene *OsLEA 3-1* has been incorporated into rice via *Agrobacterium* under the operation of different promoters (Xiao *et al.* 2007). The rice transgenics developed particularly under the control of constitutive CaMV 35S and stress-inducible *HVA1* promoters showed enhanced drought tolerance when tested under natural field conditions.

Jeanneau *et al.* (2002) examined the role of an ABA and drought regulated maize gene *ASR1* coding for an ABA stress ripening protein, and the effect of photosynthesis regulation through the ectopic expression of the *S. bicolor*

C4-phosphoenolpyruvate carboxylase gene, *C4-PEPC*, in transgenic maize. The transgenic maize lines so produced showed enhanced photosynthetic capacity, water use efficiency as well as high biomass production under mild water deficit conditions. Transgenic expression of *MYB15*, encoding a transcription factor, *R2R3 MYB*, in *Arabidopsis*, showed considerable sensitivity to exogenous ABA and enhanced tolerance to drought (Ding *et al.* 2009).

Transcription factors are specific types of proteins that bind DNA and are involved in the regulation of gene transcription, hence gene regulation. Several transcription factors have been identified, which are involved in gene regulation in plants under water limited conditions (Bartels and Sunkar 2005; Vinocur and Altman 2005). Of a number of transcription factors listed elsewhere (Gosal *et al.* 2009), dehydration-responsive element-binding factors (*DREB*) have attracted the attention of many plant researchers since Jaglo-Ottosen *et al.* (1998) and Liu *et al.* (1998) first reported the up-regulation of many genes in *DREB1/CBF* transgenic *Arabidopsis* involved in tolerance to a variety of stresses. Transgenic *Arabidopsis* plants over-expressing *DREB1/CBF3* operated by the constitutive promoter CaMV 35S also exhibited improved tolerance to drought (Kasuga *et al.* 1999). Introduction of *DREB1A* into wheat driven by *rd29A* promoter resulted in enhanced drought tolerance (Pellegrineschi *et al.* 2004). Ecotypic expression of *Arabidopsis DREB1A/(CBF3)* into transformed rice plants under the operation of constitutive promoter CaMV 35S, resulted in improved tolerance to drought (Oh *et al.* 2005). In maize, over-expression of *ZmDREB2A* under the control of consti-

tutive or stress-inducible promoter resulted in enhanced drought tolerance in plants (Qin *et al.* 2007). Bhatnagar-Mathur *et al.* (2009) generated transgenic plants of peanut over-expressing *Arabidopsis AtDREB1A*, driven by a stress-inducible promoter, *Atrd29A*.

Apart from *DREB*, other transcription factors are also known to be involved in plant stress responses. One such type is that with *APETELA2* (*AP2*)-domain. Oh *et al.* (2009) identified 42*AP2* genes in rice, which are triggered by various stresses including salinity, drought, freezing, and ABA. The transformed rice plants over-expressing *AP37* and *AP59* under the operation of the constitutive promoter *OsCcl* showed enhanced resistance to high drought at the vegetative growth stage. However, compared to *OsCcl:AP59* plants, *OsCcl:AP37* plants showed considerably higher tolerance to drought by producing 16–57% more grain yield than non-transgenic controls under severe drought conditions of the field. Recently, Jeong *et al.* (2010) reported the results of a functional genomics approach that identified a rice NAC (an acronym for *NAM* [No Apical Meristem], *ATAF1-2*, and *CUC2* [Cup-Shaped Cotyledon]) domain gene, *OsNAC10*, which improved performance of transgenic rice plants under field drought conditions. Overexpression of *OsNAC10* in rice under the control of the constitutive promoter *GOS2* and the root-specific promoter *RCc3* increased the plant tolerance to drought, high salinity, and low temperature at the vegetative stage. More importantly, the *RCc3:OsNAC10* plants showed significantly enhanced drought tolerance at the reproductive stage, increasing grain yield by 25 to 42% and by 5 to 14% over controls in the field under drought and normal conditions, respectively.

