Gene expression profiling of chickpea responses to drought, cold and high-salinity using cDNA microarray

A thesis submitted in fulfilment of the requirements for the degree of Doctor of Philosophy

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Declaration

I certify that except where due acknowledgement has been made, the work is that of the author alone; the work has not been submitted previously, in whole or in part, to qualify for any other academic award; the content of the thesis is the result of work which has been carried out since the official commencement date of the approved research program; and, any editorial work, paid or unpaid, carried out by a third party is acknowledged.

Nitin L. Mantri

30.08.2007
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It is sometimes difficult to express gratitude in words because the feelings go beyond them. These three years of my Ph.D. have changed the course of my thoughts and I have rediscovered myself with the help of some brilliant people I have been associated with.

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I appreciate the friendship, guidance and support of all my lab colleagues, in particular, Dr. Tristan Coram, Dr. Ruchira Jayasinghe, Yit Heng Chooi, Stephan Kong and Olivia Contarin.

I am indebted to my family, in particular my grandfather, who has been my model and provided me the opportunity and desire to succeed.
A cDNA microarray approach was taken to determine if the transcription of genes, from a set of putative stress-responsive genes from chickpea and its close relative grasspea (*Lathyrus sativus*), were altered in chickpea by the three abiotic stresses: drought, cold and high-salinity. For this, a cDNA microarray (Pulse Chip), constructed from chickpea unigenes, grasspea ESTs, and lentil RGAs, was firstly used to generate an expression profile of ICC 3996 (the donor of chickpea ESTs on the array) in response to drought, cold and high-salinity stresses to verify if the genes on the array responded to these abiotic stresses and showed meaningful expression profiles. Subsequently, the chickpea genotypes known to be tolerant and susceptible to each abiotic stress were challenged and gene expression in the leaf, root and/or flower tissues was studied. The transcripts that were differentially expressed (DE) among the stressed and unstressed plants in response to a particular stress were analysed in the context of their putative function and genotypes in which they were expressed. The purpose behind this was to interrogate how the genes on the array behaved in tolerant/susceptible genotypes under these abiotic stress conditions and perhaps aid in identification of putative candidates for tolerance/susceptibility to these stresses. The Pulse Chip array revealed 46, 54 and 266 ESTs as DE between stressed and unstressed ICC 3996 plants in response to drought, cold and high-salinity stresses, respectively. The putative role of these ESTs and associated pathways in response to drought, cold and high-salinity stresses is discussed. However, the identification of significant number of DE genes in response to these abiotic stresses provided the necessary impetus to explore the use of ‘Pulse Chip’ array for gene expression profiling of abiotic stress tolerant and susceptible genotypes. The transcriptional profiling of stress
tolerant and susceptible genotypes revealed 109, 210 and 386 transcripts as DE after drought, cold and high-salinity treatments, respectively. Among these, two, 15 and 30 transcripts were consistently DE in both the tolerant/susceptible genotypes under drought, cold and high-salinity stresses, respectively. The genes that were DE in tolerant and susceptible genotypes under abiotic stresses code for various functional and regulatory proteins. Significant differences in stress responses were observed within and between tolerant and susceptible genotypes highlighting the multiple gene control and complexity of abiotic stress response mechanism in chickpea. To sum up the findings of this study, the genes/pathways thought to be involved in abiotic stress tolerance mechanism of chickpea are presented. The mechanisms thought to confer drought tolerance to chickpea include delay of senescence, transport facilitation, induction of pollen tube growth, closure of stomata, suppression of CO₂ fixation, reduced energy capture, and via pathogenesis-related proteins. The mechanisms putatively involved in cold tolerance in chickpea include stress perception, Ca²⁺ signalling, regulation of ICE1, accumulation of osmolytes, delay of senescence, and transport facilitation. Subsequently, the mechanisms possibly contributing towards salt tolerance in chickpea are Ca²⁺ influx, ionic homeostasis, pH balance, suppression of aquaporins, suppression of lignification, delay of senescence, energy utilisation, and via pathogenesis-related proteins. However, these conclusions have been drawn based on previous reports on the possible role of these genes and therefore, need further confirmation via other techniques; e.g., knockouts/TILLING-mutants/overexpressing-transgenics. Nevertheless, this study is the first documentation of transcriptional profiling of chickpea in response to drought, cold and high-salinity stresses using cDNA microarray and shall aid the current and future research to understand abiotic stress tolerance mechanism in chickpea.
Thesis publications

Refereed Journals


Manuscript in preparation


Refereed Conference


Conference Poster

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Chapter 1

Introduction: Review of literature

This review is designed to shed light on the current state of knowledge regarding chickpea and the abiotic constraints that hinder its production; drought, cold and salinity. Firstly, the importance of chickpea is highlighted followed by an appraisal of the chief abiotic stresses (drought, cold and salinity) with respect to their impact, mechanisms of tolerance, and efforts to improve stress tolerance by classical breeding and molecular breeding. Thirdly, a review of how the new tools of functional genomics, specifically microarrays, promise to revolutionise the understanding of stress tolerance mechanisms and change the way stress tolerant genotypes are pursued is presented. Lastly, a detailed appraisal of cDNA microarray technology is followed by a section that highlights how microarray technology has been applied to understand more about the abiotic stress tolerance mechanisms.

In the review, the gaps in the current knowledge of abiotic stress tolerance of chickpea are identified and citations to some excellent reviews in the area are provided. The identified gaps form the basis of the PhD study and the reviewed tools and resources drive the rationale.

1.1 Chickpea

1.1.1 The crop

Chickpea (*Cicer arietinum* L.), also known as bengal gram, channa, garbanzo, cece, hommes, hamaz, nohud, lablabi, shimbra, katjang arab, gravanço, grão or grão de
bocca, is an edible legume (pulse). Chickpea is the only widely cultivated species of the
genus *Cicer* and belongs to the subfamily Faboideae of the Fabaceae family (Kupicha,
1981). The crop is a self-pollinated diploid (2n = 2x = 16) with a relatively small
genome size of 740 Mbp (Arumuganathan and Earle, 1991). Chickpea was among the
first grain crops to be cultivated, dating back to the eighth millennium BC (Zohary and
Hopf, 2000). Ladizinsky and Adler (1976) regarded *C. reticulatum* as the wild
progenitor of chickpea based on cytogenetical and seed protein analysis and
consequently nominated southeastern Turkey as its centre of origin. This claim was
supported by van der Maesen (1987) based on the presence of the closely related annual
species, *C. reticulatum* and *C. echinospermum* in southeastern Turkey.

1.1.2 Importance

The main use of chickpea is for human consumption and the seed provides an excellent
source of protein, especially for vegetarians or vegans (Taylor and Ford, 2007). The
seeds may be eaten as whole, split into halves after removing the seedcoat (dhal),
processed into flour (besan) or the young shoots may be eaten as a vegetable
(Muehlbauer and Tullu, 1997). Based on the seed type, two different trade classes are
recognised, *viz.*, *desi* and *kabuli* (Kearns, 1991; Carter, 1999). The *desi* chickpea are
usually decorticated and processed into flour while the *kabuli* type are used as whole
grains (Millan *et al.*, 2006). *Desi* chickpea has traditionally been used in the Indian
subcontinent as a dhal (milled seeds) or the flour is used to make a variety of snacks and
sweets.

Chickpea has one of the highest nutritional compositions of any dry edible grain legume
(Ahmad *et al.*, 2005). Chickpea seed contain approximately 20-30% protein, 40%
carbohydrate and 3-6% oil (Gil et al., 1996) and are a rich source of minerals (Ibrikci et al., 2003). The nutritional value of 100 g of cooked, mature chickpea seed as outlined by the United States Department of Agriculture (USDA) nutrient database is provided in Table 1.1. Chickpea is known to be a nutraceutical (or health benefiting food) because of its high nutritional value and near absence of anti-nutritive components (Williams and Singh, 1987; McIntosh and Topping, 2000; Charles et al., 2002; Millan et al., 2006). Besides, it has a traditional medicinal value (Muehlbauer and Tullu, 1997) with germinated chickpea reported as hypocholesteremic (Geervani, 1991). Desi chickpea have a very low ‘glycemic index’ making them a healthy food source for people with diabetes (Walker and Walker, 1984). Furthermore, chickpea is an additional benefit to the farmers as it fixes a substantial amount of nitrogen for the subsequent crops and adds much needed organic matter that improves soil health, long-term fertility and sustainability of the ecosystems (Ahmad et al., 2005).

1.1.3 Botany: Morphology and floral biology

Chickpea is an annual, winter-grown legume, 20 cm to 1 m tall, upright with a rather shrubby appearance (Muehlbauer and Tullu, 1997). The stems are branched with a semi-erect or semi-spreading growth habit. The leaves are glandular-pubescent with 3–8 pairs of leaflets and a top leaflet at the tip of the rachis (Cubero, 1987; van der Maesen, 1987; Muehlbauer and Tullu, 1997). They are frond-like, green or bluish-green in colour and have a serrated edge. The leaves are covered with glandular hairs that secrete malic and oxalic acid exudates, which are important in protecting the plant against insect pests (Oplinger et al., 1997). They have a robust root system that can grow up to 2 m deep. The flowers are axillary (solitary or in groups of 2-3) white, pink, purplish or blue in colour (Taylor and Ford, 2007). The pods are rhomboid ellipsoidal with 1-3 seeds. The
Table 1.1 Nutritional value of chickpea (100 gram seeds)*

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</tr>
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<td>Vitamin K (phyloquinone)</td>
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</tr>
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<tr>
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<tbody>
<tr>
<td>Carotene, beta</td>
<td>mcg</td>
<td>40</td>
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*Source: USDA Nutrient Database, 2006 (URL: http://riley.nal.usda.gov/NDL/cgi-bin/list_nut_edit.pl)
seeds are cream, yellow, brown, black or green, rounded to angular with a smooth or rough seed coat (Cubero, 1987; van der Maesen, 1987; Muehlbauer and Tullu, 1997).

The *desi* type usually have small (12–20 g/100-seeds), angular, dark-coloured seeds with a rough seedcoat (Ahmad *et al*., 2005; Taylor and Ford, 2007). They usually have pink flowers, anthocyanin pigmentation on the stems and a semi-erect or semi-spreading growth habit. They are grown in semi-arid tropics (Malhotra *et al*., 1987; Muehlbauer and Singh, 1987) and account for 85% of the cultivated area (Ahmad *et al*., 2005). The *kabuli* type have large (25–60 g/100-seeds), rams-head shaped, light-coloured seeds with a smooth seedcoat (Ahmad *et al*., 2005; Taylor and Ford, 2007). They generally have white flowers, lack anthocyanin pigmentation on the stems and have a semi-spreading growth habit. They are usually grown in temperate regions (Malhotra *et al*., 1987; Muehlbauer and Singh, 1987) and account for the remaining 15% of the cultivated area (Ahmad *et al*., 2005).

1.1.4 Climatic requirements

Chickpea is usually grown as a rainfed cool-weather crop or as a dry climate crop in semi-arid regions (Muehlbauer and Tullu, 1997). The *kabuli* type is generally grown in temperate regions whereas the *desi* type is grown in the sub-arid tropics (Malhotra *et al*., 1987; Muehlbauer and Singh, 1987). The optimum conditions for growth have been suggested to be 18-26°C day and 21-29°C night temperatures and an annual rainfall of 600-1000 mm (Duke, 1981; Smithson *et al*., 1985). However, Soltani *et al*. (2006) used quantitative data from four cultivars grown over three years to evaluate various approaches to predict chickpea phenology. They concluded that the differences among
cultivars for cardinal temperatures and critical photoperiod were small. They recorded a base temperature of 0°C, lower optimum temperature of 21°C, upper optimum temperature of 32°C, ceiling temperature of 40°C and a critical photoperiod (below which the development rate decreased due to short photoperiods) of 21 h. In fact, Smithson et al. (1985) regarded chickpea as a quantitative long-day plant capable of flowering in all photoperiods.

1.1.5 Area and production

Chickpea is the second most important legume in the world with 11.2 million ha under cultivation and with 9.1 million tonnes produced annually, it is third only to dry bean and pea (FAOSTAT, 2006; URL: http://faostat.fao.org/). Chickpea is grown in many geographical regions around the world including, south Asia, west Asia, north and east Africa, southern Europe, North America, South America and Australia (Soltani et al., 2006; Taylor and Ford, 2007). Australia is the largest exporter of chickpea whilst India is the largest producer, contributing 58% to world production (FAOSTAT, 2006; URL: http://faostat.fao.org/). India is also the largest importer of chickpea (importing ~1 million tonnes) followed by Pakistan (importing ~ 0.1 million tonnes). Following recognition of chickpea’s nutritional value, importation into Spain, Saudi Arabia, Jordan, Italy, Lebanon, Turkey, Sri Lanka and Columbia has increased considerably (Gowda and Gaur, 2004). Therefore, there is a high market demand for quality seed on many international markets. Australia and Canada are major competitors in the international marketplace for export of dry pea, lentil and chickpea (Skrypetz, 2006). In Australia alone, the 2006-2007 production was forecasted to be ~239,000 tonnes, most of which shall be exported (225,000 tonnes) (Skrypetz, 2006). Therefore, the high export potential and premium seed prices will likely drive an increase in chickpea cultivation in
Australia and elsewhere. This will involve adaptation to new agro-ecological areas for sustainability and increase in yields, and a full understanding of the potential constraints.

1.1.6 Constraints

Singh (1987) proposed that under optimum growing conditions, the yield potential of chickpea is 6 t/ha, which is very high compared to the global yield level of ~0.8 t/ha (Ahmad et al., 2005). The chief constraints to chickpea production are biotic stresses such as Ascochyta blight (Ascochyta rabiei), Fusarium wilt (Fusarium oxysporum f. sp. ciceri), and pod borer (Helicoverpa armigera) and abiotic stresses such as drought, heat, cold and salinity (Ryan, 1997). In fact, the collective yield losses due to abiotic stresses (6.4 million tonnes) are somewhat higher than due to biotic stresses (4.8 million tonnes), as estimated by Ryan (1997). The frequency of occurrence and severity of these stresses varies dependant on the climatic and geographical conditions. Berger and Turner (2007) compiled a list of biotic and abiotic stresses faced by chickpea in coarse agro-climatic zones. Several reviews cover the major biotic factors affecting chickpea production (Nene and Reddy, 1987; Reed et al., 1987; Singh et al., 1993; Ahmad et al., 2005; Millan et al., 2006).

Among the abiotic stresses, drought is almost ubiquitous to major chickpea growing regions and is exacerbated by heat stress in warmer Mediterranean and summer-dominant rainfall areas (Berger and Turner, 2007). Drought leads to a 40-50% reduction in yield globally (Ahmad et al., 2005). Cold stress at vegetative stage is common in west Asia, north Africa, Europe and central Asia and when the crop is sown in autumn or early spring. Moreover, the change from spring to winter sowing, for efficient utilisation of rainwater in Mediterranean environments, has enhanced yields but demands tolerance
to low temperatures for further yield improvements (Millan et al., 2006). Worldwide, an increasing use of irrigation is exacerbating the problem of soil-salinity and it was predicted that by 2050, 50% of all the arable land would be salinized (Wang et al., 2003b). Most of the legumes are known to be salt sensitive and die before maturity in the field where salinity rises to 100 mM NaCl (Munns et al., 2002). Therefore, it is important to produce cultivars tolerant to these abiotic stresses along with biotic stresses for sustainable increase in chickpea production.

1.2 Abiotic stresses of chickpea

Drought, cold and salinity are the major abiotic stresses affecting chickpea in order of importance (Croser et al., 2003). Here we provide an overview of these stresses with respect to their meaning, impact, tolerance mechanisms and, breeding and molecular breeding efforts to enhance stress tolerance.

1.2.1 Drought stress

1.2.1.1 Meaning

Drought is a meteorological term and an environmental event, defined as a water stress due to lack or insufficient rainfall and/or inadequate water supply (Toker et al., 2007). The seriousness of drought stress depends on its timing, duration and intensity (Serraj et al., 2003). Along with the rainfall and external water supply, drought stress depends on evapotranspiration, soil water holding capacity and the crop water requirements (Toker et al., 2007).
1.2.1.2 Impact

Worldwide, 90% of chickpea is grown under rainfed conditions (Kumar and Abbo, 2001) where terminal drought is one of the major constraints limiting productivity (Toker et al., 2007). Terminal drought is a usual feature in semi-arid tropics like south Asia and northern Australia where chickpea is grown in the post-rainy season on progressively receding soil moisture conditions (Leport et al., 1998; Siddique et al., 2000). The damage due to drought is compounded by heat stress in the warmer Mediterranean regions and regions like south Asia where temperature increases towards flowering (Singh et al., 1997) and it is difficult to differentiate between the damage caused by the individual stresses. As a result of drought stress, the growing season may be shortened affecting yield components, i.e., total biomass, pod number, seed number, seed weight and quality, and yield per plant (Toker et al., 2007). Flowering and seed set are the most critical growth stages affected by drought in chickpea (Khanna-Chopra and Sinha, 1987).

1.2.1.3 Mechanisms of tolerance

Drought resistance is a complex trait associated with several physiological attributes. In the agronomical sense, drought resistance refers to the ability of a plant to produce its economical product with minimum loss in a water-deficit environment, relative to normal water conditions. In a genetic sense, the mechanisms of drought resistance can be grouped into three categories, viz., escape, avoidance and tolerance (Turner et al., 2001; Malhotra and Saxena, 2002). These mechanisms are inter-related and there is no fixed line of demarcation.
Drought escape: Drought escape can be defined as the ability of a plant to complete its life cycle before serious soil and water deficits develop. Chickpea plants facing terminal drought at the end of the season may escape drought by early vigour, early flowering and maturity (Turner et al., 2001). The two usual approaches toward drought escape are by using early maturing (short-duration) varieties (Kumar et al., 1996) or early sowing (Toker et al., 2007), which depends on the prevalent cropping system. Accordingly, a shift of growing season from spring to winter to efficiently utilise available soil moisture was suggested (Singh, 1990).

Drought avoidance: Drought avoidance is the ability of a plant to maintain relatively high tissue water potential in a water-stressed environment. Drought stress can be avoided by maintaining water uptake and reducing the water lost by the plant. The two important traits conferring drought avoidance in chickpea are a larger/deeper root system (allowing greater water extraction) (Saxena et al., 1993) and a smaller leaf area (reducing transpirational loss) (Saxena, 2003; Toker et al., 2007). Other traits that allow drought avoidance or turgor maintenance are increased hydraulic conductance, reduced epidermal (stomatal and lenticular) conductance, leaf movement (like folding and rolling) and phenological plasticity (Mitra, 2001).

Drought tolerance: Drought tolerance is the ability of cells to metabolise at low leaf water status (Toker et al., 2007). Turgor maintenance is achieved through osmotic adjustment (accumulation of solutes in the cell), increase in cell elasticity, decrease in cell size, and protoplasmic resistance (including stabilising cell proteins) (Mitra, 2001). Membrane stability is achieved by reducing the leakage of solutes from the cell (Nayyar et al., 2005a). The cell water content is maintained by accumulating compatible solutes
like fructan, trehalose, polyols, glycine betaine, proline and polyamines that are non-toxic and do not interfere with cellular activities (Mitra, 2001). Degradation of cellular proteins due to the stress is stabilised by amino acids like proline (Munns, 2005).

1.2.1.4 Breeding for drought tolerance

Conventional breeding for drought tolerance is based on selection for yield and its components under a water-limited environment (Millan et al., 2006). The germplasm is usually screened for two important drought avoidance/tolerance traits; large root system and small leaf area (Turner et al., 2001; Saxena, 2003). Previously, more than 1500 chickpea lines were screened for drought tolerance and the genotype ICC 4958 was the most promising (Saxena et al., 1993). Subsequently, ICC 4958 was used in a three-way cross with cv. Annigeri and the Fusarium wilt resistant genotype ICC 12237. The progeny were selected for high yield and drought tolerance traits (Saxena, 2003). Several lines combining the large root trait of ICC 4958 and the small leaf area trait of ICC 5680 were reported to be more drought tolerant and yielded similarly to the high-yielding parent (Saxena, 2003). In another study, a chickpea minicore germplasm collection comprising 211 genotypes, 12 popular cultivars and 10 annual wild chickpea genotypes was screened for root traits. Several C. arietinum genotypes with more root depth than ICC 4958 were identified which could serve as an alternative source for the large root trait (Krishnamurthy et al., 2003). Also, genotypic variation for osmotic adjustment in chickpea has been reported but its correlation with yield under drought stress is unclear and the heritability was low ($h^2 = 0.20$ to 0.33) (Morgan et al., 1991; Turner et al., 2001; Moinuddin and Khanna-Chopra, 2004).
Breeding for drought tolerance is hampered by our limited knowledge about the genetic basis of drought resistance and negative correlations of drought resistance traits with productivity (Mitra, 2001). Moreover, selection for yields in chickpea is not effective in early segregating generations because of its indeterminate growth habit. Therefore breeders have to select for crosses rather than plants in F₂ and F₃ (Ahmad et al., 2005).

1.2.1.5 Molecular breeding for drought tolerance

Since selection of root traits is very laborious, molecular tagging of major genes for these traits may enable marker-assisted selection (MAS) and greatly improve the precision and efficiency of breeding (Millan et al., 2006). A RIL population from Annigeri x ICC 4958 was screened to identify molecular markers for root traits. Fifty-seven polymorphic STMS markers were mapped onto the RIL population. A quantitative trait loci (QTL) flanked by the STMS markers TAA 170 and TR 55 on LG 4A accounted for maximal phenotypic variation in root length \( R_a^2 = 33.1\% \), root weight \( R_a^2 = 33.1\% \) and shoot weight \( R_a^2 = 54.2\% \), where \( R_a^2 \) was the adjusted coefficient of determination (Chandra et al., 2004). This locus also accounted for substantial variation observed in these traits under simulated and actual field conditions. From the minicore collection, four genotypes that contrasted extremely for rooting depth and root mass were selected for development of mapping populations to identify more markers linked to QTLs governing root traits (Millan et al., 2006).

One of the most important strategies employed against terminal drought is developing short-duration, early flowering and maturing varieties (Kumar and Abbo, 2001). Two genes for flowering time, \( efl-1 \) and \( ppd \), have been reported (Or et al., 1999; Kumar and van Rheenen, 2000). Two other genes, \( nff-1 \) and \( nff-2 \), that govern node number to first
flowering (an indicator for time of flowering) have been reported (Millan et al., 2006). Two QTLs for days to 50% flowering have been located on LG 3 (Cho et al., 2002; Cobos et al., 2004).

1.2.2 Cold stress

1.2.2.1 Meaning

Cold stress is a meteorological term wherein the environmental temperature drops below the optimum required for a crop, thus limiting its growth and productivity. The cold stress has been classified into two types, chilling stress and freezing stress, based on its severity. The temperatures for chilling stress in chickpea range between -1.5°C and 15°C, whereas freezing stress temperatures are below -1.5°C (Croser et al., 2003). For a review on the implications of freezing stress on chickpea see Croser et al. (2003). For the remaining part of the review and subsequent chapters, the term ‘cold stress’ refers to ‘chilling stress’ (stress caused by temperatures between -1.5°C and 15°C).

1.2.2.2 Impact

Chickpea is constrained by cold stress across much of its geographical range and the change from summer to winter sowing of chickpea in Mediterranean regions has exposed chickpea to far colder climate than earlier (Croser et al., 2003). Cold stress limits the growth and vigour of chickpea at all phenological stages but is most devastating to yield at flowering and pod set (Srinivasan et al., 1999). During germination, cold stress results in poor crop establishment, susceptibility to soil borne pathogens and reduced seedling vigour. Prolonged periods of cold stress at the seedling stage may retard growth and cause plant death (Croser et al., 2003). At the vegetative stage, cold stress affects leaf expansion and thus limits the absorption of incident
radiation (Mwanamwenge et al., 1997). This in turn restricts the reproductive sink that the plant can support and reduces crop yield (Croser et al., 2003). Temperatures up to 15°C have been reported to cause flower and pod abortion in northern India and Australia (Srinivasan et al., 1999; Clarke and Siddique, 2004).