Wei *et al.* (2010) reported that maize plants transgenic for both *betaA* (encoding choline dehydrogenase from *Escherichia coli*) and *TsVP* (encoding V-H⁺-PPase from *Thellungiella halophila*) were produced by cross-pollination. The existence of the transgenes in the pyramided plants was demonstrated by PCR and Southern blotting. The examination of the drought resistance characteristics demonstrated that the pyramided transgenic plants had higher glycinebetaine contents and H⁺-PPase activity compared with the parental lines, which had either *betaA* or *TsVP*, and contained higher relative water content (RWC), greater solute accumulation and lower cell damage under drought stress treatment. The pyramided plants grew more vigorously with less growth retardation, shorter anthesis-silking interval and higher yields than their parental lines and the wild-type. However, most of the transgenic lines of different crops were tested under controlled laboratory or glasshouse conditions in which remarkable performance under simulated stress conditions were shown. Most drought-tolerant transgenic lines of different crops developed are based on only a single gene transformation (Table 6), and where the claims of the authors regarding the performance of the lines with respect to drought tolerance seems to be overstated, although manipulation of a number of genes predominantly involved in drought tolerance to transgenic plants seems to be a plausible approach that allows pyramiding of desirable traits to achieve considerable advance in crop drought tolerance.

Transgenics for salt tolerance

It is estimated that 20% of the irrigated land in the world is presently affected by salinity (Yamaguchi and Blumwald 2005; Ruan *et al.* 2010; Ruan and Teixeira da Silva 2011). Salinity imposes water deficit that results from the relatively high solute concentration in the soil, causes ion specific stresses resulting from altered Na⁺/K⁺ ratios, and leads to buildup in Na⁺ and Cl⁻ concentrations that are detrimental to growth and other life processes of plants (Vinocur and Altman 2005). Plant systems respond to salt stress by restricting the uptake of salt and adjust their osmotic pressure by the synthesis of compatible solutes (proline, glycinebetaine, sugars) (Greenway and Munns 1980) and

sequestering salt into the cell vacuoles for the maintenance of low cytosolic Na⁺ levels (Blumwald and Grover 2006). Transgenics that have shown a comparable level of salt tolerance to their wild types and are presented in Table 7.

Salt tolerance of transgenic tobacco engineered to over accumulate mannitol was first demonstrated by Tarczynski *et al.* (1993). The other examples of compatible solute genetic engineering includes the transformation of genes for ectoine synthesis with enzymes from the halophilic bacterium *Halomonas elongata* (Ono *et al.* 1999; Nakayama *et al.* 2000) and trehalose synthesis in potato (Yeo *et al.* 2000), rice (Garg *et al.* 2002), and sorbitol synthesis in plantago (*Plantago ovata* L.) (Pommerrenig *et al.* 2007).

Initial strategies aimed at engineering higher concentrations of proline began with the overexpression of genes encoding the enzymes pyrroline-5-carboxylate (*P5C*) synthetase (*P5CS*) and *P5C* reductase (*P5CR*). *P5CS* overexpression in transgenic tobacco dramatically elevated free proline (Kishor *et al.* 1995).

Hayashi *et al.* (1997) used choline oxidase of *Arthrobacter globiformis* to engineer glycinebetaine synthesis in *Arabidopsis* and subsequently tolerance to salinity during germination and seedling establishment was improved markedly in the transgenic lines. The enhancement of glycinebetaine syntheses in target plants has received much attention (Rontein *et al.* 2002). Huang *et al.* (2000) used COX from *Arthrobacter panescens*, which is homologous to the *A. globiformis* COD, to transform *Arabidopsis*, *B. napus* and tobacco. In this set of experiments COX protein was directed to the cytoplasm and not to the chloroplast. Improvements in tolerance to salinity, drought and freezing were observed in some transgenics from all three species, but the tolerance was variable. The results offered the possibility that the protection offered by glycinebetaine is not only osmotic but also function as scavengers of oxygen radicals.

Plants use antioxidants such reduced glutathione (GSH) and different enzymes such as superoxide dismutases (SOD), CAT, APX, glutathione-S-transferases (GST) and glutathione peroxidases (GPX) to scavenge ROS. Reduction of oxidative damage could provide enhanced plant resistance to salt stress. Transgenic tobacco plants overexpressing both GST and GPX showed improved seed germination and seedling growth under stress (Roxas *et al.* 1997). However, Xu *et al.* (1996) generated transgenic rice (cv. 'Nipponbare') over-expressing barley *hva1* gene encoding LEA protein and reported that the transgenic plants maintained a higher growth rate initially and showed better recovery on removal of salt stress. Further, Sakamoto *et al.* (1998) genetically engineered rice with the ability to synthesize GB by introducing the *codA* gene (encoding for choline oxidase obtained from *Arthrobacter globiformis*) and found that levels of GB were as high as 1 and 5 μmol per gram fresh weight of leaves in two types of transgenic plant in which choline oxidase was targeted to the chloroplasts (*ChlCOD* plants) and to the cytosol (*CytCOD* plants), respectively.

Saijo *et al.* (2000) generated transgenic rice (cv. 'Notohikari') plants over-expressing a Ca²⁺-dependent protein kinase (*OsCDPK7*). The youngest leaves wilted 3 days after salt stress of 200 mM NaCl in wild type plants, while transgenic plants exhibited greater tolerance. Mohanty *et al.* (2002) generated transgenic lines of indica rice Pusa basmati 1 (PB 1) by *Agrobacterium*-mediated transformation with *codA* gene. In this work, more than 50% of the transgenic plants could survive salt stress and set seed whereas the wild type plants failed to recover. Garg *et al.* (2002) generated transgenic indica rice PB 1, expressing the fusion gene comprising both trehalose-6-phosphate synthase and trehalose-6-phosphate phosphatase obtained from *Escherichia coli*. Compared to wild type rice, transgenic lines exhibited sustained plant growth, less photo-oxidative damage, and more favorable mineral balance under salt stress conditions. Jang *et al.* (2003) reported the generation of trehalose-producing, transgenic japonica rice plants by the introduction of a gene encoding a bifunctional fusion (*TPSP*) of

Table 7 Salt tolerant transgenic plants expressing genes involved in synthesis/over expression of ion transporters and compatible solutes.