1.2.2.3 Mechanisms of tolerance

Cold resistance, in an agronomical sense, means the ability of a plant to grow normally and produce an economical product with minimum loss from chilling relative to normal temperature conditions. In the genetic sense, the mechanisms of cold resistance may be grouped into two categories, viz., cold escape/avoidance and cold tolerance.

Cold escape/avoidance: Cold escape/avoidance may be attributed to genetic factors that allow a plant to complete its life cycle before severe cold stress or make physiological adjustments to avoid cold injury. In northern India, chickpea is sown in early winter and the temperature drops as the crop matures, causing yield losses due to chilling injury at flowering (Srinivasan, et al., 1998). Early maturing genotypes are used to escape the chilling injury (Srinivasan, et al., 1998). Another escape/avoidance mechanism is an extension of the vegetative phase under long seasons and delaying flowering until the temperature becomes warm enough for pod set. This is possible due to the indeterminate growth habit of chickpea; the delayed phenology increasing both the source and sink potential resulting in higher yield (Berger et al., 2006). Cold stress can also be avoided or compensated for by genotypes with higher pollen vigour and ovule viability at lower temperatures (Srinivasan et al., 1999). These genotypes were shown to have greater pod-setting than those lacking the features.
Cold tolerance: Cold tolerance is an active mechanism that enables cells to metabolise at low temperatures. Like drought stress, the chilling range temperatures cause dehydration, and disruption to the cell membranes and metabolism. Cold tolerance is thus the ability of cells to increase membrane fluidity and cause osmotic adjustment (Wery et al., 1993). Osmotic adjustment/dehydration avoidance is achieved by accumulating compatible solutes (cryoprotectants) such as glucose, fructose, sucrose and trehalose (Nayyar et al., 2005b). Cold acclimation or hardening is another mode of cold tolerance. Cold acclimatised chickpea seedlings were shown to be more tolerant than controls. The tolerance was mostly ABA regulated, involving an increased accumulation of cryoprotectives and scavenging reactive oxygen species (Nayyar et al., 2005b).

1.2.2.4 Breeding for cold tolerance

Singh et al. (1989) developed a screening technique to evaluate chickpea germplasm and breeding materials for cold tolerance. Only 21 out of the 3276 lines screened from 1981 to 1987 were identified as cold tolerant (Singh et al., 1989). The germplasm line ILC 8262, the mutant line ILC 8617, and the breeding line FLIP87-82C were the best sources of cold tolerance in the cultigen, with a consistent score of 3 (on a 1 to 9 scale) over years and locations (Singh et al., 1995). A pollen selection technique was developed wherein selection pressure was applied at the gametophytic stage (Clarke et al., 2004). This technique, where plant physiology knowledge was applied in breeding strategy, led to the development of two cold tolerant cultivars, Sonali and Rupali (Clarke et al., 2004). Since cold tolerance variability in the cultigen was not sufficient, wild Cicer species were also evaluated for tolerance. Most of the genotypes of C. bijugum K.H. Rech., C. echinospermum P.H. Davis, and C. reticulatum Ladiz. had significantly higher
levels of cold tolerance than the cultivated species. The comparison of cold tolerance among the wild species revealed that *C. bijugum* had the highest level of tolerance, closely followed by *C. reticulatum* and *C. ehinospermum* (Singh *et al*., 1993; Toker, 2005).

Breeding for cold tolerance is hindered by additive and non-additive effects that govern its inheritance with high narrow sense heritability (Malhotra and Singh, 1991). Cold tolerance was found to be dominant over susceptibility and selection in crosses has to be delayed until the later generations to reduce the dominance effects (Singh *et al*., 1993).

**1.2.2.5 Molecular breeding for cold tolerance**

Early identification of chilling tolerant lines combined with pollen selection has great potential to accelerate breeding for cold tolerance (Millan *et al*., 2006). Molecular markers based on amplified fragment length polymorphisms (AFLP) were linked to cold tolerance using bulked segregant analysis of F2 progeny of an intraspecific cross (Clarke and Siddique, 2003). Six pairs of primers were designed from the sequence of AFLP based markers in an attempt to develop sequence characterised amplified region (SCAR) markers. A promising set of primers amplified a 560 bp fragment containing a SSR (3 bp repeat) with nine repeats in the susceptible parent and ten in the tolerant parent (Millan *et al*., 2006). This three base-pair difference was useful in selecting tolerant progenies from the crosses between the original parents used to develop markers but was not transferable to other cultivars of the species (Millan *et al*., 2006). Therefore, there is still paucity of information to utilise molecular breeding for cold tolerance in chickpea.
1.2.3 Salt stress

1.2.3.1 Meaning
Saline soils are defined as those that have a high concentration of soluble salts ($E_{c}$ is $\geq 4$ dS/m) and the salt injury results from the high concentration of sodium chloride (NaCl) ions (Munns, 2005). The salt stress inhibits the root and shoot growth. At low concentrations this reduces the yield and at higher concentrations and/or prolonged exposure this may result in plant death (Munns, 2002). The injury due to salt stress however differs between and within the species (Munns et al., 2002). The salt injury mostly involves sodium chloride (NaCl) and it has been estimated that most of the Earth’s water contains about 30 g of NaCl per litre (Flowers, 2004).

1.2.3.2 Impact
Worldwide, over 800 million ha of land (6%) is salt affected, either by salinity (397 million ha) or the associated condition of sodicity (434 million ha) (Munns, 2005). From the total irrigated land, which produces one-third of the world’s food, 20% is salt-affected and more is on the way to being salinized (Munns, 2005). Soil salinity affects the production of most of the crops. In general, legumes are sensitive to salinity, of which chickpea, faba bean, and field pea are the most sensitive (Ahmad et al., 2005). At a field concentration of 100 mM NaCl (about 10 dS/m), most legumes species die before maturity (Munns et al., 2002). Ryan (1997) estimated that 0.9 million ton of global chickpea yield is lost to salt stress. A current estimate for yield loss due to salinity is unavailable but must have considerably increased due to the ever-increasing area of saline soil (Munns, 2005). Soil salinity adversely affects chickpea germination, resulting in poor crop establishment (Ahmad et al., 2005) and all subsequent growth stages are affected (Toker et al., 2007). Salinity increases anthocyanin pigmentation in desi types
whilst causing yellowing of leaves and stems in the *kabuli* types (Millan *et al*., 2006). Salt damage starts with necrosis of leaf margins and yellowing of older leaves that eventually abscise and die due to excess ion accumulation (Saxena *et al*., 1993).

### 1.2.3.3 Mechanisms of tolerance

Salt tolerance for a farmer would mean the ability of the plant to grow normally and produce its economic product without major yield loss in saline versus normal soils. Generally, there is no escape or avoidance of saline conditions, as it is an inherent property of the soil and does not show much seasonal variation. Therefore, in the genetic sense, the mechanisms of salinity tolerance cannot be grouped into stress escape and/or stress avoidance, as explained for drought and cold stresses. The mechanisms of salt tolerance as described by Munns *et al*. (2002) take place at three levels, *viz*., at the whole plant level, the cellular level and the molecular level.

*Control at whole plant level*: At the whole plant level, salt tolerance is the ability of the plant to control salt transportation at the following sites: a) selective uptake by root cells, limiting entry of Na$^+$ and Cl$^-$ ions, b) preferential loading of K$^+$ over Na$^+$ in the xylem (*e.g.*, the stelar cells; Gorham *et al*., 1990), c) movement of salt in the xylem to upper parts of the roots, d) stems and e) petioles and/or leaf sheaths. In many plants, Na$^+$ is retained in the upper part of the roots or lower part of the shoots. In some tolerant species, salt is not exported to the growing parts of the shoot by limiting the retranslocation of Na$^+$ or Cl$^-$ ions in the phloem. Further, there is evidence of excretion of excess salts through salt glands or bladders in the halophytes. In general, crop plants (glycophytes) rely on selective uptake by the roots, preferential loading in the xylem, and deposition of salts into upper parts of roots and lower parts of shoots.
Control at cellular level: At the cellular level, salt tolerance is achieved by excluding the salt from the cytoplasm and sequestering it into the vacuoles. This necessitates balancing the osmotic pressure from the Na\(^+\) and Cl\(^-\) ions with K\(^+\) and organic solutes in the cytoplasm. Some organic solutes (osmolytes) known to accumulate under salt stress are proline, glycine betaine and trehalose.

Control at molecular level: At the molecular level, ion transporters control the movement of salt across the cell membranes. In the absence of a Na\(^+\)-specific transporter, Na\(^+\) entry is gained passively by competition with other cations, chiefly K\(^+\). This involves both, high affinity K\(^+\) carriers and low affinity non-selective cation channels that are controlled by Ca\(^{2+}\). The Na\(^+\) may also be effluxed from the cytoplasm by Na\(^+\)/H\(^+\) antiporters that are regulated by the pH gradient across the plasmalemma. The Na\(^+\)/H\(^+\) antiporters also control the vacuolar compartmentation of Na\(^+\) driven by the pH gradient across the tonoplast. Together, these transporters control the uptake of Na\(^+\) by the cell. The mechanisms involved in Cl\(^-\) transportation are also associated with salt tolerance.

1.2.3.4 Breeding for salt tolerance

Screening for salt tolerance is limited by the large potential for interaction with other environmental stresses, which may make it difficult to separate genetic and environmental variations (Flowers, 2004; Toker et al., 2007). Therefore, carefully derived bioassays and/or field trials are required to accurately select for salt tolerant genotypes. Salt tolerance may be assessed as the percent biomass production in saline versus control conditions over a prolonged period of time (Munns et al., 2002). Another criterion is the crop yield in saline versus non-saline conditions, which has a different
pattern of response than the vegetative biomass (Munns et al., 2002). A field screening method for salt tolerance in chickpea was reported by Saxena et al. (1993). The non-field screening methods available for salt tolerance in chickpea were described by Epitalawage et al. (2003) and Maliro et al. (2007).

Several salt tolerant chickpea lines (CSG 88101, CSG 8927, CSG 8977, CSG 8962 and CSG 8943) that differed in uptake and distribution of Na\(^+\) and Cl\(^-\) ions, were identified (Dua and Sharma, 1995, 1997). A salt tolerant desi variety, Karnal Chana-1 (CSG 8963), which can be grown in saline soils with Ec between 4 to 6 dS/m, was released in India (Millan et al., 2006). Overall, the Kabuli type was more salt tolerant than the desi type, after screening 252 genotypes and breeding lines (Serraj et al., 2004). More recently, 200 genotypes and wild Cicer genotypes were screened for salt tolerance in Australia (Maliro et al., 2007). The most tolerant genotypes were CPI 060546, ILC 01302 (from Turkey), ICC 6474 and ICC 06772 (from Iran), ICC 8294, ICC 438, CPI 53008 (from India) and UC 5 (from USA) and none of the wild relatives screened were tolerant (Maliro et al., 2007). This may indicate that selection and breeding of some cultivated genotypes may have occurred on saline soils. Screening for salt tolerance is limited by its huge potential for interaction with other environmental stresses, which makes it difficult to separate genetic and environmental variations (Flowers, 2004; Toker et al., 2007).

1.2.3.5 Molecular breeding for salt tolerance

To date, the complexity of the tolerance mechanisms has limited the success achieved to incorporate this trait into conventional breeding programs (Flowers, 2004). However, since it appears to be a multigenic trait, the discovery of QTLs for salt tolerance may
result in effective pyramiding of loci within which the salt tolerance genes reside. Molecular breeding for salt tolerance in chickpea is in its infancy. Salt tolerant and sensitive varieties have been crossed in Europe (Grain Legumes Integrated Project) and are being utilised in the construction of a detailed genetic map to locate the salt tolerance QTLs and their subsequent fine mapping (Huguet and Crepsi, 2005). This is to be followed by fine mapping of QTLs for salt tolerance. Another project at International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) aims to screen the minicore germplasm for salt tolerance, investigate mechanisms for tolerance and detect QTLs for salt tolerance in existing and new mapping populations (ICRISAT, 2007; URL: http://www.icrisat.org/gt-bt/globalprj1.htm). Previously, QTLs for salt tolerance were identified in barley, citrus and rice, and were associated with ion transport under saline conditions (Flowers, 2004).

1.3 Functional genomics

1.3.1 Molecular breeding meets functional genomics

Abiotic stress tolerances are governed by multiple genes involved in multiple mechanisms that may be expressed at different plant growth stages (e.g., Foolad, 1999). The genetic background and particular environment in which a plant is growing both have significant influence on the types and locations of the quantitatively inherited and expressed genes (Flowers, 2004). Moreover, the fact that a single QTL may represent many, perhaps, hundreds of genes, poses a problem in finding the key loci that actually govern tolerance (Flowers, 2004). Sometimes it is difficult to find a marker tightly linked to a QTL and there is always a chance of identifying a false positive marker. These factors greatly hinder marker-assisted breeding, causing ‘linkage drag’ of undesirable traits due to the large regions of chromosomes identified by the QTLs
The logical way forward is to identify specific and individual candidate gene sequences that may account for the QTL effects. This would require validating the function or role of the genes associated with the QTL individually. The identification of candidate genes and elucidation of their role can be facilitated by combining QTL analysis with different sources of information and technological platforms (Wayne and McIntyre, 2002). The recent progress in genome sequencing and mass-scale profiling of the transcriptome, proteome and metabolome facilitates investigation of concerted responses of thousands of genes to a particular stress. This area of study known as ‘functional genomics’ involves development and application of global (genome-wide or system-wide) experimental approaches to assess gene function by making use of the information provided by genetic, physical and transcript maps of an organism.

1.3.2 The area of functional genomics

Functional genomics employs multiple parallel approaches including global transcriptional profiling coupled with the use of mutants and transgenics, to study gene function in a high-throughput mode (Vij and Tyagi, 2007). The basic requirements for determining gene functions are gene sequences, expressed sequence tags (ESTs) and molecular markers. Functional genomics can be broadly divided into three different categories, viz., transcriptomics, proteomics and metabolomics. Transcriptomics involves generation and analysis of gene expression profiles of an organism in response to a particular treatment (biotic or abiotic stress). Similarly, proteomics and metabolomics involve global expression profiling of the proteins or metabolites, respectively, in response to a treatment. The expression profiling of genes/proteins is possible using microarrays, serial analysis of gene expression (SAGE), massively parallel signature sequencing (MPSS), two-dimensional gel electrophoresis (2DGE),
matrix-associated laser desorption/ionisation time-of-flight (MALDI-TOF), or yeast two-hybrid expression. The gene functions detected through these approaches can be validated by overexpressing the gene through transgenics or silencing it using knockout-mutants/antisense/RNAi. Subsequently, the candidate tolerance genes may possibly be used to genetically modify a crop to help it tolerate abiotic and biotic stresses.

The area of functional genomics is extensive, and therefore, this review will focus only on different approaches to genome-wide transcriptional profiling (microarrays, SAGE and MPSS). These techniques are briefly compared followed by in-depth appraisal of microarray technology that is relevant to the current study. For information on other approaches readers are directed to some outstanding reviews in the area (2DGE – Rabilloud, 2002; Lilley et al., 2002; MALDI-TOF – Jurinke et al., 2004; Yeast two-hybrids – Miller and Stagljar, 2004; Chern et al., 2007; proteomics – van Wijk, 2001; metabolomics – Hall et al., 2002).

Microarrays have revolutionised global gene expression profiling making it possible to study all the genes of the organism in parallel (Wang et al., 2003a). The probes derived from gene sequences or ESTs, immobilised on a solid surface are used to generate expression profile of a target sample via hybridisation (Chen et al., 1998). Microarrays have been used extensively for global expression profiling of plant responses to biotic and abiotic stresses and this is discussed in detail later in the review.

The SAGE technique depends on the generation of unique transcript-specific short sequence tags of 9-17 base pairs (Saha et al., 2002). The quantification of a particular tag provides the expression level of the corresponding transcript. SAGE was originally
used to study global expression profiling of rice (Matsumura et al., 1999) and gene expression in response to cold stress in *Arabidopsis thaliana* (Jung et al., 2003; Lee and Lee, 2003). However, the lack of specificity achieved with the 9-17 base pair tags prompted the development of a revised SuperSAGE technique that uses longer (26 base pair) tags (Matsumura et al., 2003). Very recently, SuperSAGE was used in chickpea to investigate salt, drought and cold stress (Kahl et al., 2007). The authors exploited the high power approach to analyse 40,000 unique mRNAs, and identified >3,000 genes responding to the stresses applied. A disadvantage of this method is that the short sequences (26-bp) used in SuperSAGE may be homologous to hundreds of sequences in the database, making it prone to wrong annotation of transcripts. However, the identification of large sets of candidate genes responding to a certain stress enables the construction of specialised microarrays that could be used to confirm gene functions by co-expression with other known genes. This combination of SuperSAGE and microarray allows for the development of much more efficient and effective functional genomics tools to identify genes involved in stress resistance/tolerance.

The MPSS, like SAGE, obtain a representation of the transcripts in the sample related to mRNAs, ESTs or whole genome sequence, but the data generated are much larger in magnitude (Brenner et al., 2000; Pollock, 2002). A public database for MPSS resources was compiled (URL: http://mpss.udel.edu) and the MPSS resource for rice alone includes 20 libraries constructed from different tissues and in response to drought, cold and salinity (Nakano et al., 2006). Due to the high cost of MPSS, the approach not been commonly used for transcriptional profiling.
SAGE and MPSS are considered to be ‘open architecture’ systems where the information about the genomic content is obtained after completion of the assays. They are thus not dependent on available sequence information at the time of experimentation and assay coverage is not restricted to the sequences that can be detected. In contrast, the target detection in microarrays is limited to the probes present on the array at the time of the experiment and is thus referred to as a ‘closed architecture’ system (Meyers et al., 2004). The ‘closed architecture’ system is more feasible when sequence information is already known. However, factors such as scope of genetic screening, number of samples, amount of starting material, and availability of resources (chief factor) determine which technology is feasible (Clarke and Zhu, 2006).

1.4 Microarrays

Microarrays have revolutionised global gene expression profiling, making it possible to study all the genes of an organism in parallel if the entire genome is already sequenced (Wang et al., 2003a). Alternatively, a subset of probes derived from gene sequences or ESTs may be assessed. Sequences are immobilised on a solid surface and are used to generate expression profiles of a target sample via hybridisation (Chen et al., 1998). Microarrays have been used extensively for global expression profiling of plant responses to biotic and abiotic stresses. They use hundreds of highly organised probes printed on a solid surface to simultaneously interrogate the multiple RNA or DNA molecules, defined as targets, within each sample (Schena et al., 1995). The target molecules are fluorescently labelled and hybridised to the immobilised probes. The signal generated from each probe-target hybrid is quantified and the strength of signal represents: (i) target abundance (transcript level, if samples were RNA) or (ii) sequence similarity between the probes and targets (Clarke and Zhu, 2006). The ability of
microarrays to simultaneously monitor the expression of thousands of targets in a high-throughput manner facilitates recognition of global expression patterns. The comparison of expression patterns from different samples allows the association of traits with changes in gene expression, suggesting gene function (Chen et al., 2002). On a global scale, this technology has the potential to reveal the actual state the transcriptome and help understand gene regulation at the systems level.

Types of microarrays

To date three types of microarray systems have been developed based on the type of probe, viz., cDNA (spotted) microarrays, oligonucleotide (GeneChip) microarrays and tiling-path arrays. Here we briefly compare different types of microarrays followed by a detailed review of cDNA microarrays, which relates to the present study.

The cDNA arrays, as the name suggests, use cDNAs generated from mRNAs as probes. The fabrication of cDNA arrays is dependent on availability of the required clones and appropriate arraying and scanning instrumentation (Clark et al., 1999). The sequences of the cDNAs are mostly deduced and they are annotated serving as expressed sequence tags (ESTs). A detailed appraisal of cDNA microarray technology is presented later in the review.

Oligonucleotide arrays use short oligos (~60 bp) designed from known gene/DNA sequence as a probe. The fabrication of these arrays is dependent on the availability of required gene sequences and appropriate arraying and scanning instruments. The short oligos can be individually synthesised and spotted onto the array. Alternatively, oligonucleotide arrays may be fabricated using microfluidic technology, which utilises
light to direct the synthesis of short oligonucleotides onto a suitable matrix, referred to as photolithography (Pease et al., 1994). For using short oligos probes, a minimum of nine to 11 independent probes per gene sequence is necessary to accurately measure the transcript abundance without significant deterioration in performance (Zhou and Abagyan, 2002).

Recently, the availability of complete genomic sequences of some organisms has led to development of tiling-path arrays or tiling arrays. Rather than using the gene specific probes to detect gene expression, the complete genome including the intergenic regions is represented by probes on the array (Rensink and Buell, 2005). In addition to detecting transcripts, tiling arrays may be used for comparative genome hybridisations to detect deletions and polymorphisms, methylation profiling and analysis of chromatin immunoprecipitation samples (Martienssen et al., 2005). However, the use of these arrays is limited to availability of entire genomic sequence, and currently possible only in the model plants, Arabidopsis and rice. While all array technologies have their own benefits, the factors that determine choice of array platform are the objectives of experiment and the availability of the resources such as sequences/ clones, arrayer, scanner and software. An overview of cDNA microarray technology, which was mainly used because of these reasons is provided here.

1.5 cDNA microarrays

1.5.1 Fabrication

The fabrication of a cDNA microarray usually involves the generation of a cDNA library for the experimental purpose and the selection of clones to be queried. These clones can be sequenced from the 3’ and/or 5’ end and annotated by blasting the
sequence to the GenBank® databases. Clones with known function, also referred to as ESTs, are then spotted in a matrix on a solid platform (Duggan et al., 1999). Alternatively, existing EST and clone resources may be exploited as a cost effective way of generating valuable information. Once a set of corresponding PCR products have been generated, arrays can be created in multiple versions containing the entire set of available sequences or subsets of sequences resulting in smaller, ‘boutique arrays’ suitable for specific research application (Alba et al., 2004). These boutique arrays help to free up costly resources, which can then be used effectively to analyse more samples.

1.5.2 Experimental design

A schematic overview for expression profiling using cDNA microarrays was adapted from Alba et al. (2004) and is presented in Figure 1.1. Various possible microarray designs have been discussed (Churchill, 2002; Dobbin and Simon, 2002; Yang and Speed, 2002; Dobbin et al., 2003; Clarke and Zhu, 2006). The experimental designs employed in time course experiments are common reference design, direct-sequential (linear) design and direct-sequential loop design. More recently, experimental design for microarray analyses have incorporated interspecies comparisons using arrays that originate from one of the genomes being investigated (Dong et al., 2001; Horvath et al., 2003; Ventelon-Debout et al., 2003). The comparison of closely related species is most effective and informative because artefacts stemming from sequence divergence are minimised. An example of this type of comparison is co-hybridisation of cDNA derived from pepper and tomato pericarps onto a tomato TOM1 microarray to study gene expression (Alba et al., 2004).
Figure 1.1 Overview of experimental design for gene expression profiling using cDNA microarrays. (a) General scheme for gene expression profiling using cDNA microarrays. (b) Three different experimental designs for time-course experiments utilising microarrays. Abbreviations: T1........Tn, time-points 1 through n (adapted from: Alba et al., 2004).
1.5.3 Generation of hypothesis

A well-designed expression profile experiment built around a hypothesis can yield high quality results that lend themselves to validation. Microarray experiments can be categorised as hypothesis seeking or hypothesis testing (Clarke and Zhu, 2006). Hypothesis seeking begins with minimum information about the subject, followed by the gathering of information through expression profiling and building a working hypothesis to validate particular gene functions. On the other hand, hypothesis testing begins with functional information on the subject to be verified, which is tested using expression profiling.