Transgenic crop (Cultivar)	Gene	Gene product	Donor	Remark	Reference
Cotton	<i>AVP1</i>	Vacuolar pyrophosphatase	<i>Arabidopsis</i>	20% higher fibre yield of AVP1-expressing cotton plants, improved tolerance to both drought and salt stresses	Pasapula <i>et al.</i> 2010
Poplar (<i>Populus davidiana X P. bolleana</i>)	<i>TaMnSOD</i>	Superoxide dismutases	<i>Tamarix androssowii</i>	1.3–4-folds enhancement in SOD activity in transgenic plants, 8- to 23-fold increase in relative weight gains of the transgenic plants	Wang <i>et al.</i> 2010
Tobacco	<i>PcINO1</i> and <i>McIMT1</i>	<i>Myo</i> -inositol 1-phosphate synthase and inositol methyl transferase	<i>Porteresia coarctata</i> and <i>Mesembryanthemum crystallinum</i>	Elevated level of total inositol and methylated inositol and the capability of the double transgenic plants to withstand a higher degree of salt stress	Patra <i>et al.</i> 2010
Tobacco	<i>W6</i>	Ethylene responsive factor	Wheat (<i>Triticum aestivum</i> L.) landrace Xiaobaimei	Enhancement in superoxide dismutase activity and chlorophyll content in the transgenic plants	Lu <i>et al.</i> 2008
Rice (Cv. Pusa Basmati-1)	-	Cytosolic copper/zinc superoxide dismutase	<i>Avicennia marina</i>	Enhancement in SOD activity in transgenic plants	Prashanth <i>et al.</i> 2008
<i>Plantago major</i>	<i>PmSDH1</i>	Sorbitol dehydrogenase	<i>Plantago major</i>	Transgenic plants showed increased tolerance to salt stress	Pommerrenig <i>et al.</i> 2007
<i>A. thaliana</i>	<i>AtNHX1</i>	Vacuolar Na ⁺ /H ⁺ antiporter	<i>Festuca arundinacea</i>	Transgenic plants showed increased tolerance to salt stress as a result of Na ⁺ sequestration	Luming <i>et al.</i> 2006
Rice (Zhonghua no. 11)	<i>SOD2</i>	Vacuolar Na ⁺ /H ⁺ antiporter	<i>Saccharomyces pombe</i>	Transgenics had enhanced P-ATPase hydrolytic activity, increased photosynthesis and root proton exportation capacity, reduced ROS generation	Zhao <i>et al.</i> 2006a
Rice (Zhonghua no. 11)	<i>SsNHX1</i>	Na ⁺ /H ⁺ antiporter	<i>Suaeda salsa</i>	Transgenic plants increase salt stress resistance, which resulted from Na ⁺ sequestration; plants had an increase in H ⁺ -ATPase and H ⁺ -PPase activity, reduced ROS generation and increased photosynthesis	Zhao <i>et al.</i> 2006b
Rice (Zhongzhou 321)	<i>nhaA</i>	Na ⁺ /H ⁺ antiporter gene	<i>Escherichia coli</i>	Transgenics grew faster as compared to the wild types under stress conditions	Wu <i>et al.</i> 2005
Tobacco	<i>HbNHX1</i>	Vacuolar Na ⁺ /H ⁺ antiporter	<i>Hordeum brevisubculatum</i>	Transgenic plants showed increased tolerance to salt stress	Lu <i>et al.</i> 2005
Rice (Nipponbare)	<i>OsNHX1</i>	Na ⁺ /H ⁺ antiporter	<i>Oryza sativa</i>	Transgenic plants showed increased tolerance to salt stress	Fukuda <i>et al.</i> 2004
Rice	<i>TPS + TPP fusion</i>	Trehalose-6- phosphate synthase and T-6-P phosphatase	<i>Escherichia coli</i>	Trehalose levels in seeds and leaves were more in putative transgenic than control plants	Jang <i>et al.</i> 2003
<i>Arabidopsis</i>	<i>AtSOS1</i>	Plasma membrane Na ⁺ /H ⁺ antiporter	<i>Arabidopsis</i>	Transgenic plants showed increased tolerance to salt stress due to Na ⁺ extrusion	Shi <i>et al.</i> 2003
<i>Arabidopsis</i>	<i>SOD2</i>	Plasma membrane Na ⁺ /H ⁺ antiporter	<i>Schizosaccharomyces pombe</i>	Transgenic plants showed increased tolerance to salt stress due to Na ⁺ extrusion	Gao <i>et al.</i> 2003
Rice (Kinuhikari)	<i>AgNHX1</i>	Na ⁺ /H ⁺ antiporter gene	<i>Atriplex gmelini</i>	Transgenic plants survived under conditions of 300 mM NaCl for 3 days	Ohta <i>et al.</i> 2002
Rice (PB 1)	<i>codA</i>	Choline oxidase A	<i>Arthrobacter globiformis</i>	50% R1 plants survived after exposure to salt stress for 1 week	Mohanty <i>et al.</i> 2002
Rice (PB1)	<i>otsA + otsB (TPSP)</i>	Trehalose-6-phosphate synthase and trehalose-6-phosphate phosphatase	<i>Escherichia coli</i>	Transgenic plants showed enhanced tolerance both during and after stress and had longer and thicker roots	Garg <i>et al.</i> 2002
Tomato	<i>BADH</i>	Betaine dehydrogenase	<i>Atriplex hortensis</i>	Transgenic plants showed increased tolerance to salt stress	Jia <i>et al.</i> 2002
Tomato	<i>AtNHX1</i>	Vacuolar Na ⁺ /H ⁺ antiporter	<i>Arabidopsis</i>	Transgenic plants showed increased tolerance to salt stress	Zhang and Blumwald 2001
<i>Brassica napus</i>	<i>AtNHX1</i>	Vacuolar Na ⁺ /H ⁺ antiporter	<i>Arabidopsis</i>	Transgenic plants showed increased tolerance to salt stress	Zhang <i>et al.</i> 2001
Japanese permission	<i>Stpd1</i>	Sorbitol-6-phosphate dehydrogenase	Apple	Transgenic plants showed increased tolerance to salt stress	Gao <i>et al.</i> 2001
<i>Arabidopsis</i>	<i>AVP1</i>	Vacuolar H ⁺ -pyro-phosphatase	<i>Arabidopsis</i>	Transgenic plants showed increased tolerance to salt stress due to vacuolar acidification	Gaxiola <i>et al.</i> 2001
Tobacco	<i>betA</i>	Choline dehydrogenase	<i>E. coli</i>	Transgenic plants exhibited greater salt tolerance	Holmstrom <i>et al.</i> 2000
Rice (Kinuhikari)	<i>c-GS2</i>	Chloroplastic glutamine synthetase	<i>Oryza sativa</i>	over-expression reduced the increase of Na ⁺ content at high salinity	Hoshida <i>et al.</i> 2000
Tobacco	<i>EctA</i>	L-2,4-diaminobutyric acid acetyltransferase	<i>Halomonas elongata</i>	Transgenic plants exhibited greater salt tolerance	Nakayana <i>et al.</i> 2000
Rice (Notohikari)	<i>Oscdpk7</i>	Calcium-dependent protein kinase	<i>Oryza sativa</i>	Transgenic plants exhibited greater salt tolerance	Saijo <i>et al.</i> 2000
<i>Arabidopsis</i>	<i>ProDH</i>	Proline hydrogenase	<i>Arabidopsis thaliana</i>	Transgenic plants exhibited greater salt tolerance	Nanjo <i>et al.</i> 1999
Rice (Sasanishiki)	<i>Mn-SOD</i>	Superoxide dismutase	<i>Saccharomyces cerevisiae</i>	Transgenics showed enhanced tolerance to salt	Tanaka <i>et al.</i> 1999
<i>Arabidopsis</i>	<i>AtNHX1</i>	Vacuolar Na ⁺ /H ⁺ antiporter	<i>Arabidopsis</i>	Transgenic plants showed increased tolerance to salt stress	Apse <i>et al.</i> 1999