1.5.4 Sources of variation

Microarray experiments need to allow for both technical and biological variation. Technical variation may be minimised by optimising reagents and the working protocol. Biological variation remains the main concern surrounding microarray experiments, which can be divided into intra-sample variation and inter-sample variation (Bakay et al., 2002). Intra-sample variations include micro-environmental differences within the same sample, such as those between different parts of the same leaf or those caused by factors such as light intensity, humidity, nutrient partitioning and mechanical stresses like wind. Inter-sample variations include environmental differences caused by growth room/greenhouse or field effects (light, humidity, and location), watering, fertilising, soil conditions, pest pressures and human handling. Sample pooling and replication are the primary methods to account for biological variation (Clarke and Zhu, 2006).
1.5.5 Replication

Sufficient replication is an important issue in meaningful transcriptome profiling and should be based on the (i) extent of expected biological and technical variation, (ii) experimental question, (iii) desired resolution, (iv) available resources, (v) available time, and (vi) opportunities for downstream validation (Alba et al., 2004). Technical variation is minimal for in-house synthesised oligo- and cDNA-arrays, which makes biological replication a priority over technical replication when designing experiments (Zhu and Wang, 2000). Currently, a minimum of three or four biological replications with a dye-swap per time point is recommended to accommodate variation (Lee et al., 2000; Kerr et al., 2002). Dye-swap is helpful in reducing dye bias that is derived from differences in the mean brightness and background noise of individual spots, incorporation efficiencies, extinction coefficients, quantum fluorescence yield and other physical properties of the dyes (Tseng et al., 2001; Yang et al., 2001).

1.5.6 Assay, RNA extraction, target preparation and hybridisation

The cDNA microarrays are generally performed in a reference design, where mRNA from treated and untreated tissues are hybridised onto the same probe-set. Subsequently, the relative abundance of transcripts from the treated tissue is compared against those corresponding transcripts from the untreated tissue. For effective comparison, the treatment and control plants must be cultivated under exactly same conditions and differ only in the said treatment under investigation. Following treatment, total RNA is extracted from treated and control tissues using phenol-based extraction, guanidine thiocyanate, TRIZol®, silica-based extraction (e.g., RNeasy® kits, Qiagen Inc., Valencia, CA, USA) or methods that use proprietary extraction cocktails such as RNAwiz (Ambion, Austin, TX, USA). The purity and integrity of RNA is generally verified using
a spectrophotometer and gel-electrophoresis before being reverse-transcribed to cDNA targets. The treatment and control targets are then labelled with different fluorescent dyes (usually, cyanine-3 and cyanine-5) (Duggan et al., 1999) using a direct or more highly preferred indirect incorporation method. A mixture of equal amounts of labelled treatment and control targets is hybridised onto the spotted array under the coverslip. The hybridisation is performed in a special chamber (e.g., Corning® hybridisation chamber) to avoid evaporation (Coram and Pang, 2006). Generally, the hybridisation temperature ranges from 42°C (if using 50% formamide) to 70°C (if using SSC based buffers) and the incubation duration varies from several hours to overnight (Aharoni and Vorst, 2002).

1.5.7 Data acquisition, transformation and normalisation

There is a large choice in equipment and protocol for microarray data acquisition and downstream processing. A list of bioinformatics resources available for microarrays was presented in Alba et al. (2004). For data acquisition, transformation and selection of candidate genes for cDNA microarrays, slides are first washed of excess hybridisation solution and dyes, dried and scanned using a two-channel confocal microarray scanner (e.g., Affymetrix® 428™ array scanner, Santa Clara, CA) and associated software (Coram and Pang, 2006). Excitation settings used for Cyanine-3 (Cy3™) and Cyanine-5 (Cy5™) are 543/570 μm and 633-670 μm, respectively, and both image files are saved separately as ‘tif’ files. The raw image data is digitally quantified using another software (e.g., ImaGene™, BioDiscovery Inc., El Segundo, CA, USA) by overlaying the spots with a grid of same size and gene expression values are saved as ‘txt’ files.
Data processing usually involves correction for background signals, omission of flagged spots, normalisation and transformation. Data transformation and normalisation allow the detection of actual (biological) variation. Out of five common data transformation methods compared, log transformations were found to be the most reliable (Alba et al., 2004). Log transformation gave a more realistic sense of data variability by making the variation in signal ratios independent of signal magnitude and reducing skewed distribution. Log$_2$ transformation is most commonly used because it converts the expression values to an intuitive linear scale representing two-fold differences (Draghici, 2003). Normalisation is applied to minimise and standardise non-biological (technical) variation (Clarke and Zhu, 2006) and accommodates for factors like background intensity, noise levels, measurement differences, hybridisation conditions and variations caused by handling (Leung and Cavalieri, 2003). The correct use of the normalisation technique enables comparison between arrays within the experiment and possibly between arrays from separate experiments. A comparison of various normalisation methods revealed that the LOcally WEighted polynomial regreSSion (LOWESS) method was most suitable (Alba et al., 2004). The LOWESS method uses a locally weighted regression that reduces the expression ratios to the residual of the LOWESS fit of an associated intensity versus ratio curve (Cleveland and Devlin, 1988).

1.5.8 Preliminary selection of candidate genes and statistical analysis

From microarrays, candidate gene selection is generally based on gene annotation, transcript level and/or fold change. Whilst a ‘two-fold or more’ cut-off is usually preferred by molecular biologists, care should be taken while using fold-change as it can be misleading in the event of one of the candidate genes having a transcript level below the threshold or above saturation (Clarke and Zhu, 2006). Wherever possible, fold-
change data should be bolstered by using proper biological replications to enable statistical analysis (Lee et al., 2000).

Considering that microarrays typically generate tens-of-thousands of data points, the use of statistical analysis becomes imperative to determine the significance of individual data points to the observed variation. For comprehensive information on statistical tests for differential expression, readers are referred to Nadon and Shoemaker (2002), Cui and Churchill (2003), and Draghici (2003). Both parametric and non-parametric methods are used to determine real differential expression in the level of transcripts (Clarke and Zhu, 2006). The parametric methods typically employed are the Student’s $t$-test and the Welch’s $t$-test that assume equal or unequal variances, respectively. Non-parametric methods include the Wilcoxon rank sum test and the Kruskal-Wallis test that compare two and more than two groups, respectively. On the genes found to be differentially expressed after the above tests, a multiple testing correction (e.g. false detection ratio, FDR) is applied as an estimate of acceptable false positives (Draghici, 2003).

1.5.9 Grouping of differentially expressed genes and visualisation of expression patterns

The ultimate goal of expression profiling is to link a gene or set of genes to the experimental condition and determine their role in governing response to the said condition. The set of differentially expressed genes that pass statistical tests are grouped in various ways to determine those that share a similar expression pattern. The common methods of grouping include Venn diagrams, hierarchical clustering, $k$-mean clustering, self-organising maps (SOM), and principal component analysis (PCA). A review on clustering algorithms can be found in Draghici (2003). The assumption behind clustering
is that genes that cluster together are likely to be co-regulated and involved in the same or linked pathways (Rensink and Buell, 2005).

1.5.10 Verification of microarray data

Verification of microarray data can be accomplished by RNA-blot analysis, reverse transcription PCR (RT–PCR), quantitative real-time PCR (qRT-PCR), and/or comparison with EST expression databases (digital northerns). The latter is the only approach that has potential for genome-scale verification. The expression levels detected through RNA-blot are similar to those of microarrays, whilst real-time PCR is more sensitive often yielding expression levels of higher magnitude (Maguire et al., 2002; Scheideler et al., 2002; Rabbani et al., 2003; Lopez et al., 2005). Digital northerns or data mining are employed to confirm the expression of a particular gene in response to a condition by searching existing expression data in public repositories (e.g., the Gene Expression Omnibus, NCBI). These data, together with the gene annotation, provide clues to the putative role of the gene in response to a condition (Rensink and Buell, 2005).

1.6 Abiotic stress response mechanisms

The mechanisms through which plants perceive environmental signals and transmit them to cellular machinery to generate adaptive response is of fundamental importance to biology (Xiong et al., 2002). Plants sense a change in environmental condition and the signal is relayed through signalling cascades that amplify the signal and notify parallel pathways resulting in the production of effector molecules that mitigate stress (Vij and Tyagi, 2007). Drought, cold and high-salinity stresses generate complex stimuli that have different yet related attributes and may deliver quite different information to the
plant cells (Xiong et al., 2002). All these three cause osmotic stress to the plant (Verslues et al., 2006), however, cold stress also causes changes in activities of macromolecules (Xiong et al., 2002) and salt stress causes ionic stress (Munns et al., 2002, Verslues et al., 2006).

The precise mechanism(s) by which plants perceive osmotic stress is still a matter of debate. However, studies on yeast have led to identification of two types of osmosensors, SLN1 and SHO1 that feed the signal to the high-osmolarity glycerol (HOG) MAPK pathway (Bartels and Sunkar, 2005). SLN1 is likely to sense the change in turgor pressure (Reiser et al., 2003). Also, low temperature causes change in membrane fluidity (Murata and Los, 1997), which may act as a sensor and initiate a signalling cascade. Secondary signals differ from primary signals in expression time (i.e. lag behind) and in space. Secondary signals may diffuse within or among cells and their receptors may be in different subcellular locations from the primary sensors (Xiong et al., 2002). The secondary signals could also differ from primary signals in specificity as they may be shared by different stress pathways. This likely explains the interaction or crosstalk detected between stresses (Xiong et al., 2002). Drought, cold and salinity were shown to induce a transient Ca$^{2+}$ influx, which may act as one type of sensor for these stresses (as reviewed by Bartels and Sunkar, 2005; Yamaguchi-Shinozaki and Shinozaki, 2006). Downstream stress response regulation was categorised into two classes; abscisic acid (ABA) dependent and ABA-independent (Bray, 1997; Thomashow, 1999; Shinozaki and Yamaguchi-Shinozaki, 2000). The ABA-dependent gene expression functions thorough an ABA-responsive element binding (AREB) protein that binds an ABA-responsive element (ABRE) motif of the effector gene. Whereas, the ABA-independent gene expression functions through a drought-responsive
element binding (DREB) protein that binds to a drought-responsive element (DRE) motif of the effector gene. One of the genes induced by drought, cold and ABA in Arabidopsis is RD29A/COR78/LTI78 (Kreps et al., 2002). This gene is induced in both an ABA-dependent and an ABA-independent manner as it contains binding sites for both ABRE and DREB (as reviewed by Seki et al., 2003). Thereby demonstrating the inter-related nature of stress-responsive mechanism pathways.

Two different types of DREB genes are recognised, DREB1 and DREB2. Expression of the DREB1 gene is induced by cold and not dehydration or high-salinity stresses, and this motif is also referred to as a C-repeat binding factor (CBF). The converse is true for the DREB2 gene, which is only induced by drought and high-salinity stresses (Seki et al., 2003). Besides these, there are many other regulatory genes that control expression in response to these stresses such as zinc-finger proteins, salt overly sensitive-2 (SOS2) like protein kinases, Ser/Thr protein kinase (PKS5), basic/helix-loop-helix (bHLH), the APETALA2/ethylene-responsive factor (AP2/ERF) domain-containing protein RAP2, and growth factor-like proteins (Bartels and Sunkar, 2005). These genes respond rapidly and transiently to drought, cold and high-salinity stresses and their expression peaks for several hours after stress and then decreases. This is followed by synthesis of function proteins like late embryogenesis abundant (LEA) proteins, detoxification enzymes, and enzymes for osmoprotectant synthesis whose expression increases gradually after stress (Yamaguchi-Shinozaki and Shinozaki, 2006). For details on the current understanding of gene regulation in response to these stresses see Figure 1.2. Apart from osmotic stress, salinity stressed plants suffer from ionic imbalance (Verslues et al., 2006). To mitigate ionic stress and regain homeostasis for normal growth, salt tolerant plants utilise genes that can restrict Na\(^+\) from entering the cells, sequester Na\(^+\) inside vacuoles and chose K\(^+\)
over Na⁺. The genes that control salt tolerance have been recently reviewed by Munns (2005).

Figure 1.2 Transcriptional regulatory network of *cis*-acting elements and transcriptional factors involved in osmotic- and cold-stress responsive gene expression in *Arabidopsis*. Transcription factors controlling stress-inducible gene expression are shown in coloured ellipses. *cis*-acting involved in stress-responsive transcription are shown in boxes. Small filled circles reveal modification of transcription factors in response to stress signals for their activation, such as phosphorylation. Regulatory cascade of stress-responsive gene expression is shown from top to bottom. Early and emergency responses of gene expression are shown in upper part, and late and adaptive responses in the bottom. Thick gray arrows indicate the major signalling pathways and these pathways regulate many downstream genes. Broken arrows indicate protein-protein interactions (adapted from Yamaguchi-Shinozaki and Shinozaki, 2006).

1.7 Transgenics for abiotic stress tolerance

The ultimate goal of functional genomic studies on abiotic stresses is to find suitable candidates that govern stress tolerance so that they can be directly selected or used in
biotechnology approaches to improve crop performance. Generally, the latter involves
the overexpression or suppression of a candidate gene(s) within a transgenic plant that is
subsequently phenotyped for the associated stress tolerance. This also serves as a proof
of gene function.

Numerous studies were conducted to overexpress a transcriptional factor or functional
protein (e.g. osmoprotectants) to induce abiotic stress tolerance. Most involved
interrogating the role of downstream components (effectors) like those coding for
antiporters, heat-shock proteins, superoxide dismutases or LEA proteins, as opposed to
upstream components (regulators) like those coding for various kinases. A
comprehensive list of such transgenic studies was compiled and analysed (Bartels and
Sunkar, 2005; Vij and Tyagi, 2007). However, there is still a need for the identification
of further stress-induced promoters rather than constitutive promoters (e.g. Cauliflower
mosaic virus, CaMV 35S promoter) and much more research is required to decipher the
actual mechanisms for stress tolerance before breeders and farmers can reap benefits
from this work.

1.8 Microarray studies for abiotic stress responses
Microarrays were previously used to profile genes expressed in response to drought,
cold and high-salinity stresses, mostly using Arabidopsis (Table 1.2). Most of the studies
were conducted on Arabidopsis as it was granted the status of model plant at the
beginning of functional genomics research. Following Arabidopsis, rice has been used
as a model for monocot species because of its compact genome and importance as a
food crop. The availability of gene sequences and EST resources in these and other
<table>
<thead>
<tr>
<th>Species</th>
<th>Growth conditions</th>
<th>Stress Treatments</th>
<th>Time points</th>
<th>Tissues analysed</th>
<th>Comments</th>
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<tr>
<td>Rice</td>
<td>Grown hydroponically at 28°C/25°C day/night temperatures, 50% relative humidity, and 12 h light. Grown until roots and shoots measured ~7 and 10 cm, respectively</td>
<td>Salt (150mM NaCl)</td>
<td>0.25 h - 7 d</td>
<td>Roots</td>
<td>Salt tolerant and sensitive cultivars compared. Early time - ABA-induced genes, later times - defence-related genes; water channels - all times. Tolerant cultivar differed from susceptible in timing of gene expression; early in tolerant.</td>
<td>Kawasaki et al., 2001</td>
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<td>Arabidopsis</td>
<td>Grown for 14 - 37 days depending on treatment type</td>
<td>Osmotic (200 mM mannitol); Salt (100 mM NaCl); Cold (4°C); wounding; pathogen attack; jasmonic acid</td>
<td>Differs from 0 h to 5 d depending on treatment type</td>
<td>Leaves, roots and floral organs separately</td>
<td>mRNA levels of previously characterised genes changed significantly in response to other treatments, suggesting multifunctional nature. Out of 43 transcription factors induced during senescence, 28 were induced by different stresses, suggesting overlap.</td>
<td>Chen et al., 2002</td>
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<td>Arabidopsis (wild type and transgenics)</td>
<td>Grown in controlled environment at 22°C for 11 d</td>
<td>Cold (4°C)</td>
<td>0.5-24 h, 7 d</td>
<td>Whole plant</td>
<td>Transcript level of ~8000 genes studied. 306 genes were &gt;3-fold DE at one or more time points. Extensive down-regulation during cold acclimation, indicating, in addition to gene induction, gene repression is likely to play a key role in cold acclimation.</td>
<td>Flower and Thomashow, 2002</td>
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<td>Arabidopsis</td>
<td>7 day old seedlings were grown in hydroponic media for 3 weeks, 12 h light.</td>
<td>Hyperosmotic (200 mM mannitol); Salt (100 mM NaCl); Cold (4°C)</td>
<td>3 h, 27 h</td>
<td>Leaves and roots separately</td>
<td>2409 genes &gt;2-fold DE. 30% transcriptome regulated under stress conditions. Compared to 3 h time point, less number of shared responses were observed at 27 h. 68% of genes expressed were common to those of known circadian clock related genes.</td>
<td>Kreps et al., 2002</td>
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<td>Species</td>
<td>Growth conditions</td>
<td>Stress Treatments</td>
<td>Time points</td>
<td>Tissues analysed</td>
<td>Comments</td>
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<td>Barley</td>
<td>For drought - pots with sand, For salinity - hydroponically until 3 weeks</td>
<td>Drought (desiccation); Salt (150 mM NaCl)</td>
<td>6 - 24 h, depending on stress</td>
<td>Leaves and roots</td>
<td>Transcripts induced under drought stress included jasmonate responsive, metallothionein-like, LEA and ABA-responsive proteins. Most of the genes related to photosynthesis were repressed. Ozturk et al., 2002</td>
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<tr>
<td>Arabidopsis</td>
<td>Grown for 3 weeks in growth chamber at 22°C under 16 h light</td>
<td>Dehydration (desiccated); Cold (4°C); Salt (250 mM NaCl)</td>
<td>1h, 2 h, 5 h, 10 h, 24 h</td>
<td>Whole plant</td>
<td>Builds up on earlier study - Seki et al., 2001. ~7000 independent full length cDNAs used. 53, 277 and 194 genes induced &gt;5-fold after cold, drought and high-salinity treatments, respectively. Various transcriptional regulatory mechanisms thought to function upon stress imposition. Seki et al., 2002</td>
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<td>Arabidopsis</td>
<td>Grown hydroponically until the development of full rosette</td>
<td>Salt (80 mM NaCl); K⁺ starvation; Ca²⁺ starvation</td>
<td>2-96 h</td>
<td>Roots</td>
<td>1096 Arabidopsis transporter genes studied. Cation stress led to changes in transcript level of many genes across transporter families. Several novel putative regulatory motifs were discovered within the sets of co-expressed genes. Maathuis et al., 2003</td>
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<td>Rice</td>
<td>Grown under controlled conditions - 28°C/25°C day/night temperature, 12h light, 83% humidity</td>
<td>Drought; Cold (4°C); Salt (250 mM NaCl); ABA (100μM)</td>
<td>5 h, 10 h, 24 h</td>
<td>Whole plant</td>
<td>From 73 stress-inducible rice genes, 51 were reported in Arabidopsis. Possible cis-acting elements were searched in stress inducible genes. More genes commonly induced by high-salinity, drought and ABA stresses than cold and high-salinity, or cold and ABA. Rabbani et al., 2003</td>
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<td>Barley</td>
<td>Grown on pods at 18°C/13°C day/night, 10 h light for 7 d</td>
<td>Dehydration (desiccation); Cold (4°C); Salt (175 mM NaCl); high light; copper toxicity</td>
<td>5 h to 53 h, depending on treatment</td>
<td>Leaves</td>
<td>99 genes DE in at least one condition. Plants challenged with combined stresses showed different response than for individual stress conditions. Atienza et al., 2004</td>
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<td>Species</td>
<td>Growth conditions</td>
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<td>Time points</td>
<td>Tissues analysed</td>
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<td>Poplar</td>
<td>In-vitro cultured clones were grown in pots with sand for 2 months. These plants were transferred to hydroponic media and grown for another month</td>
<td>Salt (300 mM); after withdrawal of salt stress</td>
<td>0.5-72 h; 1-48 h after withdrawal</td>
<td>Whole plants</td>
<td>Gene expression during salt stress and recovery from stress compared. Transcripts induced by salt stress were associated to ionic and osmotic homeostasis like magnesium transporter-like, syntaxin-like, plasma membrane intrinsic, cytochrome 450 proteins. Photosynthesis related transcripts repressed after 72 h of stress but recovered after the stress was removed.</td>
<td>Gu <em>et al.</em>, 2004</td>
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<tr>
<td><em>Arabidopsis</em> and <em>Thelungiella halophila</em></td>
<td>Grown on MS plates with 1.2% agar and 3% sugar for 2-3 weeks</td>
<td>Salt (250 mM NaCl)</td>
<td>2-24 h</td>
<td>Whole plant</td>
<td>Fewer number of genes induced in <em>T. halophila</em> after salt stress. The genes expressed by <em>Arabidopsis</em> after salt stress were expressed by <em>T. halophila</em> in normal conditions, before stress imposition.</td>
<td>Taji <em>et al.</em>, 2004</td>
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<td>Barley</td>
<td>Seedlings were grown hydroponically for 15 d under 13 h light, 70% relative humidity, 25°C/22°C day/night temperatures</td>
<td>Osmotic (20% w/v PEG); Salt (200 mM NaCl)</td>
<td>1h, 24 h</td>
<td>Leaves and roots separately</td>
<td>Different set of genes were DE under osmotic stress than salt stress. Most of the early salt responsive genes were similar to those of osmotic stress regulated ones suggesting plants suffer osmotic stress in initial phase of salt stress.</td>
<td>Ueda <em>et al.</em>, 2004</td>
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<td>Potato</td>
<td>Grown hydroponically for 5 weeks, 16 h/8 h - day/night, 25°C</td>
<td>Cold (4°C); heat (35°C); Salt (100 mM NaCl)</td>
<td>3 h, 9 h, 24 h</td>
<td>Leaves and roots separately</td>
<td>~12000 clones cDNA microarray used. 3314 clones were DE in total including those associated with signal transduction and heat shock proteins. General and stress specific responses identified.</td>
<td>Rensink <em>et al.</em>, 2005</td>
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<tr>
<td>Rice</td>
<td>Cultured in tanks filled with soil and irrigated with nutrients for 22 d</td>
<td>Salt (5:1 NaCl and CaCl₂ - 7.4 dS/m)</td>
<td>30 d</td>
<td>Whole plant; main shoot dissected to get growing point and crown tissue</td>
<td>Salt tolerant and sensitive cultivars compared. Affymetrix rice GeneChip used (55,515 probes). Genes related to flavonoid biosynthesis were DE only in tolerant genotype. Cell wall-related genes were responsive in both genotypes, suggesting cell wall restructuring as adaptive mechanism. More genes expressed in tolerant genotype than susceptible one.</td>
<td>Walia <em>et al.</em>, 2005</td>
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crops has been explored through transcriptional profiling to improve our understanding on molecular mechanisms of abiotic stress adaptation and tolerance.

Significant overlap was detected among the genes expressed under drought, cold and high-salinity stresses (Kreps et al., 2002; Rabbani et al., 2003), suggesting the existence of some sharing in the stress pathways. On the other hand, many genes were identified that were expressed only in response to a particular stress (e.g., between Kreps et al., 2002 and Seki et al., 2001, 2002; between Seki et al., 2001, 2002 and Flower and Thomashow, 2002). In Arabidopsis, whilst Seki et al. (2001, 2002) reported fewer genes to be induced by cold-stress than drought and high-salinity stresses, Kreps et al. (2002) found cold-stress induced nearly double the number of genes than high-salinity stress. These inconsistencies may be attributed to the biological differences among the genotypes used, plant growth conditions, stress treatment conditions and/or their detection methodologies. Others focused on comparing the responses between tolerant and susceptible genotypes to a particular stress. Kawasaki et al. (2001) compared the genes expressed by a rice salt tolerant genotype (Pokkali) to those expressed by a salt susceptible genotype (IR29) in response to salt stress. They concluded that the two genotypes differed in the timing of gene expression upon stress. The delayed gene expression by the salt susceptible genotype (IR29) was assumed to be responsible for salt sensitivity (Kawasaki et al., 2001). In another study, the transcriptome of the salt tolerant rice genotype (FL478) was compared to the salt sensitive genotype (IR29). The greater number of genes expressed by FL478 than IR29 was believed to be associated with FL478 being able to maintain a low Na\(^+\) to K\(^+\) ratio (Walia et al., 2005). Further, Taji et al. (2004) extended the concept of comparative transcriptomics to a species level by comparing the expression profiles of Arabidopsis thaliana with a halophyte
(Thellungiella halophila), which have 90-95% microsynteny at the cDNA level. The chief difference in gene expression was that *T. halophila* expressed a number of salt-responsive *A. thaliana* genes even before the stress was imposed, again revealing the importance of the timing of gene expression for stress tolerance. In general, comparison of gene expression profiles between contrasting genotypes provides much information in understanding the spatial and temporal patterns of gene expression required for abiotic stress tolerance.

1.9 Crosstalk between abiotic and biotic stress responses

The gene expression profiling using microarrays has served as an excellent platform to compare genes expressed by plants in response to various abiotic and biotic stresses. As described above this has led to detection of stress specific and shared pathways. The abiotic stress specific pathways and crosstalk between abiotic stress responses has been reviewed (Knight and Knight, 2001; Seki et al., 2003). On the other hand, Chen et al. (2002) studied expression profiles of various transcription factor genes in various organs at different developmental stages under biotic and abiotic stresses. They conducted >80 experiments representing 57 independent treatments with cold, salt, osmoticum, wounding, jasmonic acid and different types of pathogens at different time points. The mRNA levels of a number of previously characterised transcriptional factor genes changed significantly in association to other regulatory pathways, suggesting their multifunctional nature (Chen et al., 2002). Moreover, Cheong et al., (2002) used an *Arabidopsis* Genome GeneChip array (Affymetrix, Santa Clara, CA) to generate transcriptional profiles of *Arabidopsis* in response to wounding, pathogen, abiotic stress and hormonal responses. They identified a significant number of genes and transcription factors to be commonly regulated by all of the stress conditions assessed. Munns (2005)
also appraised that many genes identified by salt-stress expression studies were also expressed during pathogen infection. Recently, the crosstalk between abiotic and biotic stress responses and their points of convergence in stress signalling networks were reviewed (Fujita et al., 2006). Several transcriptional factors and kinases are thought to be promising candidates for crosstalk between stress signalling pathways. In fact, hormone signalling pathways regulated by abscisic acid, salicylic acid, jasmonic acid and ethylene, as well as reactive oxygen species (ROS) signalling pathways are suggested to play key roles in crosstalk between biotic and abiotic stress signalling (Figure 1.3, Fujita et al., 2006).

1.10 cDNA library resources at RMIT University

A cDNA library was generated at RMIT University after challenging a chickpea germplasm line ICC 3996 (resistant to Ascochyta blight) with the fungus. From the 1021 clones sequenced, 571 (56%) showed significant homology to existing database entries (Coram and Pang, 2005). The 1021 ESTs were clustered and assembled into 516 unigenes (Figure 1.4). Based on putative functions of these ESTs they were categorised into those associated to defence, cellular communication/signalling, transcription, energy metabolism, cell rescue/death, protein synthesis, cell cycle/DNA processing, transport facilitation, and those with unknown and unclear functions (Coram and Pang, 2005).

Another cDNA library was generated at RMIT University after challenging a Lathyrus sativus (a close relative of chickpea) line ATC 80878 (resistant to Mycosphaerella pinodes) with the fungus. Of the 818 clones sequenced, 431 (53%) showed high similarity to existing database entries (Skiba et al., 2005). These were categorised into
Figure 1.3 Convergence points in abiotic and biotic stress signalling networks (adapted from: Fujita et al., 2006).
Figure 1.4 Functional classification of the 516 non-redundant \textit{C. arietinum} ESTs.
different functional groups based on their putative function (Figure 1.5, Skiba et al., 2005). Additionally, numerous defence related resistance gene analogs (RGAs) from lentil (\textit{Lens culinaris}) were available (Barkat Mustafa, pers. comm.).

![Figure 1.5 Functional classification of the 818 \textit{L. sativus} ESTs.]

1.11 Rationale

Chickpea, the third most important grain legume, loses more than 50\% of yield globally to abiotic stresses (Ahmad \textit{et al.}, 2005). The chief abiotic constraints in their order of importance are drought, cold and high-salinity (Croser \textit{et al.}, 2003). The cultivated
chickpea has a high morphological but narrow genetic variation (Udupa et al., 1993) making it difficult for breeders to produce elite cultivars with durable resistance to the major biotic and abiotic stresses. Molecular breeding (or MAS) is limited by the fact that abiotic stresses are inherited in a more quantitative manner and may be subjective to assess under field conditions due to confounding environmental factors, which makes it difficult to screen for and quantitate tolerance. Moreover, quantitating the effects of abiotic stresses involves the measurement of various factors like survival rate, yield, dry matter production, days to maturity, flower/pod survival, root mass and transpiration ratio. This feature of abiotic stresses represents a major obstacle to developing molecular markers.

Marker-assisted breeding is increasingly targeted toward tracking the candidate genes responsible through gene identification and functionality studies (Tuberosa and Salvi, 2004). Candidate genes, identified and characterised through whole genome sequencing projects or expressed sequence tag (EST) libraries may be assessed for their comparative transcriptional activity against biological reactions to specific plant stresses via microarray technologies. Analysis of the expression and function(s) of stress inducible genes facilitates understanding of the molecular mechanisms underlying the stress tolerance responses. This approach has potential to assist molecular plant breeders in improving stress tolerance by gene selection and/or genetic manipulation. In order to obtain a complete picture of a plant’s response to stress, it would be ideal to study the expression profiles of all the genes in its genome. Currently, this is only possible for model crops like *Arabidopsis thaliana* (thale cress), *Oryza sativa* (rice), *Medicago truncatula* (barrel medic), *Populus trichocarpa* (black cottonwood) whose genomes have been sequenced. In the near future it will also be possible for *Brachypodium*
distachyon, Lotus japonicus (lotus), Manihot esculenta (cassava), Lycopersicon esculentum (tomato), Solanum tuberosum (potato), Sorghum bicolor and Zea mays (corn) whose genome sequencing shall be soon completed (Plant Genome Central – Genome Projects in Progress; URL: http://www.ncbi.nlm.nih.gov/genomes/PLANTS/PlantList.html). Until this is available for other crops, researchers have to rely on information generated by studying these model crops and explore the EST/cDNA sequences from the same or closely related species generated by various studies.

A set of chickpea unigenes and Lathyrus ESTs were available at RMIT University. Although the ESTs for these libraries were derived from plant tissue challenged with a particular biotic stress (pathogen), it was clear from annotation of the ESTs that many may also be associated with abiotic stresses (as seen in Kreps et al., 2002; Seki et al., 2002; Rabbani et al., 2003). In fact, a considerable amount of interaction was revealed between wounding, pathogen, abiotic stress and hormonal responses in Arabidopsis by transcriptional profiling (Cheong et al., 2002). Munns (2005) also reported that many genes identified by salt-stress expression studies were common with pathogen infection, whilst Fujita et al. (2006) reviewed abiotic and biotic stress responses in plants and concluded that a significant amount of crosstalk existed in the stress signalling networks. Therefore, in the absence of a purely abiotic stress related cDNA library for chickpea, a boutique pulse array constructed from available EST and RGA resources was considered an excellent tool for studying the chickpea transcriptome in response to abiotic stresses.

Considering the gaps in knowledge regarding the mechanisms of abiotic stress tolerances in chickpea and the opportunities for study identified in this review, the aims of this study were to:
1. Construct a boutique pulse microarray (in association with Mr. Tristan Coram, RMIT University) representing all the chickpea ESTs (unigenes), defence related ESTs from close relative *Lathyrus sativus*, and RGAs from *Lens culinaris*.

2. Design assays for challenging chickpea plants with chief abiotic stresses, namely, drought, cold and high-salinity. Challenge the chickpea genotype ICC 3996 (the donor of chickpea ESTs) with drought, cold and high-salinity stresses, and interrogate the changes in its transcript levels using the pulse microarray. This study shall reveal if the boutique pulse array is capable of detecting transcriptional changes in response to the abiotic stresses being queried.

3. Select the genotypes tolerant and susceptible to drought, cold and salinity stresses. Challenge a group of stress tolerant and susceptible genotype with particular stresses and compare the transcripts that are differentially expressed. This study shall help formulate a hypothesis regarding what genes may be potentially involved in tolerance or susceptibility to each abiotic stress.

4. Challenge a second group of tolerant and susceptible genotypes with the particular stresses and compare the transcripts that are differentially expressed. Perform a two-way comparison of the differentially expressed transcripts in the two groups of tolerant and susceptible genotypes. This study shall help determine if a particular set of genes are expressed only in tolerant/susceptible genotypes, which might bolster their proposed link to tolerance/susceptibility. Additionally, it might reveal how the genes being interrogated behave in different tolerant and susceptible genotypes under the same stress condition.

5. Interpret the results from transcriptional profiling in context of putative gene functions and genotypes in which they were expressed to try and uncover the mechanisms and pathways involved in abiotic stress tolerance in chickpea.
Chapter 2

Construction of a boutique ‘Pulse Chip’ microarray to study transcriptional changes in ICC 3996 in response to major abiotic stresses; drought, cold and high-salinity

2.1 Introduction

Abiotic stresses, mainly, drought, cold and high-salinity greatly affect chickpea production (refer to section 1.1.6). As described in Chapter 1, the efforts to improve abiotic stress tolerance in chickpea has involved screening of germplasm, breeding and marker-assisted selection. These techniques have mostly relied on selection of particular traits known to be involved in stress tolerance; e.g., selection of higher root density for drought tolerance. However, multiple genes govern abiotic stress tolerance quantitatively, making it difficult to screen for tolerance (refer to section 1.3.1). Hence, identification of the actual number of genes involved in abiotic stress tolerance and their mechanisms of action is vital for effective breeding strategies.

Plants have evolved a number of mechanisms to cope with different biotic and abiotic stresses. To survive against these stresses, plants respond and adapt with complex mechanisms, including developmental, morphological, physiological, and biochemical strategies (Taji et al., 2004). One important step in the control of stress response is transcriptional activation and repression of genes. The products of these genes function not only in stress tolerance but also in stress response (Yamaguchi-Shinozaki and Shinozaki, 2006). Studies on molecular mechanisms of abiotic stress tolerance have unravelled number of genes involved, right from stress perception to actual
response or adaptation (refer to section 1.6). The speed and coordination of stress perception, signal transduction and transcriptional activation is vital for successful stress tolerance. At the genomic level, plant stress responses are complex and diverse, and every gene involved in the tolerance response, from perception to signalling to direct involvement, forms part of a coordinated response network.

Our overall understanding of the coordinated tolerance response at the molecular level can be improved by analysing the gene/protein/metabolite expression profiles in response to stress (refer to section 1.3.2). One such approach involves generating gene expression profiles in response to a particular stress using microarrays (refer to section 1.4). This valuable tool has been exploited in a number of crops to visualise the coordinated response of a large set of genes in response to abiotic stresses (refer to section 1.8). However its use has been limited by the availability of various resources, mainly gene or EST sequences. Crops such as *Arabidopsis thaliana*, *Oryza sativa*, and *Medicago truncatula* that were nominated as model plants were principally benefited by the availability of the whole genome sequences, which were subsequently used in expression studies. There is lack of sequencing initiative in most of the other crops (like chickpea) and therefore they instead use information from the study of these model species and sequence resources from other research projects in same or related species.

ICC 3996 is a *desi* chickpea germplasm line with reportedly high capacity for *Ascochyta* blight resistance (Nasir *et al.*, 2000; Collard *et al.*, 2001). Therefore, as reported in section 1.10, this was used in construction of a blight resistance cDNA library from which 1021 clones were sequenced and annotated (Coram and Pang,
2005). Further, 818 ESTs from a grasspea (*Lathyrus sativus*, close relative of chickpea) cDNA library generated in response to *Mycosphaerella pinodes* (Skiba *et al*., 2005) were available. These EST libraries at RMIT University were not subtracted libraries, thus retaining many genes involved in cellular metabolism, protein synthesis, transcription, cell rescue, signalling and communication, energy metabolism and transport facilitation. The annotation of these ESTs suggested that many might also be associated with abiotic stresses (as seen in Kreps *et al*., 2002; Ozturk *et al*., 2002; Seki *et al*., 2002; Jang *et al*., 2004; Ueda *et al*., 2004). In fact, a considerable amount of interaction was revealed between wounding, pathogen, abiotic stresses and hormonal responses in various crops (refer to section 1.9). In addition to above, a RGA sequence resource from lentil (*Lens culinaris*) was available with The University of Melbourne (Barkat Mustafa, pers. comm.).

Hence the aims of the experiments described in this chapter were to:

(i) Construct a boutique ‘Pulse Chip’ microarray representing all the chickpea ESTs (unigenes), ESTs from grasspea, and RGAs from lentil in association with Mr. Tristan Coram at RMIT University.

(ii) Design assays for challenging chickpea plants with major abiotic stresses, namely, drought, cold and high-salinity.

(iii) Challenge the chickpea genotype ICC 3996 (donor of chickpea ESTs for the microarray) with drought, cold and high-salinity stresses, and interrogate the changes in its transcript levels using the ‘Pulse Chip’ microarray.

This study will determine if the boutique Pulse Chip array is capable of detecting transcriptional changes in response to the abiotic stresses being queried. This shall
help to determine if the use of ‘Pulse Chip’ array generated mainly from biotic stress related ESTs could be expanded to study expression profiles of other chickpea genotypes, tolerant and susceptible to the abiotic stresses being interrogated.

2.2 Materials and Methods

2.2.1 Spotted cDNA array preparation

The 516 non-redundant chickpea ESTs (Coram and Pang 2005), 156 grasspea ESTs (Skiba et al. 2005), 41 *Lens culinaris* resistant gene analogs (RGAs; Barkat Mustafa, 2005, pers. comm.), 43 chickpea cDNAs whose sequencing reactions failed and 12 controls were spotted on the array. The 12 controls included negative, printing, and blank buffer controls. Thus, a total of 768 features were printed on the array according to Minimum Information about a Microarray Experiment (MIAME) guidelines (Brazma et al. 2001). The complete list of the 768 features is presented in Appendix 1.

Mr. Tristan Coram (RMIT University) designed the array and Mr. Barkat Mustafa (The University of Melbourne) provided the lentil RGAs. Only the construction of ‘Pulse Chip’ array described below that formed a part of this study was performed in association with Mr. Tristan Coram.

2.2.1.1 Probe preparation: PCR amplification, purification and resuspension

The purified pGEM®-T Easy (Promega, Madison, WI) vector plasmids extracted from the cDNA library were used in 110 µL PCR reactions, as follows: 2.2 µL purified vector, 11 µL 10X PCR buffer (Invitrogen Life Technologies, Carlsbad, CA), 2.2 µL 10 mM dNTP (Invitrogen Life Technologies, Carlsbad, CA), 3.3 µL 50 mM MgCl₂, 5.5 µL of 10 µM PCR primer (Clontech, Mountain View, CA), 0.15 µL *Taq* polymerase (Invitrogen Life Technologies, Carlsbad, CA) and made up to 110 µL
with sterile MilliQ water. The PCR amplifications were performed in a ThermoHybaid PCRExpress™ thermocycler (ThermoHybaid, Franklin, MA) using following temperature regime: initial denaturation at 94°C for 2 min followed by 35 cycles of denaturation for 45 s at 94°C, annealing at 55°C for 30 s, extension at 72°C for 1.5 min, followed by a final extension step of 10 min at 72°C. The second and third replicate 110 µL PCRs were performed after substituting the purified plasmid with 2.2 µL of PCR products from first PCR reactions.

Considering that *L. sativus* cDNA clones were present in the same vector as the chickpea clones, the cDNA inserts (probes) of all ESTs were amplified to >2000 ng and purified as above. The 41 RGA sequences were amplified to >2000 ng from lentil DNA using specific primers designed to target potential plant resistance gene motifs (Barkat Mustafa, pers. comm.). The RGA probes were then purified and prepared for printing as for the EST probes.

The PCR reaction products were combined and purified using Montage™ PCRµ96 plates (Millipore, Billerica, MA) and a vacuum manifold (Qiagen, Valencia, CA). All the PCR products were visualised on 1.5% agarose gels to confirm the presence of single bands (Figure 2.1). The pellets of each well were resuspended in 10 µL 50% (v/v) dimethylsulphoxide (DMSO), the preferred buffer for cDNA probes, with overnight shaking on a platform mixer at 250 rpm and at 4°C. The samples were then transferred to a V-bottom polypropylene 384-wells plate (Corning Incorporated Life Sciences, Acton, MA) and stored at 4°C until printing of the array.
Figure 2.1 Example of cDNA inserts from pGEM®-T Easy Vector (Promega, Madison, WI) plasmids amplified using clontech primers (Clontech, Mountain View, CA). The first lane in each row represents 1 kb DNA ladder (Fermentas Life Sciences, Maryland, USA).
2.2.1.2 Printing of array

Microarray grids were printed onto Gamma Amino Propyl Silane (GAPS) II slides (Corning Incorporated Life Sciences, Acton, MA) using a BioRobotics® MicroGrid II Compact (Genomic Solutions, Ann Arbor, MI) and four Microspot™ 2500 pins (Genomic Solutions, Ann Arbor, MI) at RMIT University (Victoria, Australia). For each sub-grid, probes and controls were deposited once with a volume of approximately 6 nL and diameter of 200 µm. The array had subgrids that comprised 14 x 14 grids from one pin. Four such pins printed side-by-side to contain 784 grids. These four pins together formed a metagrid. Each metagrid contained all 768 features (the remaining 16 spaces being vacant). Each array had six replicates of the metagrid representing six technical replicates per spot.

After printing, slides were treated according to the guidelines for GAPS II coated slides, which involved steaming of the array surface by holding the array side down over a beaker of boiling sterile water for 5 s and snap-drying it for 5 s at 100°C on a heating block (printed side up). This action rehydrated the probes to ensure even distribution of DNA within spots. The spotted DNA was then immobilised by UV cross-linking at 70 mJ and baking at 80°C for 3 h. Finally, the slides were stored in a dust-free desiccated environment for no longer than two months before use.

2.2.2 Assays to challenge chickpea plants with drought, cold and high-salinity

The assays to challenge chickpea plants with drought, cold and high-salinity were carefully designed in consultation with the specialists in each respective area. The assay for imposing drought stress in chickpea was designed under the guidance of Drs. David Hoisington and Vadez Vincent (International Crop Research Institute for the
Semi-Arid Tropics, AP, India). Dr. Heather Clarke (Centre for Legumes in Mediterranean Agriculture, WA, Australia) advised on setting up the cold stress assay. Mr. Moses Maliro (Faculty of Land and Food Resources, The University of Melbourne, Victoria, Australia) provided clues on challenging chickpea plants with high-salinity stress.

The experimental design of this study was carefully chosen to target adaptive genes and attempted to simulate natural conditions. This was achieved by cultivating plants in a glasshouse instead of a growth chamber, and by applying uniform and prolonged stress before harvesting the tissue samples. Moreover, it was known that chickpea is most sensitive to drought and cold stresses at flowering (Khanna-Chopra and Sinha, 1987; Srinivasan et al., 1999; Clarke and Siddique, 2004). Therefore, this study examined both the leaf and flower response for drought and cold stress. However, considering that plants usually encounter salinity stress from the vegetative stage (if grown on saline soils), the high-salinity stress was applied only at the early growth stage. Further, the time-points chosen for tissue collection after high-salinity stress were based on the results of a pilot experiment that showed two-week old chickpea plants could not prevent salt from reaching leaves after 48 h of stress with 150 mM NaCl (as evidenced by appearance of water-soaked lesions on lower leaves). Subsequently, in all the treatments, the collection of dying tissues, such as yellowing leaves and aborting flowers, was avoided to capture active tolerance responses.

2.2.2.1 Challenging chickpea with drought stress and collection of tissues

Seeds of ICC 3996 were obtained from the Australian Temperate Fields Crop Collection (Horsham, Victoria, Australia). The seeds were first surface sterilised by
placing them in 70% ethanol for two minutes followed by three washes with sterile water. The seeds were then germinated on moist filter paper in Petri dishes. Germinated seeds were planted in 15 cm plastic pots containing autoclaved potting mix (Yates, Homebush, NSW, Australia). Five treatment and five control plants were grown (one plant per 15 cm pot). The plants were grown normally in the glasshouse with temperature set-up between 15 and 25°C. The plants were watered to keep them moist but excess watering was avoided. They were fertilised twice with urea (seven and 20 days after sowing) during establishment and once with Nitroso® (Amgrow, Australia) at 45 days after sowing. The drought stress was imposed two weeks after flowering, as follows:

All the plants were saturated with water late in the evening. The next morning, the pots were bagged such that no water was allowed to further evaporate from the pots. A one ml pipette tip was cut slightly at the tip and inserted in the pot to allow addition of water (Figure 2.2). The pot weights at this stage were recorded as the initial pot weights. The amount of water (water content) in each pot was estimated to be 30% of the initial pot weight. From the subsequent day onwards, the control pots were maintained at 80% water content. However, the treatment pots were allowed to lose 5-10% of their water content per day and any extra water lost (>10%) was replenished. The leaf, root and flower/early-pod tissues were collected individually when the treatment pots reached 30% water content, indicative of a drought or high water deficit condition (Ray and Sinclair, 1998; Dr. V. Vincent, 2005, pers. comm.; Dr. D. Hoisington, 2005, pers. comm.). The tissues from the control plants were also collected at the same time. The tissues were snap frozen in liquid nitrogen and preserved at –80°C until RNA extraction.
2.2.2.2 Challenging chickpea with cold stress and collection of tissues

The seeds of ICC 3996 were germinated and the plants cultivated as described in section 2.2.2.1. The cold stress treatment commenced two weeks after flowering (Figure 2.3).

The treatment plants were exposed to a 12 h day and 12 h night temperature cycle of 15-25°C and 5°C, respectively. The control plants were maintained in same conditions in glasshouse, i.e., with temperature set-up between 15 to 25°C. The leaf and flower/early-pod tissues were collected after the seventh night at 5°C. The tissues from the control plants were also collected at the same time (Croser et al., 2003;
Clarke and Siddique, 2004; Dr. H. Clarke, 2005, pers. comm.). The tissues were snap frozen in liquid nitrogen and preserved at –80°C until RNA extraction.

Figure 2.3 ICC 3996 plant at the commencement of cold stress treatment.
2.2.2.3 Challenging chickpea with high-salinity stress and collection of tissues

The seeds of ICC 3996 were germinated as described in section 2.2.2.1. Germinated seeds were grown in a hydroponic system using 50 L plastic crates. Two crates were set-up, one each for treatment and control. Forty holes (8 x 5) of 5 cm diameter were drilled in the crates’ lid and rockwool plugs were fixed in them. Ten germinated seeds were transplanted in rockwool plugs within each crate. The seedlings were watered normally from above for four days. The following day, the crates were filled with ½ strength modified Hoagland’s nutrient medium (pH 6.5; Taiz and Zeiger 2002; Appendix 2). The medium was aerated using two aquarium pumps per crate. The nutrient medium was subsequently replaced with full strength solution (pH 6.5) after a further seven days. At the 18th day, the nutrient medium for the treatment plants was replaced with full-strength modified Hoagland’s + 150 mM sodium chloride (NaCl) (pH 6.5), a salinity concentration known to be toxic to chickpea (data not shown; Munns et al., 2002). The control plants continued to grow in replaced full-strength modified Hoagland’s solution (pH 6.5) (Figure 2.4). Leaf/shoot and root tissues were collected from five treatment and control plants at 24 and 48 hours after the high salt solution was added to the treatment plants. The tissues were snap frozen in liquid nitrogen and preserved at –80°C until RNA extraction.