Table 7 (Cont.)

Transgenic crop (Cultivar)	Gene	Gene product	Donor	Remark	Reference
Rice (Nipponbare)	<i>ch-codA</i> , <i>cycodA</i>	Choline oxidase A	<i>Arthrobacter globiformis</i>	Transgenic plants had high levels of glycine betaine and grew faster compared to wild types on removal of stress	Sakamoto <i>et al.</i> 1998
<i>Arabidopsis</i>	<i>COX</i>	Choline oxidase	<i>Arthrobacter globiformis</i>	Transgenics showed enhanced tolerance to salt	Hayashi <i>et al.</i> 1997
Rice (Nipponbare)	<i>hva 1</i>	LEA protein	<i>Hordeum vulgare</i>	Transgenic seedlings maintained a higher growth rate during stress and plants showed faster recovery on removal of stress	Xu <i>et al.</i> 1996

the trehalose-6-phosphate (T-6-P) synthase (TPS) and T-6-P phosphatase (TPP) of *E. coli*, under the control of the maize *ubiquitin* promoter. Increased trehalose accumulation in transgenic plants resulted in increased tolerance to salt.

Considering that mechanisms that reduce cytosolic Na⁺ concentrations could provide a degree of tolerance to relatively low NaCl concentrations (Blumwald and Grover 2006). Ohta *et al.* (2002) engineered salt sensitive rice cultivar Kinhuikari using the Na⁺/H⁺ antiporter gene from *Atriplex gmelini* (*AgNHX1*). The activity of the vacuolar-type Na⁺/H⁺ antiporter in the transgenic rice plants was 8-fold higher than in wild type rice plants. Salt tolerance assays followed by non-stress treatments showed that the transgenic plants over-expressing *AgNHX1* could survive under conditions of 300 mM NaCl for 3 days while the wild type plants could not. Zhao and Zhang (2006) generated transgenic rice plants with *SsNHX1* from *Suaeda salsa* which showed markedly enhanced tolerance to salt stress compared with non transgenic controls grown under outdoor conditions. Yanga *et al.* (2009) produced six different transgenic *Arabidopsis* plants that overexpress *AtNHX1*, *SOS3*, *AtNHX1+SOS3*, *SOS1*, *SOS2+SOS3*, or *SOS1+SOS2+SOS3*. Northern blot analyses confirmed the presence of high levels of the relevant gene transcripts in transgenic plants and reported that transgenic *Arabidopsis* plants over-expressing *AtNHX1* alone did not present any significant increase in salt tolerance, contrary to earlier reports. However, transgenic plants overexpressing *SOS3* exhibit increased salt tolerance similar to plants overexpressing *SOS1*.