2.2.3 Detection of ESTs differentially expressed under various abiotic stress conditions

2.2.3.1 Biological replication and total RNA extraction

Each stress treatment experiment was performed in three biological replications. The tissues from five treatment or control plants for each biological replication were pooled before RNA extraction. Leaf, flower/early-pod, and root tissues were pooled
The total RNA was extracted using the Qiagen® RNeasy™ Plant Mini Kit (Qiagen, Valencia, CA). The procedure mentioned by the manufacturer was followed. The RNA yield and purity were checked on a spectrophotometer (Cary 50 Bio, Varian, Palo Alto, CA) and its integrity verified using gel electrophoresis. A 2 µL aliquot of total RNA, mixed with 8 µL of RNase-free water (Qiagen, Valencia, CA) and 3 µL 5X RNA loading buffer (Appendix 3), was pipetted into wells of a 1.2% formaldehyde agarose (FA) gel (Appendix 3) and run in 1X FA gel running buffer (Appendix 3) at 100 V. The gels were post-stained by soaking in a solution of 300 mL 1X TBE containing 40 µL of 10 mg/mL ethidium bromide for 20 min, followed by destaining in MilliQ water for 20 min. Stained gels were viewed under UV-light transilluminator and the images captured using a Gel-Doc™ system (Bio-
Figure 2.5 Flow-chart showing the stress treatment procedure and tissue sample processing to generate gene expression profiles. The high-salinity stress treatment included two time points (24 h and 48 h) at which the tissues were harvested.
Rad, Hercules, CA). Figure 2.6 shows an example of good quality total RNA isolated from the harvested tissue samples. Subsequently, 5 µL aliquots of total RNA were diluted 1:200 in DEPC water (Appendix 4) and assessed by reading the absorbance at 260 and 280 nm. An absorbance of 1 unit at 260 nm corresponded to 40 µg of RNA and an OD$_{260}$/OD$_{280}$ ratio of >1.9 was considered to be good quality RNA.

![Figure 2.6](image)

**Figure 2.6** Example of good quality total RNA samples extracted from chickpea tissue, run on a 1.2% formaldehyde gel and stained with ethidium bromide. The first lane on the left represents a 100 bp DNA Ladder Plus (Fermentas Life Sciences, Maryland, USA).

2.2.3.2 cDNA target synthesis

From the total RNA for each treatment condition and corresponding control sample, 50 µg of RNA per sample was concentrated to 5.5 µL in a laminar air flow for use in reverse transcription. Briefly, 5 µg of Oligo dT 15 (Roche Diagnostics, Mannheim,
Germany) was mixed with total RNA. The mixture was incubated at 70°C for 10 min and then chilled on ice for 10 min before adding the first strand buffer (Invitrogen Life Technologies, Carlsbad, CA) to a final concentration of 1X, aa-dUTP/dNTPs mix (final concentrations of 0.5 mM dATP, 0.5 mM dGTP, 0.5 mM dCTP, 0.2 mM dTTP, 0.3 mM aa-dUTP), DTT (Invitrogen Life Technologies, Carlsbad, CA) to a final concentration of 10 mM, and 150 units of Superscript II reverse transcriptase (Invitrogen Life Technologies, Carlsbad, CA) in a total reaction volume of 30 µL made up using DEPC-treated water (Appendix 4). Reverse transcription was carried out at 42°C for 2 h in a Thermo Px2™ thermal cycler (Thermo, Milford, MA). After reverse transcription, excess RNA template was hydrolysed by adding 10 µL of 1 M NaOH and 10 µL of 0.5M EDTA (pH 7.0) to each tube and incubating for 15 min at 65°C. This mixture was then neutralised with 25 µL of 1 M HEPES (pH 7.0).

2.2.3.3 Labelling of cDNA targets and hybridisation

The cDNA targets were purified and post-labelled using a Qiagen® QIAquick™ PCR purification kit (Qiagen, Valencia, CA) and Cy3/Cy5 mono-NHS esters (Amersham Pharmacia, Buckinghamshire, UK) resuspended in 0.1 M NaHCO₃ (pH 9.0). Briefly, cDNA targets were applied to QIAquick columns and washed/dried according to manufacturer’s instructions, before adding the appropriate resuspended CyDye to the column membrane and incubating for 1 h at room temperature in the dark. Following incubation, labelled samples were eluted, appropriate Cy3 and Cy5 targets combined (to represent a stress treated sample and control sample from corresponding tissue and time point), and purification was repeated.
Slides were pre-hybridised by blocking in 5X SSC, 0.1% SDS, 25% formamide, 1% BSA for 45 min at 42°C, rinsed in distilled water, and dried with an air gun (see Appendix 4 for SSC and SDS stock solutions). Purified combined targets were resuspended in 2X hybridisation buffer (5X SSC, 0.2% SDS, 50% formamide), 25 µg Human Cot1 DNA (Invitrogen Life Technologies, Carlsbad, CA), 0.4 mg polyA (Sigma-Aldrich, St Louis, MO), 0.5 mg salmon sperm DNA (Sigma-Aldrich, St Louis, MO), and made up to 40 µL with sterile water. The resuspended combined targets were denatured at 100°C for 2 min and hybridised onto the array (containing six metagrids) by pipetting below a 25 x 25 mm Lifter slip (Grale Scientific, Australia) that was placed on the array slide. The slide was placed in a waterproofed and humidified hybridisation chamber (Corning Incorporated Life Sciences, Acton, MA) and incubated in a water bath at 42°C for 16-20 h in dark.

2.2.3.4 Scanning of array and data transformation

The slides were washed for 5 min in each of 1X SSC/0.2% SDS and 0.1X SSC/0.2% SDS, and twice for 2 min in 0.1X SSC. Washed slides were rinsed in distilled water and immediately dried with an air gun. Slides were scanned at 532 nm (Cy3, green laser) and 660 nm (Cy5, red laser) using an Affymetrix® 428™ array scanner (Santa Clara, CA). The images were captured with Affymetrix® Jaguar™ software (v. 2.0, Santa Clara, CA). Using Jaguar™ software, slides were first preview scanned at 20 µm resolution to locate the grids on the slide surface. All the metagrids were then scanned at 10 µm resolution with a line average of three (three repeats per image line), and a gain setting of 65 db for both Cy3 and Cy5 channels. Jaguar™ software generated a separate image file for each channel per scan, which were subsequently saved as ‘.tiff’ files.
Image analysis was performed using Imagene™ v. 5.5 image analysis software (Biodiscovery, Marina Del Rey, CA). Both the Cy3 and Cy5 images produced by Jaguar™ were opened using Imagene™ and overlaid to produce a composite image. Spot diameter (pixels) within the image was determined with the ‘ruler’ tool before generating a grid defined by the number of columns, rows and spot diameter (14.0 pixels). The grid was then positioned over the sub-grid by the ‘automatically place grid’ tool (local flexibility set to 5.0 pixels) to ensure optimal spot recognition. Some grid spots had to be manually adjusted by visual inspection of their alignment with array spots. The gene ID file generated using Microsoft® Excel (Microsoft, Redmond, WA), was then loaded to assign a particular identification to each spot within the array. Spots were individually quantified using the fixed circle method; sample values were measured as the mean of pixels within the spot circle and the local background in a three-pixel diameter ring that began three pixels outside the spot circle.

During quantification, auto segmentation was performed, which partitioned the image into regions of specified meaning, namely spot versus background. This view showed which pixels were valued as signal, and which were background and thus ignored in the quantification process. Once the segmentation was complete, suspicious spots were identified and flagged by various types of automated and manual flagging. Under the ‘quality flags’ tool, options selected for automatic flagging included:

1. Empty spots: Low-expressed or missing spots were flagged based on the sensitivity threshold \( R < 4 \), where \( R = (\text{signal mean} - \text{background mean}) \times \text{standard deviation}^{-1} \). The \( R \) threshold was adjusted until all negative control spots were flagged as ‘empty’.
2. Negative spots: Spots with signal mean lower than background mean were flagged.
3. Poor spots: Five criteria were used including background contamination (confidence level set to 0.9995), signal contamination (confidence level set to 0.9995), high-ignored pixel percentage (set to >25%), high open perimeter percentage (set to >25%), and significant offset from expected position (set to >60%). Automatic multichannel flagging was set to flag a spot in both channels if it was ‘poor’ in one channel, ‘empty’ in both channels, or ‘negative’ in both channels. Spots with mean signal intensity less than two times the local background were manually flagged by opening the data file using Microsoft® Excel (Microsoft, Redmond, WA), flagging the required spots, and then resaving the data file as text delimited (as required for post-image analysis).

Quantification data was imported into Genesight™ 3 (Biodiscovery, Marina Del Rey, CA) for post-image analysis. Using the dataset builder the quantification data was loaded into experimental groups so that the replicate data could be combined. The data set was organised into ratio data for Cy3 and Cy5 for each tissue type or time point. The ‘data preparation’ tool was used to perform a series of specific data transformations:

1. Local background correction: The background intensity of each spot was subtracted from the signal intensity. This was the most accurate way of background correction as it allowed for variations of background intensity over the slide area.

2. Omit flagged spots: Flagged spots from Imagene™ were filtered out of the dataset, ensuring only high quality spots remained.
3. Normalisation: Global normalisation using LOcally WEighted polynomial regreSSion (LOWESS) was used which divides the data into number of overlapping intervals and fits a polynomial function.

4. Ratio: A ratio between treatment and control mean signal intensities was created.

5. Log transformation: This feature allowed the conversion of ratio values into log$_2$ values, where a gene up-regulated by a factor of two in a treated sample had a value of 1.0 and a gene down-regulated by a factor of 2 had a value of -1.0.

6. Combine replicates: Data for replicate spots was combined by taking the average of the replicated spots to produce a single value with a coefficient of variation (cv). Substituting a set of values with single value caused loss of information, but to alleviate this, a cv was also calculated.

2.2.3.5 Identification of differentially expressed ESTs

The identification of differentially expressed (DE) genes can be divided into ranking and selection. Ranking involves the specification of a statistic measure, which captures evidence for DE genes on a per gene basis. Whilst, selection requires specification of procedure (e.g. stipulation of a critical value) for arbitrating what constitutes ‘significant’ DE gene (Yang et al., 2005).

The ranking method employed was based on fold change (FC) cut-off for expression. A stringent FC cut-off value of two-fold was used in the current experiments (Maguire et al., 2002; Scheideler et al., 2002; Lopez et al., 2005; Clarke and Zhu, 2006). Specifically, the expression datasets were used to determine the 95% confidence interval for mean expression ratio of each array feature, and those ESTs whose confidence interval extended beyond the determined FC cut-off were identified as DE.
The two-fold cut-off can be misleading in the event of one gene having transcript level below threshold or above saturation (Clarke and Zhu, 2006). Therefore, two-fold cut-off should be bolstered by using proper biological replications to enable statistical analysis. Subsequently, $t$ statistics were used, accounting for gene-specific variation across arrays (Yang et al., 2005), which is commonly used for assessing DE in plant microarray studies (Dudoit et al., 2002; Fujiwara et al., 2004; Gibly et al., 2004; Buchanan et al., 2005; Salzman et al., 2005). The use of $t$ statistic could be inappropriate if the sample size is small (Draghici, 2003). However, the increased number of technical and biological replicates used in this study ($n=18$, where $n$ represents the number of data points for each array feature) ensured that $t$ statistics could be reliably employed without experiencing large effects from outliers. Additionally, equality of variance tests between channel means was performed for each array feature using the F distribution. In all cases, equal variances were observed, enabling the pooling of sample variances. Students $t$ statistics were then calculated for each feature, and $P$ values were obtained from the $t$ distribution for use in the selection of DE ESTs. Subsequently, False Discovery Ratio (FDR) multiple testing corrections were applied after ranking by FC cut-off and $t$ statistics. Overall, DE ESTs were then identified as those with a 95% confidence interval for mean fold change (FC) that extended beyond the two-fold cut-off and also passed the Students $t$ test ($P<0.05$) and FDR correction (see Appendix 5 for the ranking method employed to identify DE ESTs).

The list of DE ESTs for each treatment and tissue-type/time-point were then compiled and sorted according to their putative functions. The gene expression values were
analysed in the context of the putative function of the genes and the stress condition in which they were expressed, to interpret their possible involvement in stress response.

2.2.4 Quantitative real-time PCR confirmation of DE ESTs

The microarray expression results were validated by performing quantitative real-time PCR (qRT-PCR) on a set of selected ESTs/genes from the list of resultant DE ESTs. This set was chosen to represent different stresses, tissue-types, time points and expression values (up/down-regulation). The primers were designed using Primer3 (Rozen et al., 2000) and possessed a GC content of 40-60%, Tm >50°C, primer length 20–25 nucleotides, and expected amplicon sizes were 100-250 bp. The comparative C\textsubscript{T} method of quantitation (\textDelta\textDeltaC\textsubscript{T} method) was used with the actin gene as a reference. The relative fold-change for each of the selected genes was detected from the C\textsubscript{T} values. For each tissue-type/time-point, 5 µg of total RNA from one of the biological replicates was converted into cDNA using oligodT 15-mer (Roche Diagnostics, Mannheim, Germany) and Superscript II reverse transcriptase (Invitrogen Life Technologies, Carlsbad, CA). The cDNA was purified using the Qiaquick PCR purification kit (Qiagen, Valencia, CA) and diluted to 250 µL in sterile water. The comparative C\textsubscript{T} method (\textDelta\textDeltaC\textsubscript{T} method) eliminated the need for standard curves, but could only be used if PCR efficiencies are relatively equal between target and reference (actin) (Applied Biosystems, 2005). Therefore, validation experiments were performed on 5 to 6 log dilutions of each of the target and reference to determine if their amplification efficiencies were equal. Triplicate qRT-PCR reactions were performed using iQ\textsuperscript{TM} SYBR\textsuperscript{®} Green Supermix (Bio-Rad, Hercules, CA), 0.4 µM of forward and reverse primers, and required amount of cDNA template. The PCRs were performed in a Bio-Rad MyiQ\textsuperscript{TM} (Bio-Rad, Hercules, CA). The temperature regime
used was 95°C for 10 min followed by 40 cycles of 45 s at 95°C, 45 s at 55°C and 1 min at 72°C. Melting curve analysis by applying decreasing temperature from 95°C to 45°C (0.5°C/10 s) and gel electrophoresis of the final product were used to confirm single amplicons. Negative control reactions using untranscribed RNA were run with the main reactions to confirm absence of genomic DNA. Relative fold change for a particular target was determined by comparing the C_T values of each treatment with that of the control. The C_T values were normalised using the C_T reference (actin) prior to comparison.

Validated targets were then used to detect relative fold changes between treated and control samples (10^{-4} dilution). Mean C_T and C_T standard deviations were calculated from the triplicate qPCRs for each sample. \( \Delta C_T \) values were then calculated for target and control samples by deducting the C_T value from the corresponding C_T for reference sample (\( \Delta C_T = C_T_{\text{target}} - C_T_{\text{reference}} \)). The C_T standard deviation (s) values were calculated using: \( s = \sqrt{(s_1^2 + s_2^2)} \). The \( \Delta \Delta C_T \) values could then be calculated by: \( \Delta \Delta C_T = \Delta C_T_{\text{treated sample}} - \Delta C_T_{\text{control sample}} \). The fold difference in expression of treatment relative to control was calculated as \( 2^{\Delta \Delta C_T} \) (Applied Biosystems, 2005; URL: http://www.appliedbiosystems.com/support/apptech/#rt_pcr).

2.3 Results and discussion

2.3.1 Experimental design

A standardised system of plant growth, stress imposition and replication was developed in order to minimise experimental variability and ensure accurate measurements of changes in mRNA abundance (Figure 2.5). The experiments were conducted in reference design where respective tissues from unstressed plants served
as control. A stringent two-fold cut-off combined with Students $t$ test ($P<0.05$) ranking and FDR multiple testing correction selection was used to select ESTs DE between treatment and control plants. This was done even if few genes were missed instead of including false positives. All MIAME guidelines were followed and the datasets were deposited into the Gene Expression Omnibus, National Center for Biotechnology Information (series no. GSE8554).

2.3.2 Spotted cDNA array construction and analysis

A cDNA array (Pulse Chip) was generated using clones from previously characterised chickpea (*Cicer arietinum* L.) (Coram and Pang, 2005) and grasspea (*Lathyrus sativus* L.) (Skiba et al., 2005) cDNA libraries. The PCR-amplified products contained single inserts, as revealed by gel-electrophoresis. A total of 768 features including 516 non-redundant chickpea ESTs along with 156 grasspea ESTs, 41 lentil (*Lens culinaris*) RGAs, 43 chickpea bad reads and 12 controls (see Appendix 1) were spotted on the array. The array had 14 x 14 grids that formed one sub-grid. Four such sub-grids were printed side-by-side to form one meta-grid containing 784 grids. Each meta-grid had all 768 features on it (remaining 16 spaces being vacant). Each array had six replicates of the meta-grid printed on it (representing six technical replicates for each spot). Figure 2.7 shows an example of a scan viewed using Imagene™ v. 5.5 (BioDiscovery, Marina Del Rey, CA). Transcript level for each cDNA was calculated as the average intensity of the six technical replicates, then the average intensity of the three biological replicates. A FC cut-off of 2-fold, Students $t$ test ($P<0.05$) ranking with FDR multiple testing correction selection was used to select ESTs DE between treatment and control plants for all tissue-types, time-points, and stress conditions.
Figure 2.7 Example of a scan view of the ‘Pulse Chip’ array with Imagene™ v. 5.5 (BioDiscovery, Marina Del Rey, CA).
2.3.3 Abiotic stress treatments

The ICC 3996 plants were cultivated, challenged with drought, cold and high-salinity stresses, and tissue samples collected as described in section 2.2. Drought stress caused yellowing of older leaves and abortion of some floral buds. Cold stressed plants did not show any visible injury. This is not surprising because chickpea is known to have a strong indeterminate growth habit (Wang et al., 2006) and may recover from overnight cold-stress if the temperatures return to normal during the day (Heather Clarke, pers. comm.). The high-salinity stressed plants showed water-soaked lesions on older leaves at 48 hours post treatment (hpt), indicating accumulation of salt in older leaves. The salt is known to accumulate in older leaves (crown region) when the roots fail to restrict it (Munns et al., 2002).

2.3.4 Identification of shared and stress-specific responses

The ESTs with an altered up- or down-regulated transcription level were observed following each of the stress responses among the tissue-types assessed. Figure 2.8 illustrates the breakdown by stress for the 756 probes (representing ESTs and RGAs) identifying a 2-fold or greater change in expression. A total of 317 ESTs were more than 2-fold DE by either of the stresses assessed. The number of DE transcripts affected in response to high-salinity (266) was approximately five-times higher than those affected in response to drought (46) and cold (54) stresses. In Arabidopsis, Seki et al. (2002) revealed more transcripts to be DE by drought stress (desiccation), followed by high-salinity stress (250 mM NaCl) and cold stress (4ºC). However, also in Arabidopsis, Kreps et al. (2002) found more transcripts to be DE in response to cold stress (4ºC), followed by high-salinity (100 mM NaCl) and osmotic/drought stress (200 mM Mannitol). Therefore, it is proposed that the number of DE transcripts
in response to a particular stress depends on the method of stress induction and its severity. Moreover, high-salinity stress response was studied at two time-points compared to one time-point for drought and cold stresses, which may have contributed to the detection of more DE transcripts under high-salinity stress.

The transcription level of several ESTs was altered by more than one of the stresses assessed, which may indicate crosstalk or shared pathways among the biological responses involved in these stress reactions. The Venn diagram revealed three ESTs
that were DE under both drought and cold stresses, whilst 22 and 18 ESTs were DE under drought and high-salinity, and cold and high-salinity stresses, respectively. Furthermore, three ESTs were DE under all the three stress conditions.

2.3.5 Drought stress response

The leaf, root and the flower tissues were collected after drought stress as described in section 2.2.2.1. The root samples yielded small quantities of poor quality RNA. The RNA from three extractions was pooled together to produce enough quantity for hybridisation; even this failed to generate good quality, score-able spots. Therefore, only leaf and flower tissues were used in subsequent analysis.

Six microarrays were hybridised for each of the 12 treatment/control x tissue-type x biological replication conditions, producing 72 microarray images for analysis of DE ESTs. The list of ESTs DE in response to drought stress is presented in Table 2.1. The number of ESTs DE in leaf tissues (34) were approximately twice the number DE in flower tissues (13). The number of microarray probes that were undetected (mean fluorescence intensity less than two times the mean local background intensity in all tissue-types and replications) in ICC 3996 varied according to the source of the probes. In general, the levels of undetected features for *L. sativus* probes were higher than the *C. arietinum* probes. All lentil RGA sequence probes were undetected in all the tissue-types assessed.

The transcripts that were >2-fold DE between the treatment and control plants in response to drought stress were associated with various functional and regulatory proteins (Table 2.1). Globally, the number of transcripts repressed (43) was eight-
Table 2.1 List of ESTs differentially expressed by ICC 3996 in response to drought stress.

<table>
<thead>
<tr>
<th>Clone ID</th>
<th>Species*</th>
<th>GenBank Accession</th>
<th>Category</th>
<th>Putative Function</th>
<th>Log2 Ratio</th>
<th>P value</th>
<th>Tissue type*</th>
</tr>
</thead>
<tbody>
<tr>
<td>LS0093</td>
<td>LS</td>
<td>DY396284</td>
<td>Cell cycle &amp; DNA processing</td>
<td>Histone Deacetylase 2 isoform B</td>
<td>-1.10</td>
<td>2.62E-06</td>
<td>F</td>
</tr>
<tr>
<td>LS0297</td>
<td>LS</td>
<td>DY396324</td>
<td>Cell rescue/death/ageing</td>
<td>Dehydrin-cognate</td>
<td>1.11</td>
<td>8.74E-06</td>
<td>F</td>
</tr>
<tr>
<td>LS0297</td>
<td>LS</td>
<td>DY396324</td>
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<td>Dehydrin-cognate</td>
<td>-1.06</td>
<td>0.000295</td>
<td>L</td>
</tr>
<tr>
<td>U133</td>
<td>CA</td>
<td>DY475172</td>
<td>Cell rescue/death/ageing</td>
<td>Phosphate-induced protein</td>
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<td>3.51E-11</td>
<td>L</td>
</tr>
<tr>
<td>U151</td>
<td>CA</td>
<td>DY475190</td>
<td>Cell rescue/death/ageing</td>
<td>S-adenosylmethionine synthetase enzyme (EC 2.5.1.6)</td>
<td>-2.64</td>
<td>1.39E-08</td>
<td>L</td>
</tr>
<tr>
<td>LS0160</td>
<td>LS</td>
<td>DY396300</td>
<td>Cellular communication/Signalling</td>
<td>ATHP3 (histidine-containing phosphotransfer protein like)</td>
<td>-1.38</td>
<td>7.21E-06</td>
<td>L</td>
</tr>
<tr>
<td>LS0551</td>
<td>LS</td>
<td>DY396350</td>
<td>Cellular communication/Signalling</td>
<td>Nonspecific lipid-transfer protein precursor</td>
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<td>1.86E-05</td>
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<td>LS0124</td>
<td>LS</td>
<td>DY396291</td>
<td>Cellular communication/Signalling</td>
<td>Putative ARF1 GTPase activating protein</td>
<td>-1.97</td>
<td>1.13E-13</td>
<td>L</td>
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<tr>
<td>U265</td>
<td>CA</td>
<td>DY475302</td>
<td>Cellular metabolism</td>
<td>4-alpha-glucanotransferase (EC 2.4.1.25)</td>
<td>-1.97</td>
<td>3.89E-14</td>
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</tr>
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<td>LS</td>
<td>DY396337</td>
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<td>Alpha-amylase precursor</td>
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<td>U458</td>
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<td>DY475475</td>
<td>Cellular metabolism</td>
<td>Asparagin synthetase (EC 6.3.5.4)</td>
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<td>CA</td>
<td>DY475477</td>
<td>Cellular metabolism</td>
<td>Asparagine synthetase (glutamine hydrolysing)</td>
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<td>L</td>
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<td>U398</td>
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<td>DY475415</td>
<td>Cellular metabolism</td>
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<td>DY475393</td>
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<td>CA</td>
<td>EB085031</td>
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<td>Cytochrome P450</td>
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<td>DY475498</td>
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<td>Glucosyltransferase</td>
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<td>1.06E-05</td>
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<td>LS0930</td>
<td>LS</td>
<td>DY396408</td>
<td>Cellular metabolism</td>
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<td>LS0060</td>
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<td>Defence</td>
<td>Putative auxin-repressed protein</td>
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<td>0.000738</td>
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<td>DY396277</td>
<td>Defence</td>
<td>Singleton</td>
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<td>2.68E-05</td>
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<td>LS</td>
<td>DY396374</td>
<td>Defence</td>
<td>Subtilisin inhibitors I and II (ASI-I and ASI-II)</td>
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* Species: CA is *Cicer arietinum* L. and LS is *Lathyrus sativus*. Tissue-type: L is leaf tissues and F is flower/early-pod tissues.
times those induced (5) in response to drought stress. The interesting ones included
the phosphate-induced protein (DY475172) and S-adenosylmethionine synthetase
(DY475190) transcripts related to senescence that were >2-fold and >6-fold repressed
in the leaves of ICC 3996, respectively. The switching-off of death/senescence related
genes might signify effort being made by the stressed plants to delay death. In fact,
delay of senescence has been considered as one of the mechanisms of drought
tolerance in other crops (Borrell et al., 2000; Yan et al., 2004). Further, a dehydrin-
cognate transcript (DY396324) associated with cell rescue was >2-fold induced in
flowers but >2-fold repressed in leaves of ICC 3996. Plant dehydrins are part of a
large group of highly hydrophilic proteins known as late embryogenesis abundant
(LEA) proteins (Rorat, 2006). They have conserved amino acid motifs and are
induced in plants by dehydration or treatment with ABA (Robertson and Chandler,
1994). However, in pea, a different type of dehydrin (B61) was reported whose
expression was repressed by dehydration stress and ABA application (Robertson and
Chandler, 1994).

The transcripts associated with starch metabolism, namely, 4-alpha-glucanotransferase
(DY475302) and alpha-amylase precursor (DY396337) were about 3-fold repressed in
leaves of drought stressed plants. These enzymes have been shown to be involved in
degradation of starch to hexose–sugars in the leaves (Chia et al., 2004; Asatsuma et
al., 2005). Hexose sugars like sucrose function as osmoprotectants and accumulate in
the leaves under osmotic stress (Bartels and Sunkar, 2005). The repression of starch
degradation might thus make ICC 3996 plants more susceptible to drought stress.
Alternatively, they might be using other osmoprotectants like proline or polyamines to
combat osmotic stress.
The transcripts associated with cytochrome P450 (EB085431) and cytochrome C biogenesis protein (DY475393) were repressed in leaves of drought-stressed plants. Plants utilise a diverse range of cytochrome P450 monooxygenases in their biosynthetic and detoxification pathways (Schuler, 1996). The biosynthetic P450s have an important role in the synthesis of lignin intermediates, sterols, terpenes, flavonoids, isoflavonoids, furanocoumarins and a variety of secondary products. Whilst, catabolic P450s convert toxic products into non-toxic or vice-versa (Schuler, 1996). The reason for repression of these cytochromes under drought stress may become clearer after additional studies.

The transcript associated with asparagine synthetase (DY475475) was repressed whilst glutamate-hydrolysing asparagine synthetase (DY475477) was induced in the leaves of drought stressed plants. Both of these enzymes are involved in nitrogen metabolism, where glutamate-hydrolysing asparagine synthetase (GHAS) leads to production of ammonia which is transferred to other active sites for asparagine synthesis (Tesson et al., 2003). Induction of GHAS but repression of asparagine synthetase may mean that the ammonia produced was being channelled for use in other processes.

The transcripts associated with energy metabolism/photosynthesis (EB085050, DY475518, DY475316, DY475116 and DY475069) were all repressed in the leaves of drought stressed plants. The genes involved in photosynthesis are known to be repressed in shoots following the treatment of plants with NaCl (salt stress), PEG (osmotic stress) or ABA. This response is consistent with the closure of stomata in
response to high ABA or osmotic stress, inhibition of CO$_2$ fixation and reduced need for energy capture by photosynthetic ETC (Buchanan et al., 2005).

Among the regulatory proteins, the transcript associated with a lipid-transfer protein precursor (DY396350) was induced in the leaves of drought stressed plants. Lipid-transfer proteins (LTPs) are known to be induced by osmotic and cold stress and have a role in stress adaptation (Yamaguchi-Shinozaki and Shinozaki, 2006). The exact role of LTPs is not known but they are thought to be involved in cutin biosynthesis, surface wax formation, pathogen-defence reactions, or the adaptation of plants to environmental changes (Kader, 1997).

Interestingly, a transcript associated with a transcription factor of the AP2/EREBP1 DNA binding domain (CV793594) was repressed in the leaves of drought stressed plants. The AP2/EREBP transcription factor was reported to contain a dehydration responsive element binding (DREB) domain (Zhifang et al., 2001). Moreover, the AP2-domain transcription factor was shown to act as a repressor of the ABA response in Arabidopsis (Pandey et al., 2005). The ABA signalling pathway is an important part of drought stress adaptive response in plants (refer to section 1.6). Thus, the repression of the AP2/EREBP1 transcription factor here may indicate that ICC 3996 plants were using an ABA-dependent pathway for drought-stress adaptation.

Further, the transcript associated with the histidine-containing phosphotransfer protein ATHP3 (DY396300) was repressed in the leaves of drought-stressed plants. The ATHPs (or AHPs) are thought to be involved in stress sensing and relay signal transduction, where ATHP1 is thought to sense osmotic stress and transfer the signal
via ATHP2/ATHP3 to the Arabidopsis Response Regulators (ARRs) (Urao et al., 2000). The amino acid sequences of ATHP2 and ATHP3 show 81% identity, suggesting possible functional redundancy (Hwang et al., 2002). Moreover, overexpression of ATHP2 was shown to cause cytokinin hypersensitivity, affecting root and hypocotyl elongation (Suzuki et al., 2002). Hence, the repression of ATHP3 may be important to sustain leaf growth under stress.

Subsequently, the transcript associated with putative auxin-repressed protein (DY396359) was >4-fold repressed in the leaves of drought stressed plants. The plant hormone auxin regulates the growth and development processes by controlling the expression of auxin-responsive genes. One of the ways is by down-regulating auxin-repressive gene to effect growth (Park and Han, 2003). The down-regulation of this gene in drought stressed plants may mean an attempt to continue growth under stress.

Several transcripts associated to proteins with unknown/unclear functions were induced and/or repressed in leaves and flowers of drought stressed plants. Further studies on drought stress adaptation using these transcripts may reveal their possible involvement and role.

### 2.3.6 Cold stress response

The leaf and flower tissues were harvested from cold stressed and unstressed plants (as described in section 2.2.2.2) and used to analyse genes that were DE between stressed and unstressed plants. Six microarrays were hybridised for each of the 12 treatment/control x tissue-type x biological replication conditions, producing 72 microarray images for analysis of DE ESTs. The list of ESTs DE in response to cold
stressed is presented in Table 2.2. As seen for drought stress, the number of ESTs DE in leaf tissues (38) were approximately twice those DE in flowers (21). The number of microarray probes that were undetected (mean fluorescence intensity less than two times the mean local background intensity in all tissue-types and replications) in ICC 3996 varied according to the source of the probes. As seen for drought stress, the levels of undetected features for L. sativus probes were higher than the C. arietinum probes. All lentil RGA sequence probes were undetected in all tissue-types assessed.

Globally, most (78%) of the transcripts DE in response to cold stress were repressed (Table 2.2). The interesting ones included two phosphate-induced protein transcripts (DY475076, DY475172) that were 3- to 16-fold induced in the leaves and flowers of cold stressed plants. Mitogen activated protein kinases (MAPKs) play a central role in abiotic and biotic stress signalling, and are also involved in cold acclimation of plants (Chinnusamy et al., 2006). Evidence for the activation of MAPKs by phosphate-induced cell-cycle entry of tobacco cells was previously reported (Wilson et al., 1998). Hence, the phosphate-induced proteins may be involved in activation of the MAPK signalling cascade, leading to cold acclimation of ICC 3996 plants.

Among the cellular metabolism related transcripts, carbonic anhydrase-like protein (EC 4.2.1.1) responsible for reversible hydration of carbon dioxide (DY475403) was repressed in the leaves of cold stressed plants. Carbonic anhydrase (CA) is involved in diverse biological processes including pH regulation, ion exchange, CO₂ transfer, respiration and photosynthetic CO₂ fixation (Tiwari et al., 2005). Biosynthesis of CA is dependent upon photon flux density, CO₂ concentration and Zn availability. Cold stress causes disruption of respiration and photosynthesis (Wolk and Herner, 1982;
Table 2.2 List of ESTs differentially expressed by ICC 3996 in response to cold stress.

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<th>Species</th>
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<th>Category</th>
<th>Putative Function</th>
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<td>Energy</td>
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<td>DY475510</td>
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<td>DY475174</td>
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<td>-1.58</td>
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</table>

* Species: CA is *Cicer arietinum* L. and LS is *Lathyrus sativus*. Tissue-type: L is leaf tissues and F is flower/early-pod tissues.
van Heerden and Kruger, 2000), which may have led to reduced CO₂ content in leaves affecting CA production. The disruption of photosynthesis is also evidenced by the repression of transcripts related to the chlorophyll a/b binding protein (DY475454), and thioredoxin (DY396330) in flowers and leaves of cold stressed plants, respectively.

The transcript associated with fructose 1,6-bisphosphate aldolase (DY475547) was repressed in the leaves of cold-stressed plants. Fructose 1,6-bisphosphate (FBP) aldolase plays a key role in glycolysis (FBP cleavage) and gluconeogenesis (FBP synthesis) and is under indirect regulation of ATP (EMBL-EBI database. URL: http://www.ebi.ac.uk/interpro/DisplayIproEntry?ac=IPR011289). When the concentration of ATP in the cell is low, AMP would then be high, which inhibits fructose 1,6-bisphosphatase and thus gluconeogenesis. This implies, at low ATP concentration, the cell does not expend energy in synthesising glucose. Thus, the leaves of cold stressed plants may have been trying to conserve energy by repressing fructose 1,6-bisphosphate aldolase.

The transcript related to homogentisate 1,2 dioxygenase (DY475551) was repressed in the leaves of cold-stressed plants. Homogentisate 1,2 dioxygenase (HGO) is involved in tyrosine catabolism pathway and increased transcription of related enzymes has been associated with senescence and compartmentalisation (Dixon and Edwards, 2006). Thus, the cold stressed plants may be repressing this transcript in an attempt to delay senescence.
Importantly, the transcripts associated with ubiquitins (DY396278, DY396303) were repressed in the leaves of cold stressed plants, whilst a transcript related to polyubiquitin (DY396328) was >4-fold repressed. Cold acclimation induces the expression of C-repeat binding factors (CBF), which in turn activate the downstream genes that confer chilling tolerance (Chinnusamy et al., 2006). The transcription of CBFs and other cold-induced regulons is regulated by a constitutively expressed transcription factor, inducer of CBF expression 1 (ICE1), which is proposed to be negatively regulated by ubiquitination (Chinnusamy et al., 2006). Hence, repression of ubiquitins in leaves and flowers of cold stressed plants may be related to activation of ICE1, leading to cold acclimation.

Further, the transcript associated with L-ascorbate peroxidase (DY396435) was repressed, whilst the transcript related to cationic peroxidase (DY475306) was induced in the leaves of cold stressed plants. Ascorbate peroxidase (AP) is the main enzyme responsible for hydrogen peroxide ($H_2O_2$) removal in the chloroplasts and cytosol of higher plants (Dalton, 1991). Cationic peroxidases (CP) have been associated with defence against pathogens (Young et al., 1995) but recently, a CP was shown to be cold-stress inducible and was implicated in stress tolerance (Llorente et al., 2002).

Interestingly, a transcript related to UDP-glucose 4-epimerase (DY475149) was induced in the leaves of cold stressed plants. UGE (UDP-glucose 4-epimerase) catalyses the inter-conversion of UDP-Galactose and UDP-Glucose (Zhang et al., 2006). Both these nucleotide sugars act as activated sugar donors for the biosynthesis of cell wall polysaccharides such as, cellulose, xylo-glucans, (1,3;1,4)-$\beta$-D-glucan and
pectins. Thus, the induction of UGE in leaves of cold stressed plants may be an adaptive response by strengthening cell walls.

The transcript associated with zinc-binding dehydrogenase (DY475500) was highly (>6-fold) repressed in the leaves of cold stressed plants. Zinc-binding dehydrogenases (ZBD) are alcohol dehydrogenases (AD) that catalyse the oxidation of alcohol to acetaldehyde or ketone derivatives. Low temperature is known to induce the accumulation of AD in *A. thaliana*, a cold-tolerant plant (Jarillo, 1993). It has been demonstrated that AD is not required for development of freezing tolerance and that cold-induced anaerobic metabolism and abscisic acid are responsible for its induction (Jarillo, 1993). However the induction of ZBD showed the successful imposition of cold-stress in chickpea.

Among the transcripts related to defence, *Avr9/Cf9* rapidly elicited protein (CV793589) was induced in the leaves and flowers of cold stressed plants. The pathogen avirulence genes (*Avr*) are known to be specific effectors that trigger *R*-gene mediated plant defences (Dixon *et al*., 1994). The *Avr9/Cf9* protein was first identified from *Lycopersicon esculentum-Cladosporium fulvum* interaction as being induced upon interaction of the *Cf9* protein and *Avr9* avirulence gene product according to the gene-for-gene hypothesis (Durrant *et al*., 1999). However, the induction of the related transcript in leaves and flowers of cold-stressed plants needs further investigation.

Interestingly, two transcripts associated with auxin-repressed protein (DY396289, DY396292) were repressed in the leaves of cold-stressed plants. These transcripts were also repressed in leaves under drought stress. The plant hormone auxin regulates
the growth and development processes by controlling the expression of auxin-responsive genes. One way is by down-regulating auxin-repressive genes to effect growth (Park and Han, 2003). The repression of this gene in cold-stressed plants may indicate that the plant was attempting to continue growth under stress.

From the transcripts associated with transport facilitation, a cyclic ion channel protein (DY475468) was repressed in the leaves and flowers, whereas, aquaporins (DY475174 and DY396334) were repressed only in leaves of cold stressed plants. However, a transcript associated with DNA-J like protein involved in intracellular protein transport (DY475488) was ~8-fold induced in leaves of cold-stressed plants. Prolonged chilling range temperatures are known to affect membrane permeability. The water content of the tissues is affected which causes alteration/inhibition of protein functions (McWilliam, 1983; Cooper and Ort, 1988).

Among, the transcripts related to regulatory proteins, a protein kinase (DY475103) was induced in the flowers of cold-stressed plants. Cold stress regulates the expression and activity of various kinases of the MAPK pathway, which is necessary for cold acclimation in plants (Teige et al., 2004). Interestingly, transcripts associated with the hypothetical transmembrane protein (DY475478) and membrane related protein CP5 (DY475119) were repressed in flowers and leaves of cold stressed plants, respectively. Cold stress is known to cause change in fluidity of plasma membrane at the micro-domain, leading to stress perception (Chinnusamy et al., 2006). Also, a WD-repeat protein (DY475550) was repressed in the leaves of cold-stressed plants. WD-repeat (WDR) proteins are essentially involved in different cellular and organismal processes, including cell division and cytokinesis, apoptosis, light
signalling, flowering, floral development, and meristem organisation (van Nocker and Ludwig, 2003). The repression of these proteins in response to cold stress needs further investigation.

Several transcripts associated to proteins with unknown/unclear functions were induced and/or repressed in the leaves and flowers of drought stressed plants. Further studies on cold stress adaptation using these transcripts may reveal their possible involvement and role.

### 2.3.7 High-salinity stress response

The shoot and root tissues were harvested from the high-salinity-stressed and unstressed plants (as described in section 2.2.2.3) and used to assess the genes that were DE between the stressed and unstressed plants. Six microarrays were hybridised for each of the 24 treatment/control x tissue-type x time-point x biological replication conditions, producing 144 microarray images for analysis of DE ESTs. The list of ESTs DE in response to high-salinity stress is presented in Table 2.3. More ESTs were DE in roots (115) than the shoots (94) at 24 hpt, whilst the converse was true at 48 hpt when more ESTs were DE in the shoots (108) than roots (82). The number of microarray probes that were undetected (mean fluorescence intensity less than two times the mean local background intensity in all tissue-types and replications) in ICC 3996 varied according to the source of the probes. As seen for drought and cold stress responses, the levels of undetected features for *L. sativus* probes were higher than the *C. arietinum* probes. All lentil RGA sequence probes were undetected in all tissue-types/time-points assessed. Globally, the number of ESTs repressed (291) in all tissue-types and time-points was approximately thrice the number of induced ESTs (109).
Table 2.3 List of ESTs differentially expressed by ICC 3996 in response to high-salinity stress

<table>
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<tr>
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<th>Species</th>
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<th>Category</th>
<th>Putative Function</th>
<th>Log2 Ratio</th>
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<td>DNA binding protein</td>
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<td>3.07E-06</td>
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<td>DY475266</td>
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<td>DY475419</td>
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* Species: CA is *Cicer arietinum* L. and LS is *Lathyrus sativus*. Tissue-type: S 24 is shoot tissues at 24 hpt; R 24 is root tissues at 24 hpt; S 48 is shoot tissues at 48 hpt; R 48 is root tissues at 48 hpt.
The complete list of transcripts DE at 24 and 48 hpt is presented in Table 2.3. The number of ESTs DE in roots was more than shoots at 24 hpt and converse was true at 48 hpt. This is in agreement with the fact that initially the roots try to restrict the salt from entering the plant and only when that fails, the salt travels to shoots and leaves, where it is attempted to be compartmentalised (Munns et al., 2002). This was also evident from the appearance of water soaked lesions on the older leaves at 48 hpt.

Salinity is known to cause ionic stress in addition to osmotic stress, and plants have to regain ionic homeostasis for normal growth (Munns, 2005). An interesting observation related to this was that the transcript associated with aluminium-induced protein (DY475138) was 2- to 9-fold induced in shoots and roots at 24 and 48 hpt. The induction of aluminium-induced protein (AIP) may be a part of cationic shock experienced by plants under salt stress which is known to cause accumulation of reactive oxygen species (Kawano et al., 2005). Aluminium stress is also known to affect root growth and cause DNA damage due to increased superoxide dismutase accumulation and peroxidase activities (Meriga et al., 2004). They also reported that plants tried to be localise Al$^{3+}$ more in roots than shoots. In fact, DY475138 was highly induced in roots at 24 hpt and shoots at 48 hpt, supporting the assumption that initially salt stress was mitigated at root level and only when that failed, it reached the shoots, which tried to compartmentalise it. Moreover, the transcript related to metallothionein-like protein (DY396295) was >3-fold induced in roots of high-salinity-stressed plants at 24 and 48 hpt. On the contrary, transcripts related to metallothionein-like protein 1 (DY396373, DY396322, DY396406) were repressed in shoots and roots at 24 hpt, and in shoots at 48 hpt. Metallothioneins (MT) are low molecular weight, metal-binding proteins that help to maintain metal-ion
concentrations in the plants (Jin et al., 2006). Hence, the expression of MTs in salt stressed plants may be viewed as an effort being made by the plants to attain ion homeostasis.

Importantly, the transcripts related to auxin-repressed protein (DY475137, DY475078, DY396292) were 2- to 9-fold induced in roots at 24 and 48 hpt, and shoots only at 48 hpt. The auxin-repressive gene negatively controls the growth and development of plants (Park and Han, 2003). The induction of this gene in high-salinity-stressed plants may mean that their growth was checked under stress. Moreover, this transcript was not induced in shoots until 48 hpt, which may indicate that the shoots faced more stress later on. A related observation includes repression of transcripts associated with endoxyloglucan transferase (DY475207) and gibberellin-regulated protein precursor (DY396423) in shoots at 48 hpt. Endoxyloglucan transferase (EXGT) catalyses the cleavage and molecular grafting of xyloglucan polymers (Akamatsu et al., 1999) and reduced transcription of EXGT has been linked to reduced internodal length (Hanzawa et al., 1997). Similarly gibberellin is associated with plant growth and development and its reduced levels lead to dwarfism (Sakamoto et al., 2004). The repression of these transcripts further bolsters the assumption that the plants actively reduced shoot growth at 48 hpt.

Interestingly, the transcript associated with ubiquitin conjugating protein involved in the regulation of photomorphogenesis and senescence (DY475328) was >3-fold repressed in the shoots at 24 and 48 hpt. Delay of death/senescence has previously been reported as a mode of plant salt tolerance (Munns, 2005).
Among the transcripts associated with cellular metabolism, 4-alpha-glucanotransferase (DY475302) was 4- to 19-fold repressed in shoots at 24 and 48 hpt, whilst it was >2-fold induced in roots at 48 hpt. Alpha-glucanotransferase (AGT) is associated with the breakdown of starch into sucrose (Zeeman et al., 2004). Another transcript associated with starch degradation, alpha amylase (DY396337) (Asatsuma et al., 2005) was repressed in shoots at 24 and 48 hpt. Starch and sucrose molecules were reported to serve as reciprocal fluxes to each other (Zeeman et al., 2004). Sucrose is a known osmolyte that accumulates in salt-stressed plants (Munns, 2005). The repression of starch degradation pathways may mean that sucrose was being produced by alternative pathway or some other osmolyte may have been deployed to maintain cell-turgor under salt-stress. One observation related to this assumption is induction of the transcript associated with sucrose synthase (DY475105) in roots at 24 and 48 hpt. Sucrose synthase (SS) catalyses the reversible reaction of sucrose synthesis from glucose and fructose. Another observation was >4-fold induction of the transcript related to glutamate dehydrogenase (DY475308) in roots at 24 and 48 hpt. A study on salinity tolerance in wheat revealed that under high-salinity conditions, glutamate dehydrogenase is preferentially employed for production of proline. Proline is an osmolyte and transgenic plants engineered to over-accumulate proline showed enhanced salt tolerance (Zhu et al., 1998; Hong et al., 2000).

An important observation was that at 48 hpt, the transcript associated with cysteine protease (DY475066) was induced in roots, whilst the transcript associated with cysteine protease 15A precursor (DY396396) was repressed in shoots. Cysteine protease (CP) activation is known to be instrumental in programmed cell death (PCD)
(Solomon et al., 1999). Hence, the induction of CP in roots and repression in shoots at 48 hpt may imply that the root cells started to die while the shoots tried to delay death.