Recently, Patra *et al.* (2010) reported that co-expression of PcINO1 (L-*myo*-inositol 1-phosphate synthase or MIPS coding gene from the wild halophytic rice, *Porteresia caractata*) or McIMTI (inositol methyl transferase, IMTI coding gene from common ice plant *Mesembryanthemum crystallinum*) gene in transgenic tobacco plants either in cytosol or in chloroplasts accumulate higher amount of total inositol (free and methyl inositol) compared to non-transgenic plants. These transgenic plants were more competent in terms of growth potential and photosynthetic activity and were less prone to oxidative stress under salt stress. A positive correlation between the elevated level of total inositol and methylated inositol and the capability of the double transgenic plants to withstand a higher degree of salt stress compared to the plants expressing either PcINO1 or McIMTI alone. Additionally, Kim *et al.* (2010) reported that overexpression of *AtABCG36* improves drought and salt stress resistance in transgenic *Arabidopsis* and produced higher shoot biomass and less chlorotic leaves than the wild type.

TRANSGENICS FOR HERBICIDE RESISTANCE

The use of herbicides to reduce loss in crop yield due to weed competition has become an integral component of modern agriculture. Developments in plant genetic engineering and knowledge of biochemical action of herbicides on plants spurred innovative approaches to engineer crops to withstand herbicides. These strategies usually involve isolation and introduction of a gene from other organisms, mostly bacteria, which is able to overcome the herbicide-induced metabolic blockage (Kim *et al.* 1999). A number of

other genes have been identified that can alleviate the herbicide action through various ways (such as detoxification, sequestration, etc.) and thus confer resistance to the plants carrying them. Thus genetic engineering technology has made it possible to tailor crop varieties to resist specific herbicides by introducing relevant genes (Padgett *et al.* 1995). Consequently, the range of selective herbicides has now greatly expanded, wherein specific genotypes and varieties can confer resistance rather than generic crops displaying resistance to specific herbicides.

Over the last two decades, extensive efforts were put into generating glyphosate-resistant crops, culminating in the use of the *CP4* gene from *Agrobacterium* spp., which encodes a glyphosate-resistant form of 5-enolpyruvyl-shikimate-3-phosphate synthase (*EPSPS*) (Padgett *et al.* 1996). All commercial glyphosate-resistant crops except some maize varieties contain this gene. Glyphosate-resistant canola also contains a gene that encodes a glyphosate oxidoreductase (*GOX*) from the microbe *Achrobacterium anthropi* (strain LBAA). This enzyme degrades glyphosate to glyoxylate, a ubiquitous and safe natural product, and aminomethylphosphonate (*AMPA*), a non-toxic compound. However, accumulation of *AMPA* in glyphosate-resistant soybeans has been correlated with mild phytotoxicity to the crop (Reddy *et al.* 2004).

One of the first selectable transformation marker genes was the *bar* gene from *Streptomyces hygrosopicus*, the same organism that produces phosphinothricin, the natural form of glufosinate. This gene makes plants resistant to glufosinate by inactivating this herbicide through acylation (Thompson *et al.* 1987; Lydon and Duke 1999). To date, only five transgenes have been used in commercial crops to confer resistance to herbicides: *CP4*, *GOX* and the mutated maize *EPSPS* for glyphosate resistance, the gene encoding a nitrilase for bromoxynil resistance, and the *bar* gene for glufosinate resistance (Duke 2005).

FIELD TRIALS: SUCCESSES AND FAILURES

Data from the biotech industry suggest that since wide-scale planting started in 1996, the area of transgenic crops grown globally has increased from 2 to 134 Mha in 2009 (James 2009), of which 131 Mha are grown in eight countries: USA, Brazil, Argentina, India, Canada, China, Paraguay and South Africa. The release of the first transgenic events with insect resistance (*Bt*) (Bates *et al.* 2005) was not engineered to increase yield directly, but experience has shown that, by reducing losses from pests these varieties have in many cases delivered increased yields when compared with conventional crops. For *Bt* cotton, Fernandez-Cornejo and Caswell (2006) reported that the increases in cotton yields in the Southeast United States were associated with the adoption of HT and *Bt* cotton in 1997. The same authors quote a 2001 US government survey data showing that maize yield was 9% higher for *Bt* maize than for conventional maize. Gianessi (2008) reported the outcome of a study in Mississippi over 3 years, in which *Bt* cotton produced higher lint yields and had an economic advantage when compared with conventional cotton varieties. In China, *Bt* cotton was first approved in 1997 and by 2004 accounted for 69% of cotton grown in China, with 100%

adoption in Shandong province, where pest pressure was greatest (James 2008). Approval came later in India, in 2002, but as early as 2006, India's *Bt* cotton area exceeded that of China, and in 2008 accounted for 80% of India's cotton output (James 2009). Karihaloo and Kumar (2009) noted that between 2003–04 and 2006–07 cotton yields in India indicate a significant yield advantage of more than 30% with *Bt* cotton compared with conventional varieties with corresponding increase in farm income. Transgenic cotton that produced one or more *Bt* insecticidal proteins was planted on over 15 million ha in 11 countries in 2009 and has contributed to a reduction of over 140 million kg of insecticide active ingredient between 1996 and 2008. As a highly selective form of host plant resistance, *Bt* cotton effectively controls a number of key lepidopteran pests and has become a cornerstone in overall integrated pest management (IPM).

A study by Fernandez-Cornejo and McBride (2002) suggests that for HT soya bean, a 10% increase in adoption in the USA would lead to a 0.3% yield increase. Better results were obtained for HT corn where a 10% increase in adoption generated a 1.7% increase in yield and a 1.8% increase in net returns (Park *et al.* 2010). The Canola Council of Canada reported yield increases of up to 10% for transgenic compared with conventional varieties of canola. Direct comparison between mean yields of adopters versus non-adopters needs treating with caution as the adopters could be the more productive farmers anyway. HT Canola was grown commercially in Canada for the first time in 1997. Within 6 years of the transgenic varieties being available, over 90% of the area was HT Canola and the overall area of the crop grown had increased from 12 to 16 Mha. One of the main reasons for adoption was that HT canola is used as a 'cleaning crop'. In this way, the need for fallow is removed and farmers can have one more crop in the rotation.

CONCLUSION

The tremendous potential of biotechnology as an applied science that uses biological knowledge to meet practical needs and the great advantages that will come to humankind from its applications, makes it likely that GT technology will continue to flourish. It could be considered as the 'silver bullet' that will solve the problems of 21st century arising from abiotic and biotic stress including human malnutrition. To realize the full potential of this technology, concerted efforts in research and development are further needed to enhance the efficiency of various procedures/techniques used in different crops against multiple stresses, as witnessed with the success stories *Bt* cotton, brinjal, maize, canola, soybean, tobacco, etc. that have been transformed with one or more economic traits so far. Recent advances in the field of molecular biology and transgenic technologies have enabled the plant tailors to know the pitfalls regarding the expression of transgenes, emerging trends involving fusion proteins, deployment of antimicrobial peptides, stacked genes and various genes regulating metabolic pathways require special attention. Further, large-scale field trials are needed to test whether expression of the introduced genes will affect yields, quality, or agronomic traits. Although the introduced genes are well-defined, the field trials also provide the opportunity to ascertain whether any unexpected or undesirable consequences have resulted from the transformation procedure. Genetically engineered crops are just beginning to make their way into the hands of breeders. Their potential for changing the characteristics of plants have already been demonstrated to a great extent. It remains for the market place to put a value on those traits and, ultimately, on the technology that makes these changes possible.

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