The transcripts associated with UDP-glucose 4-epimerase (DY475149, DY475221) were induced only in roots at 24 hpt but in both, roots and shoots at 48 hpt. UDP-glucose 4-epimerase (UGE) catalyses the interconversion of UDP-Gal to UDP-Glc, both of which are involved in biosynthesis of cell-wall polysaccharides such as cellulose, xyloglucans, (1,3;1,4)-β-D-glucan and pectins. Thus, the induction of UGE in roots at 24 hpt, and in roots and shoots at 48 hpt may be an adaptive response by strengthening cell walls. Moreover, the transcript associated with xylose isomerase (DY475309) was induced only in roots at 24 and 48 hpt. Xylose isomerase catalyses the inter-conversion of xylose to xylulose (Fuxreiter et al., 1995), which may possibly be involved in strengthening the roots by xylose deposition.

Among the defence related transcripts, class 10 pathogenesis related protein (CV793610) and disease resistance protein (CV793593) were >5-fold induced only in roots at 24 and 48 hpt. Whereas, a transcript related to SNAKIN 2 antimicrobial peptide (CV793606, CV793608) was >3-fold induced only in shoots at 24 and 48 hpt. Other defence related transcripts were repressed in shoots and/or roots at 24 and/or 48 hpt. Many defence related genes have been reported to be induced by abiotic stresses but their involvement in the stress response is unclear (refer to section 1.8). However, the shoot or root specific induction of some transcripts may warrant further study.

Amongst the transcripts related to transport facilitation, aquaporins (DY475174, DY396334), potassium channel regulatory factor (DY475169), and tonoplast intrinsic
protein (DY396419) were repressed in shoots and/or roots at 24 and 48 hpt. Also, a transcript associated with cyclic ion channel protein (DY475468) was repressed only in shoots at 24 and 48 hpt. However, the transcript related to DNA-J like protein involved in intra-cellular protein transport (DY475488) was induced in shoots at 24 and 48 hpt. All of these proteins are associated with transport of various molecules within and between cells. Their repression could mean disruption in their role under stress condition. Alternatively, they could be repressed in an attempt to regain homeostasis by regulating the movement of related molecules in and out of the cell.

Also interesting is the fact that the transcript associated with superoxide dismutase (DY475155) was >5-fold repressed in roots at 24 hpt, while being >2-fold repressed in shoots and roots at 48 hpt. Superoxide dismutase (SOD) is involved in the programmed cell death pathway where its repression allows the accumulation of reactive oxygen species that signal and contribute to cell death (Neill et al., 2002). Hence, the repression of SOD under high-salinity stress may possibly be related to promotion of cell-death pathways under stress.

The transcripts associated with energy metabolism/photosynthesis electron transport chain (ETC) (DY475345, DY475142, DY475116, DY475305) were repressed in shoots at 24 and 48 hpt. Interestingly, the ETC-related transcript ferredoxin (DY475487) was highly repressed only in roots at 24 and 48 hpt. The genes involved in photosynthesis have been reported to be repressed in shoots following the treatment of plants with NaCl (Salt stress), PEG (Osmotic stress) or ABA. This response is consistent with the closure of stomata in response to high ABA or osmotic stress, inhibition of CO₂ fixation and reduced need for energy capture by photosynthetic ETC
(Buchanan et al., 2005). However, the transcript related to chloroplast DNA (EB085019, EB085054) was highly repressed in shoots at 24 and 48 hpt whilst being induced in roots at these times. Further studies may reveal if this feature is specific to high-salinity stress response. Similarly, in-depth studies may unveil if any of the several transcripts associated to proteins with unknown/unclear functions expressed here have a role in high-salinity stress adaptation.

2.3.8 Validation of microarray results – qRT-PCR

Eight genes with different expression values were selected, representing different stresses, tissue-types and/or time-points. The comparative C_T method (ΔΔC_T method) was used to calculate fold-change values. Figure 2.9 shows an example of a validation plot achieved for one target. The C_T values were automatically generated by the MyiQ™ instrument (Bio-Rad, Hercules, CA). Figure 2.10 shows example of amplification curves and C_T values determination. The melt curve analysis showing single peak (Figure 2.11) and gel electrophoresis indicated specific amplification of single product. All the genes revealed similar expression pattern for microarray and qRT-PCR values of fold-change (Table 2.4). This confirmed the reliability of microarray data. However, the fold change values obtained through qRT-PCR were generally more exaggerated than corresponding microarray values. Similar observations were reported in other microarray studies (Dowd et al., 2004; Lopez et al., 2005; Coram and Pang, 2006).
$y = -0.0143x + 8.8802$

Figure 2.9 Example of a validation plot generated over a dilution series for the target gene DY475384 (Serine/Threonine protein kinase). The equation of the red trendline for the data shows that the absolute value of slope is $<0.1$.

Figure 2.10 Example of amplification curves (coloured lines) generated by the MyiQ™ instrument (Bio-Rad, Hercules, CA). The solid orange line represents the threshold used to calculate $C_T$ values.
Figure 2.11 Example of Melt Curves generated by the MyiQ™ instrument (Bio-Rad, Hercules, CA). The presence of sharp single fluorescence peaks in this example indicated the presence of single amplicons.
Table 2.4 Expression ratios of selected transcripts assessed by microarray and qRT-PCR. Array values indicate mean log$_2$ fold change (FC) ratio relative to untreated controls and qRT-PCR values indicate log$_2$ ratios of $2^\Delta\Delta$Ctreatment$/\Delta$Ctreatment). A set of DE genes with different expression values from different stress treatments, tissue-types and/or time-points were chosen for qRT-PCR confirmation.

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<td>DY475403</td>
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2.3.9 Comparison of abiotic and biotic stress responses of ICC 3996

DNA microarrays have been considered to be an excellent platform for comparison of genes expressed by plants under biotic and abiotic stresses. As described in section 1.9, stress specific and shared pathways have been unveiled by such comparisons allowing the detection of points of cross-talk between these stress responses. The
‘Pulse Chip’ array was constructed in association with Mr. Tristan Coram, who used it to generate expression profile of chickpeas in response to *Ascochyta* blight pathogen (Coram and Pang, 2006). ICC 3996, which is *Ascochyta* blight resistant genotype, was one of the genotypes studied by Coram and Pang (2006). Hence, the comparison of genes DE by ICC 3996 in response to abiotic stresses from this study and biotic stress from Coram and Pang (2006) was considered, to detect genes commonly expressed under these stresses.

The comparison of genes DE by ICC 3996 in response to drought, cold, high-salinity and *Ascochyta* blight stresses in different tissue-types and/or time-points is presented in Figure 2.12. Globally, 46, 54, 266, and 51 transcripts were DE in at least one tissue-type or time-point in response to drought, cold, high-salinity, and *Ascochyta* blight stresses, respectively. The comparison among transcripts DE in response to drought, cold and high-salinity is presented in section 2.3.4, and is not discussed here. The numbers indicated in the blocks were transcripts exclusively DE for that particular combination and were not repeated in subset/superset combinations. As seen in the figure, thirty transcripts were uniquely DE in response to *Ascochyta* blight stress, whilst no transcript was DE under all the four stresses being compared.

Twenty-one transcripts were commonly DE between the biotic stress (*Ascochyta* blight) and one or more of the abiotic stresses (drought, cold and high-salinity). The number of transcripts that were commonly DE under *Ascochyta* blight and high-salinity stresses (16) was about twice and thrice those commonly DE under *Ascochyta* blight and cold stresses, and *Ascochyta* blight and drought stresses, respectively (Table 2.5). This may be due to number of reasons. Firstly, the response of ICC 3996
Figure 2.12 Venn diagram comparing the transcripts that were DE by ICC 3996 in response to drought, cold, high-salinity and *Ascochyta* blight stresses.
Table 2.5 The ESTs commonly DE by ICC 3996 in response to drought, cold, high-salinity, and *Ascochyta* blight stresses.

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**Cold, High-salinity and Ascochyta blight**

**Drought, Cold, High-salinity and Ascochyta blight**

None

* DL = Drought leaves; DF = Drought flowers; CL = Cold leaves; CF = Cold flowers; SS 24 = High-salinity shoots 24 hpt; SS 48 = High-salinity shoots 48 hpt; SR 24 = High-salinity roots 24 hpt; SR 48 = High-salinity roots 48 hpt; AS 12 = Ascochyta blight shoots 12 hpt; AS 24 = Ascochyta blight shoots 24 hpt; AS 48 = Ascochyta blight shoots 48 hpt; AS 72 = Ascochyta blight shoots 72 hpt.
to both, *Ascochyta* blight and high-salinity stress was studied at seedling stage, whereas drought and cold stresses were studied at flowering stage. Secondly, for both, *Ascochyta* blight and high-salinity stresses, the shoot tissues (stem and leaves pooled together) were studied, whilst for drought and cold stresses, leaf tissues were studied. Thirdly, the sheer number of transcripts DE in response to high-salinity stress (266) was about five-times those DE under drought and cold stresses.

Among the transcripts commonly DE under various combinations of biotic and abiotic stresses, the transcript associated with SNAKIN2 antimicrobial peptide (CV793606) was highly induced in shoots under high-salinity and *Ascochyta* blight stress, whilst the S1-3 protein homolog (CV793591) was repressed in leaves/shoots under cold and *Ascochyta* blight stresses. Interestingly, the transcripts associated with wound-induced protein (DY475220) and RNA/ssDNA binding protein (DY475357) were repressed in shoots under high-salinity and *Ascochyta* blight. Several transcripts associated with the cellular metabolism like the transcripts related to S-adenosylmethionine synthetase (DY475190) and 4-alpha-glucanotransferase (DY475302) were repressed in leaves/shoots under drought, salt and *Ascochyta* blight stress. Alternatively, the transcripts associated with the WD repeat protein (trp-asp domains) (DY475550) and carbonic anhydrase (DY475403) were repressed in leaves/shoots after cold, salt, and *Ascochyta* blight stress.

All of the above transcripts identified as commonly DE between biotic and abiotic stresses are related to downstream genes and may be involved in stress adaptation. The biological roles of these genes were discussed in sections 2.4.2, 2.4.3, and 2.4.4. The genes related to defence and cellular metabolism were previously reported to be
commonly expressed under biotic and abiotic stresses (Cheong et al., 2002; Munns, 2005). Although this provides an indication of the pathways that may be shared among these stress responses it would be more useful to identify upstream genes that govern responses to multiple stresses. Unfortunately, no regulatory genes (transcription factors/signalling molecules) were found to be commonly DE in these studies. Since the array used represented only a limited number of transcription factors from the chickpea genome, it would be worthwhile to identify the complete set of transcription factors for chickpea and use those for comparing responses among biotic and abiotic stresses.

2.4 Conclusions

A spotted cDNA array (Pulse Chip) was manufactured from 516 non-redundant chickpea ESTs along with 156 grasspea ESTs, 41 lentil RGAs, 43 chickpea bad reads and 12 controls and used to generate expression profiles of ICC 3996 in response to drought, cold and high-salinity stresses. Overall, 46, 54 and 266 ESTs were identified as DE under drought, cold, and high-salinity stresses, respectively. The important genes DE in response to drought stress included induction of transcripts associated with dehydrin-cognate, lipid-transfer protein precursor, and glutamate-hydrolysing asparagine synthetase, whilst repression of transcripts associated with senescence, photosynthesis/energy metabolism, auxin-repressed protein, starch metabolism, AP2/EREBP1 DNA binding domain, putative ARF1 GTPase activating protein, and histidine-containing phosphotransfer protein ATHP3. The interesting transcripts DE in response to cold-stress included induction of phosphate-induced protein, cationic peroxidase, UDP-glucose 4-epimerase, Avr9/Cf9 rapidly elicited protein, DNA-J like protein involved in intracellular protein transport, and protein kinase, whilst repression
of transcripts associated with a hypothetical transmembrane protein, membrane related protein CP5, lipid-transfer protein precursor, WD repeat protein and several transcripts associated with cellular metabolism, cell cycle and DNA processing, protein synthesis and photosynthesis/energy metabolism. Under high-salinity stress, several transcripts were DE only in roots at 24 hpt but DE in shoots or both, shoots and roots at 48 hpt, relating to the theory of upward movement of salt to shoots at later stages when roots fail to restrict it. The important transcripts DE in response to high-salinity stress included induction of aluminium-induced protein, auxin-repressed proteins, metallothionein-like protein, glutamate dehydrogenase, sucrose synthase, UDP-glucose 4-epimerase, xylose isomerase, class 10 pathogenesis related protein, disease resistance protein, SNAKIN 2 antimicrobial peptide, and DNA-J like protein involved in intra-cellular protein transport. Whilst high-salinity stress caused the repression of transcripts associated with cell rescue/death, cell cycle/DNA processing, cellular metabolism, photosynthesis/energy metabolism, and transport facilitation. As discussed in section 2.3, several of the above transcripts have been previously implicated to be associated with abiotic stress response in other crops. The annotation of these transcripts implies that the experimental design and downstream analysis employed in this study may be useful for identification of candidates for tolerance to these stresses. Hence, this experimental design and analysis procedure shall be used in the subsequent study to interrogate the possible involvement of the 756 probes on the Pulse Chip array in conferring tolerance/susceptibility to these stresses.
Chapter 3

Comparative transcriptional profiling of drought tolerant and susceptible genotypes to reveal potential gene candidates for drought tolerance/susceptibility

3.1 Introduction

Drought is a meteorological term and an environmental event, defined as a water stress due to lack or insufficient rainfall and/or inadequate water supply (Toker et al., 2007). Worldwide, 90% of chickpea is grown under rainfed conditions (Kumar and Abbo, 2001) where terminal drought is one of the major constraints limiting productivity (Toker et al., 2007). For the production year 2006-2007 in Australia, rainfall during the main crop growing months of June to October was much below average and the lowest on record with the exception of some regions (Skrypetz, 2006). A similar trend of reduced rainfall and higher overall temperatures has been observed recently in the rest of the world. This concerns the food production of all the crops around the globe, including chickpea. In chickpea, flowering and seed set are the stages of development most sensitive to drought (Khanna-Chopra and Sinha, 1987).

As explained in section 1.2.1.3, chickpea plants cope with drought via three mechanisms including drought escape, drought avoidance, and drought tolerance. Two traits, namely, a large root system and smaller leaf area have been widely used for the selection of drought tolerant lines (Turner et al., 2001; Saxena, 2003). However, efforts in breeding for drought tolerance are hampered by our limited knowledge about the genetic basis of drought tolerance and the negative correlation of tolerance
traits with productivity (Mitra, 2001). Molecular mapping has identified two QTLs on LG 3 for days to 50% flowering (Cho et al., 2002; Cobos et al., 2004) in a bid to help plants escape drought by producing early flowering varieties. However, as reported in Chapter 1, drought tolerance is a complex trait governed quantitatively by multiple genes and only improved understanding of the genetic basis of drought tolerance may assist in formulation of efficient breeding strategies.

Studies on the molecular mechanisms for drought tolerance has led to the identification of a number of genes including osmosensors (SLN1 and SHO1), Ca$^{2+}$ signalling cascades, various transcription factors (including MYC, MYB, NAC), regulatory elements (DREB), and response proteins (e.g. osmoprotectants like proline, trehalose, etc.) that function in a ABA-dependent or ABA-independent manner (refer to section 1.6). The timing of expression of these genes in response to osmotic stress has led to the identification of two groups with different expression profiles (Yamaguchi-Shinozaki and Shinozaki, 2006). In one group, the gene expression was rapid and transient and reached a maximum in several hours, and then decreased. In the second group, gene expression slowly and gradually increased after stress treatment within 10 hours (Yamaguchi-Shinozaki and Shinozaki, 2006). However, there is a paucity of information concerning the number and types of genes involved in drought tolerance and how they interact to produce effective tolerance.

Microarrays have been the method of choice for generating gene expression profiles in response to stress (refer to section 1.8). Many genes and pathways have been associated with drought stress response and probably tolerance using microarray platforms (as seen in Seki et al., 2001, 2002; Kreps et al., 2002; Rabbani et al., 2003).
Some studies have expanded the use of microarrays to compare abiotic stress response in stress tolerant and susceptible genotypes (e.g. Kawasaki et al., 2001; Walia et al., 2005). The comparison of expression profiles of contrasting genotypes has the potential of leading us to understanding the spatial and temporal pattern of gene expression required for stress tolerance. The study in Chapter 2 demonstrated that the ‘Pulse Chip’ array could be effectively used for gene expression profiling of chickpea responses to drought stress. To date, there is no report on gene expression profiling of contrasting chickpea genotypes in response to drought stress.

Hence, the aims of the experiments detailed in the current chapter were to:

1. Challenge two groups of drought tolerant and susceptible genotypes with drought stress and compare the transcripts that are differentially expressed in them. Perform a two-way comparison of the differentially expressed transcripts in the two groups of tolerant and susceptible genotypes. This study shall help determine if a particular set of genes are expressed only in tolerant/susceptible genotypes, which may indicate that they are associated with stress tolerance/susceptibility. Additionally, it may reveal how the genes being interrogated behave in different tolerant and susceptible genotypes under the stress condition.

2. Interpret the results from transcriptional profiling in the context of putative gene functions and genotypes in which they were expressed to try and uncover the mechanism and pathways involved in drought tolerance in chickpeas.
3.2 Materials and methods

3.2.1 Selection of genotypes

The drought tolerant and susceptible genotypes were selected after consultation with Dr. Bob Redden (Curator, Australian Temperate Fields Crop Collection, Horsham, Victoria, Australia). The drought tolerant genotypes used in the present study were BG-1103 (ATC 48111) and BG-362 (ATC 48104), where ATC is the Australian Temperate Crop identification number. Both BG-1103 and BG-362 are desi, with erect growing habit, brown seeds and medium duration (130 days to maturity). BG-362 is tolerant to drought while BG-1103 is highly tolerant to drought and heat, both yielding 3 t/ha (Bob Redden, pers. comm.). The drought susceptible genotypes used in the present study were Kaniva (ATC 40030) and Genesis-508 (ATC 45226). Kaniva is kabuli, with large cream seeds, medium plant height, and late flowering variety usually grown in South Australia. It yields about 2 t/ha in areas with >500 mm rainfall but produces only 0.77 t/ha in area receiving <400 mm rainfall (McMurray, 2006). Genesis 508 is desi, with small dark-brown seeds, short plant height, and mid-late flowering, released for cultivation in Victoria and South Australia. It yields about 2 t/ha in areas receiving >500 mm rainfall, but performs poorly producing 0.80 t/ha in areas receiving <400 mm rainfall (McMurray, 2006).

3.2.2 Experimental design, stress treatment and analysis of differentially expressed genes

The first group of drought tolerant and susceptible genotypes used was BG1103 and Kaniva. The second group of drought tolerant and susceptible genotypes used was BG-362 and Genesis-508, respectively. Five treatment and five control plants per genotype were cultivated and drought stressed as described in section 2.2.2.1. The
leaf, root and flower/bud tissues were harvested when the treatment plants reached 30% water content, snap frozen and stored at –80°C until RNA extraction. The drought stress treatments for all the genotypes were performed thrice (three biological replications). The tissues from five experimental replicate plants per biological replication were pooled before RNA extraction. Leaf, flower and root tissues were pooled separately. This RNA was used to prepare cDNA targets for expression analysis using microarray and quantitative real-time PCR (qRT-PCR). The total RNA extraction, preparation of targets, labelling and hybridisation were conducted as described in section 2.2.3. Figure 3.1 shows the experimental design for drought stress treatments.

The microarray was designed with six technical replicate spots per EST. The scanning, data transformation and identification of differentially expressed (DE) genes was performed as explained in section 2.2.3. Briefly, the transcript level for each EST/cDNA was firstly calculated as the average intensity of the six technical replicates and then the average intensity of three biological replicates. Data analysis included LOcally WEighted polynomial regreSSion (LOWESS) normalisation to adjust for differences in quantity of initial RNA, labelling and detection efficiencies. A dye swap in one biological replicate adjusted dye bias, if any. The DE ESTs were identified as those with a 95% confidence interval for mean fold change (FC) that extended beyond the two-fold cut-off and also passed the Students t test ($P < 0.05$) and false detection ratio (FDR) correction. These cut-offs translate into induced ESTs having a log$_2$ ratio $\geq 1$ and repressed ESTs a ratio of $\leq -1$. 

Figure 3.1 Flow-chart showing a model for the analysis of drought stress response in stress tolerant and susceptible genotypes.

*Group II was processed in the same way as Group I. Susceptible genotypes were challenged and processed in the same way as shown for tolerant genotypes.
A list of DE ESTs for each genotype and tissue-type was then compiled and sorted according to their putative functions. The ESTs DE in the first group of tolerant and susceptible genotypes were compared to identify the ESTs uniquely DE in the tolerant/susceptible genotype. The ESTs found to be uniquely DE in the first group of drought tolerant and susceptible genotypes were validated by comparing the expression of these ESTs in the second group of tolerant and susceptible genotypes. Finally, a two-way comparison of genes that were DE in both the tolerant and susceptible genotypes was conducted (Figure 3.2) to identify genes that were consistently DE only in the drought tolerant/susceptible genotypes. The differential expression of two genes was further validated using qRT-PCR. The qRT-PCR was conducted by comparative $C_T$ method as described in section 2.2.4. Subsequently, the ESTs DE in the two groups of drought tolerant and susceptible genotypes were analysed based on their putative functions and genotypes in which they were expressed to reveal the possible mechanisms of drought tolerance/susceptibility in chickpea.

### 3.3 Results and discussion

#### 3.3.1 Drought stress treatment

The design and implementation of the drought stress treatment was the same as shown in Figure 2.1. The treatment plants were allowed to lose 5-10% water content daily, whilst holding the control plants at 80% water content. A comparison of drought stressed (at 30% water content) and unstressed (at 80% water content) Kaniva plants is presented in Figure 3.3. The drought stress caused yellowing of older leaves, wilting of fully-grown leaves, and abortion of buds and flowers. The yellowing and pod
abortion was prominent in susceptible genotypes. The yellowing and wilting of leaves is presented in Figure 3.4, whilst pod abortion is presented in Figure 3.5.

**Figure 3.2** Schematic representation of two-way comparison between the ESTs DE in the two groups of tolerant and susceptible genotypes to reveal the ESTs consistently DE in both the tolerant/susceptible genotypes.
Figure 3.3 Comparison of drought stressed and unstressed Kaniva plants.

A. Unstressed plants maintained at 80% water content show no signs of yellowing.

B. Drought stressed plants at 30% water content show yellowing of lower leaves and flower abortion.
Figure 3.4 A close-up view of yellowing of older leaves in Genesis-508 caused by drought stress.
Figure 3.5 A close-up view of bud abortion caused in Kaniva (A) and Genesis-508 (B) by drought stress treatment. The arrows in the pictures point towards aborted buds.
3.3.2 Analysis of drought stress response

The drought tolerant and susceptible genotypes used in the first group were BG-1103 and Kaniva, respectively. The leaf, root and the flower tissues were collected after drought stress as described earlier. The root samples yielded small amounts of poor quality RNA. The RNA from three root-tissue extractions was pooled together to produce sufficient amounts for hybridisation; however this failed to generate good quality, score-able spots. Therefore, only the leaf and flower tissues were used for further analysis. The second group of drought tolerant and susceptible genotypes studied was BG-362 and Genesis-508, respectively.

Six microarrays were hybridised for each of the 48 genotype x treatment/control x tissue-type x biological replication conditions, producing 288 microarray images for analysis of DE ESTs. The analysis consisted of two-way comparison to finally identify ESTs that were consistently DE only in the tolerant/susceptible genotypes. The number of microarray probes that were undetected (mean fluorescence intensity less than two times the mean local background intensity in all tissue-types and replications) in each chickpea genotype (tolerant and susceptible) varied according to the source of the probes. In general, the levels of undetected features for *L. sativus* probes were higher than the *C. arietinum* probes. All lentil RGA sequence probes were undetected in all genotypes.

Overall, 109 transcripts were >2-fold DE in all the genotypes and tissue-types examined. The Venn diagram shown in Figure 3.6 illustrates one of the many ways in which this large data set can be sorted to reveal potential insights. This diagram provides an important overview showing the distribution of changes into genotype-
specific responses. Globally, the number of transcripts DE in drought tolerant genotypes were more than that of susceptible genotypes. No transcript was commonly DE in all the tolerant and susceptible genotypes. The expression data for drought stress response has been deposited in Minimum Information about a Microarray Experiment (MIAME) compliant format at Gene Expression Omnibus, National Center for Biotechnology Information (Series number GSE7416).

**Figure 3.6** The number of transcripts DE by the drought tolerant and susceptible genotypes assessed.

* Tolerant-1 is BG-1103; Tolerant-2 is BG-362; Susceptible-1 is Kaniva; Susceptible-2 is Genesis-508.
Globally, the number of ESTs repressed was three to 10 times more than the ESTs induced for the genotypes and tissue types studied (Figure 3.7). Tolerant-1 (BG-1103) and tolerant-2 (BG-362) had a similar number of induced ESTs (6 and 7) but tolerant-2 had twice (45) the number of ESTs repressed than tolerant-1 (21). The susceptible-1 (Kaniva) had thrice the number of induced ESTs than susceptible-2 (Genesis-508) (6 and 2), whereas both the susceptible genotypes had a similar number of repressed ESTs (20 and 21). The differences may be attributed to genotype x environmental factors because the plants were grown in the glass house where the environmental conditions like temperature, humidity, and light intensity were approximately but not exactly the same.

**Figure 3.7** The number of ESTs DE between the drought stressed and unstressed plants of the tolerant and susceptible genotypes assessed.
The ESTs that were more than 2-fold DE (between treatment and control plants of all genotypes) included genes related to cell cycle, cell rescue, cellular metabolism, signalling and communication, transport facilitation, defence, energy metabolism, and protein synthesis (Table 3.1). Most of the DE ESTs belonged to cellular metabolism followed by genes with unknown function, genes related to defence, energy metabolism, cell rescue, protein synthesis, etc. The genes expressed from various functional categories did not show a particular trend related to the tolerant and susceptible genotypes.

The list of transcripts DE between treatment and control plants of all genotypes in response to drought stress is extensive and therefore presented in Appendix 6. However, a list of transcripts highly DE (>5-fold) in response to drought stress is presented in Table 3.2. The transcripts DE in response to drought stress coded for various functional and regulatory proteins, most of which were repressed. The interesting ones included those associated with senescence such as, auxin-responsive protein IAA9 (DY396315), dehydration-stress induced protein (DY396321), magnesium chelatase subunit (DY396339), phosphate-induced protein (DY475076 and DY475172), senescence-associated protein DIN1 (DY396338), and salt-inducible protein (DY396320) that were repressed in the shoots and flowers of tolerant genotypes. The switching off of death/ageing related genes may be an indication of the effort being made by plants to delay death. In fact, delay of senescence has been considered as one of the mechanisms of drought tolerance in other crops (Borrell et al., 2000; Yan et al., 2004). Out of these, only the phosphate-induced protein was repressed in the flowers of susceptible genotypes, which may contribute towards their susceptibility.
Table 3.1 Classification of drought regulated ESTs into functional categories based on sequence similarity to known genes.

<table>
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*T1 is tolerant-1, T2 is tolerant-2, S1 is susceptible-1, and S2 is susceptible-2.
^Total% of Genotype is the percentage of ESTs DE for the particular Functional Category from the total ESTs DE in the genotype.
Table 3.2: The ESTs that were >5-fold differentially expressed in the drought tolerant and susceptible genotypes of Group I and Group II

<table>
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<tr>
<th>GenBank Accession</th>
<th>Category</th>
<th>Group I* (Log₂ ratio)</th>
<th>Group II* (Log₂ ratio)</th>
<th>Putative Function</th>
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<td></td>
<td></td>
<td>Tolerant leaves</td>
<td>Susceptible leaves</td>
<td>Tolerant flowers</td>
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<td>Cell cycle &amp; DNA processing</td>
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<td>DY475477</td>
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<td>Asparagine synthetase (glutamine hydrolysing) (EC 6.3.5.4) – induced by the dark</td>
</tr>
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<td></td>
<td>-3.84</td>
<td>Fructose-1,6-bisphosphatase (EC 3.1.3.11)</td>
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<td>-2.37</td>
<td>beta-1,3-glucanase enzyme implicated in pathogen defence (EC 3.2.1.39)</td>
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* Group I had BG 1103 (ATC 48111) and Kaniva (ATC 40030) as tolerant and susceptible genotypes, respectively. Group II had BG 362 (ATC 48104) and Genesis 508 (ATC45226) as tolerant and susceptible genotypes, respectively.
Further, several transcripts associated with ubiquitin and polyubiquitin were repressed only in the leaves and flowers of tolerant genotypes. Ubiquitins are involved in diverse range of signalling cascades including photomorphogenesis and senescence (Downes et al., 2003). Their repression in tolerant genotypes may possibly be related to suppression of senescence contributing towards stress tolerance. Moreover, ubiquitins are known to negatively control the expression of stress related genes with a drought responsive element binding (DREB) motif (Chinnusamy et al., 2006). The Pulse Chip array lacked DREB transcripts; therefore the involvement of ubiquitin suppression in drought tolerance from this perspective needs to be further queried.

The transcript associated with protein-transport protein (DY475074) was 3-fold induced in flowers of tolerant-2, whilst aquaporin-like transmembrane channel protein (DY396334) and DNA-J like protein involved in intracellular protein transport (DY475488) were repressed in the flowers of susceptible-1. Moreover, the lipid-transfer protein precursor transcript (DY396350) was induced in the leaves of tolerant-2 genotype. Lipid-transfer proteins (LTPs) are known to be induced by osmotic and cold stress and have a role in stress adaptation (Yamaguchi-Shinozaki and Shinozaki, 2006). The exact role of LTPs is not known but they are thought to be involved in cutin biosynthesis, surface wax formation, pathogen-defence reactions, or the adaptation of plants to environmental changes (Kader, 1997). Although this was not confirmed in the remaining tolerant and susceptible genotypes, the suppression of protein and other solute transport in the susceptible genotype, whilst its induction in tolerant genotype may be contributing towards tolerance/susceptibility of these genotypes.
Importantly, two putative auxin-repressed protein transcripts (DY396289, DY396359) were highly (5-fold and 40-fold) repressed in the flowers and leaves of tolerant-2 genotype, respectively, whilst, this transcript was induced in the flowers and leaves of the susceptible-1. The plant hormone auxin regulates the growth and development processes by controlling the expression of auxin-responsive genes. One of the ways is by down-regulating the auxin-repressive gene to effect growth (Park and Han, 2003). The down-regulation of this gene in the tolerant genotype and up-regulation in the susceptible genotype may be because the susceptible genotype’s growth was suppressed due to drought stress while the tolerant one continued its growth. Moreover, the auxin-repressible gene has cis-elements responsible to sucrose in its promoter region and its regulation is controlled by sucrose (Park and Han, 2003). The sucrose-responsive transcription factor was >4-fold induced in the flowers of tolerant-2 where the auxin-repressed protein was >40-fold repressed. Therefore, it may possibly mean that sucrose was playing a key role in the drought-stress response of tolerant-2.

Among the pathogen-responsive transcripts involved in plant defense, a pea (pi230) disease resistance response protein (DY396390) and a multi-resistance protein ABC transporter (CV793605) were induced in the flowers of tolerant-1 and tolerant-2, respectively. On the contrary, the pathogenesis-related protein (DY396305 and DY396343), nematode-resistance protein (CV793603), Cf-9 gene cluster (DY396352) and disease resistance response protein transcripts (DY396276 and DY396276) were repressed in the flowers of tolerant and susceptible genotypes. The pathogenesis-related proteins have been shown to be expressed in response to abiotic stresses (Buchanan et al., 2005) but their exact role still remains unknown.
Several transcripts associated with energy metabolism such as, ATP synthase (DY475245), ferredoxin (electron transport protein) (DY475487), NADH dehydrogenase (DY396279, DY475316), NADH ubiquinone oxidoreductase (DY475294) and thioredoxin-related genes (DY475069, DY396293, DY396330) were repressed in the tolerant and susceptible genotypes. The genes involved in photosynthesis are known to be repressed in the shoots following the treatment of plants with NaCl (Salt stress), PEG (Osmotic stress) or ABA. This response is consistent with the closure of stomata in response to high ABA or osmotic stress, inhibition of CO₂ fixation and reduced need for energy capture by photosynthetic ETC (Buchanan *et al.*, 2005).

Interestingly, a RAC-GTP binding protein was induced in the flowers of a tolerant genotype. The RAC/ROP-GTP binding proteins are involved in diverse range of functions including defence, cell polarity and morphogenesis, and pollen tube growth (Brembu, 2004). Therefore, the induction of RAC-GTP binding protein in the flowers of tolerant genotype might be related to maintaining the pollen tube growth under drought stress to promote successful fertilisation and seed production.

Several transcripts with unknown/unclear functions were induced and/or repressed in the flowers and leaves of all the genotypes. The role/involvement of the genes with unknown/unclear functions will become clear only after subsequent studies. For instance, suppression of the DY475051 transcript only in the flowers of susceptible genotypes may contribute towards their susceptibility.
3.3.3 ESTs consistently DE in drought tolerant/susceptible genotypes

The main objective of this study was to find a suite of ESTs/genes that are consistently DE in both the tolerant/susceptible genotypes in response to the drought-stress condition. For this, the ESTs that were uniquely DE between the tolerant-1 and susceptible-1 genotypes were compared with those uniquely DE between tolerant-2 and susceptible-2. This was followed by a two-way comparison where, the genes uniquely DE between tolerant-1 and susceptible-2 were compared with those of tolerant-2 and susceptible-1. This led to identification of ESTs that were consistently DE only in the tolerant/susceptible genotypes.

Only two transcripts were consistently DE under drought stress. The cytosolic fructose 1,6-bisphosphatase (DY475548) associated with cellular metabolism and a transcript with unknown function (DY475051) were >2-fold repressed in the flowers of drought susceptible genotypes. This highlighted the global complexity of understanding the response to drought stress. The drought tolerant and susceptible genotypes tested here differed in their response to drought, which may possibly be due to genetic differences or interaction with other environmental factors as the stress treatments were carried out in glass house (15-25°C) at different times for the two groups of genotypes. Alternatively, the genotypes may differ in their timing of gene expression, which could not be captured here because the tissues were harvested at a single time-point.

Interestingly, two cytosolic fructose 1,6-bisphosphatase transcripts (DY475548, DY475543) were repressed only in the flowers of both susceptible genotypes. Fructose 1,6-bisphosphatase is involved in gluconeogenesis and is subject to indirect regulation by ATP. When the concentration of ATP in the cell is low, AMP would
then be high, which inhibits fructose 1,6-bisphosphatase and thus gluconeogenesis. This means at low ATP concentration, cell does not spend energy in synthesizing glucose. This may indicate that the susceptible genotypes were short of ATPs affecting glucose synthesis in their flowers/pods.

3.3.4 qRT-PCR confirmation

Two transcripts that were DE in both the susceptible genotypes were selected for qRT-PCR validation. The PCR amplification efficiency was verified using a validation curve analysis. The $C_T$ values were automatically generated by the MyiQ™ instrument (Bio-Rad, Hercules, CA). The melt curve analysis showed a single peak and gel electrophoresis indicated specific amplification of single product. The comparative $C_T$ method ($\Delta\Delta C_T$ method) was used to determine fold change values (as described in section 2.2.4). The fold-change values obtained through qRT-PCR show similar expression pattern to those obtained using microarray (Table 3.3). As observed in Chapter 2, the qRT-PCR fold-change values were generally exaggerated compared to the corresponding microarray values.

3.4 Conclusions

In summary, this study represented the first use of cDNA microarrays in chickpea to study drought stress response in the tolerant and susceptible genotypes. Expression profiles were generated for 756 probes including chickpea unigenes, *Lathyrus* ESTs, and lentil RGAs in conferring tolerance/susceptibility to drought stress. The results indicated that significant differences exist between the response of drought tolerant and susceptible genotypes. This highlighted the multiple gene control and complexity of drought tolerance mechanism. Only two transcripts were found to be consistently
Table 3.3 Table 3.3 Expression ratios of selected transcripts assessed by microarray and qRT-PCR. Array values indicate mean log$_2$ fold change (FC) ratio relative to untreated controls and qRT-PCR values indicate log$_2$ ratios of 2$^\Delta$Ctcontrol/2$^\Delta$Cttreatment. A set of DE genes that were expressed in both the susceptible genotypes were chosen for qRT-PCR confirmation of expression.

<table>
<thead>
<tr>
<th>Treatment/Genotype/Tissue-type</th>
<th>GenBank Accession</th>
<th>Putative Function</th>
<th>Group I*</th>
<th>Group II*</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Array</td>
<td>qRT-PCR</td>
</tr>
<tr>
<td>Drought susceptible flowers</td>
<td>DY475477</td>
<td>Asparagine synthetase (glutamine hydrolysing) (EC 6.3.5.4) - induced by dark.</td>
<td>-2.66</td>
<td>-2.37</td>
</tr>
<tr>
<td>Drought susceptible flowers</td>
<td>DY475051</td>
<td>Unknown function</td>
<td>-1.47</td>
<td>-2.53</td>
</tr>
</tbody>
</table>

* Group I had Kaniva (ATC 40030), whilst Group II had Genesis-508 (ATC45226) as susceptible genotypes, respectively.

DE from the 109 transcripts expressed in all genotypes and tissue types studied. Nevertheless, this study still provides an important insight into how the 756 genes studied here behave in different tolerant and susceptible genotypes under drought stress. The key findings include repression of the transcripts associated with senescence like auxin-responsive protein IAA9, magnesium chelatase, phosphate-induced protein, and senescence-associated protein in the tolerant genotypes may contribute towards drought tolerance in chickpea. This corroborates the claim that one of the mechanisms involved in drought stress tolerance includes delay of senescence (Borrell et al., 2000; Yan et al., 2004). Further, the induction of a protein-transport protein and a lipid-transfer protein, that facilitate solute transport, may be essential for drought tolerance. Importantly, the repression of transcripts associated with photosynthesis is an indication of closure of stomata, inhibition of CO$_2$ fixation and reduced need for energy capture under osmotic stress that may indicate successful
stress imposition. Subsequently, the induction of RAC-GTP binding protein that facilitates pollen tube growth may contribute towards drought tolerance by promoting successful fertilisation and seed production. One of the limitations of this study is that the drought stress response at different time-points could not be assessed due to lack of resources. The inclusion of additional time-points could have captured more transcriptional changes and probably revealed the difference in the timing of gene expression between the tolerant and susceptible genotypes. Hence, the study of more genotypes and transcriptional changes at several time points may provide a better picture of the involvement of the genes being interrogated here in drought tolerance/susceptibility. Subsequently, the functionality of candidate tolerance genes detected through this approach could be validated by overexpressing the genes through transgenics or silencing them using knockout-mutants/antisense/RNAi. Nevertheless, this study shall serve as a basis for further investigation of drought stress response in chickpea.
Chapter 4

Comparative transcriptional profiling of cold tolerant and susceptible genotypes to reveal potential gene candidates for cold tolerance/susceptibility

4.1 Introduction

Cold stress is a meteorological term wherein the environmental temperature drops below the optimum required for the crop, thus limiting its growth and productivity. Chickpea faces two types of low temperature stresses, namely, chilling stress (-1.5°C to 15°C) and freezing stress (below -1.5°C) (Croser et al., 2003). The chilling stress is prevalent across much of the chickpea producing areas and is the subject of this study. Therefore, the term ‘cold stress’ here applies to chilling range temperature (-1.5°C to 15°C). Cold stress limits the growth and vigour of chickpea at all phenological stages but is most devastating to yield at flowering and pod setting (Srinivasan et al., 1999). The impact of cold stress on the chickpea crop was discussed in section 1.2.2.2.

As explained in section 1.2.2.3, chickpea plants cope with cold stress via two mechanisms, cold escape/avoidance and cold tolerance. Cold escape/avoidance is the ability of chickpea plants to complete their reproductive phase before or after severe cold stress whilst, cold tolerance involves active mechanisms allowing the plant cells to improve membrane fluidity and osmotic adjustments to survive cold (Wery et al., 1993). Breeding efforts for cold tolerance in chickpea have mainly involved selection for yield and its components (e.g. high pollen vigour, high pod setting) in cold stressed environments (Singh et al., 1987). However, breeding for cold tolerance has
been set back by additive and non-additive effects that govern it and its dominance over susceptibility that delays selection in early generations (Malhotra and Singh, 1991; Singh et al., 1993). Additionally, the few efforts to develop molecular markers for cold tolerance identified a single SSR marker, which was not transferable to other populations (Millan et al., 2006). Hence, an improved understanding of genetic basis of cold tolerance is imperative for future plant breeding strategies.

Cold acclimation involves precise regulation of expression of transcription factors and effector genes collectively known as cold-regulated (COR) genes (Chinnusamy et al., 2006). Significant progress has been made in identifying transcriptional, post-transcriptional, and post-translational regulators of cold-induced expression of COR genes. Cold stress is thought to be sensed by membrane rigidification that probably increases the cytosolic Ca$^{2+}$ levels triggering the expression of COR genes (Sangwan et al., 2001). Cold-induced expression of reactive oxygen species (ROS) is putatively involved in activation of mitogen-activated protein kinase (MAPK) cascades that act as transcriptional regulators for freezing tolerance (Chinnusamy et al., 2004). The cold stress response involves expression of C-repeat binding transcription factors (CBF), which activate downstream adaptive genes and the expression of CBFs, is under the control of the inducer of CBF expression 1 (ICE1). The putative adaptive genes induced in response to cold are RD29A, COR15, COR47, RD22, and pyrroline-5-carboxylate synthetase. However, we still lack complete understanding of the signalling process from sensors to transcription factors to actual response, particularly in reproductive tissues (Chinnusamy et al., 2006).
Recent studies using gene expression profiling have captured a large amount of transcriptional changes in response to low temperature stress (as seen in Flower and Thomashow, 2002; Kreps et al., 2002; Seki et al., 2002). Transcriptome analysis using microarray technology is a powerful technique, which has been useful in discovering stress-inducible genes involved in the stress response and tolerance (Yamaguchi-Shinozaki and Shinozaki, 2006). The use of microarrays can be expanded to generate expression profiles of stress tolerant and susceptible genotypes to reveal differences in gene expression that contribute to tolerance/susceptibility (as seen in Kawasaki et al., 2001; Walia et al., 2005). The study described in Chapter 2 demonstrated that the ‘Pulse Chip’ array could be effectively used for gene expression profiling of chickpea responses to cold stress. To date, there is no report on gene expression profiling of contrasting chickpea genotypes in response to cold stress.

Hence, the aims of the experiments described in current chapter were to:

1. Challenge two groups of cold tolerant and susceptible genotypes with cold stress and compare the transcripts that are differentially expressed in them. Perform a two-way comparison of the differentially expressed transcripts in the two groups of tolerant and susceptible genotypes. This study shall help determine if a particular set of genes are expressed only in the tolerant/susceptible genotypes, which may mean they are associated with stress tolerance/susceptibility. Additionally, it may reveal how the genes being interrogated behave in different tolerant and susceptible genotypes under the stress condition.
2. Interpret the results from transcriptional profiling in the context of putative
gene functions and genotypes in which they were expressed to try and uncover
the mechanism and pathways involved in cold tolerance in chickpeas.

4.2 Materials and methods

4.2.1 Selection of genotypes

The cold tolerant and susceptible genotypes were selected after consultation with Dr.
Heather Clarke (Centre for Legumes in Mediterranean Agriculture, CLIMA, WA,
Australia) and Dr. Bob Redden (Curator, Australian Temperate Fields Crop
Collection, Horsham, Victoria, Australia). The cold tolerant genotypes used in the
present study were Sonali (ATC 48113) and ILC-01276 (ATC 40021), where ATC is
the Australian Temperate Crop identification number. The cold susceptible genotypes
used in the present study were Amethyst (ATC 42331) and Dooen (ATC 40874).
Sonali is a very early flowering, desi variety, with medium dark brown seeds, and
medium plant height released for cultivation in Western Australia in 2004 as a cold
tolerant genotype (McMurray, 2006). It was developed by pollen selection for cold
tolerance at hybridisation in CLIMA (Clarke et al., 2004). ILC-01276 is a desi
germplasm line with yellow seeds, medium plant height, and cold-tolerance (Bob
Redden, pers. comm.) Amethyst and Dooen are cold sensitive desi cultivars from
Australia (Clarke and Siddique, 2004). The growth rate of pollen tubes in Amethyst
and Dooen was significantly retarded at 4°C leading to cold sensitivity (Clarke and
Siddique, 2004). Additionally, whilst Amethyst and Dooen crops matured in 100 days
at optimum temperatures (25/20°C), the plant growth was retarded at low temperatures
(18/8°C), producing the first pod around 90 days after sowing and taking 200 days to
mature (Heather Clarke, pers. comm.).
4.2.2 Experimental design, stress treatment and analysis of differentially expressed genes

The first group of cold tolerant and susceptible genotypes used was Sonali and Amethyst, respectively. The second group of cold tolerant and susceptible genotypes used was ILC-01276 and Dooen, respectively. Five treatment and five control plants per genotype were cultivated and cold stressed as described in section 2.2.2.2. The leaf and flower/bud tissues were harvested after seven nights of cold stress to the treatment plants. The tissues were snap frozen and stored at −80°C until RNA extraction. The cold stress treatments for all the genotypes were performed with three biological replications. The tissues from five experimental replicate plants per biological replication were pooled together before RNA extraction. Leaf and flower/bud tissues were pooled separately. This RNA was used to prepare cDNA targets for expression analysis using microarray and quantitative real-time PCR (qRT-PCR). The total RNA extraction, preparation of targets, labelling and hybridisation were conducted as described in section 2.2.3. The experimental design for cold stress treatments was same as shown in Figure 3.1 except that only the leaf and flower/bud tissues were harvested and used for analysis. The ESTs DE in all the tolerant and susceptible genotypes were identified as described in section 3.2.2.

A list of DE ESTs for each genotype and tissue-type was then compiled and sorted according to their putative functions. The ESTs DE in the first group of tolerant and susceptible genotypes were compared to identify the ESTs uniquely DE in the tolerant/susceptible genotype. The ESTs found to be uniquely DE in the first group of cold tolerant and susceptible genotypes were validated by comparing the expression of
these ESTs in the second group of tolerant and susceptible genotypes. Finally, a two-way comparison of genes that were DE in both the tolerant and susceptible genotypes was conducted (see Figure 3.2) to identify genes that were consistently DE only in the cold tolerant/susceptible genotypes. The differential expression of two genes was further validated using qRT-PCR. The qRT-PCR was conducted by comparative $C_T$ method as described in section 2.2.4. Subsequently, the ESTs DE in the two groups of cold tolerant and susceptible genotypes were analysed based on their putative functions and genotypes in which they were expressed to reveal the possible mechanisms of cold tolerance/susceptibility in chickpea.

4.3 Results and discussion

4.3.1 Cold stress treatment

The cold-stress treatment was performed as described by stressing the treatment plants with 15-25°C/5°C (day/night temperature) for seven days, whilst maintaining the control plants at 15 to 25°C. The cold stressed plants did not show any chilling injury and no obvious phenotypic difference was observed between cold stressed and unstressed plants of all genotypes. This was expected because chickpea has a strong indeterminate growth habit (Wang et al., 2006) and may recover from overnight cold-stress if the temperatures return to normal during the day (Heather Clarke, pers. comm.). However, the objective of the study was to assess the adaptive response of chickpea to cold-stress, and therefore, the tissue samples were collected after the seven consecutive nights of cold stress. The Figure 4.1 shows the plants of cold tolerant (Sonali) and susceptible (Amethyst) genotypes during cultivation, whilst Figure 4.2 shows plants before cold stress treatment.
Figure 4.1 The plants of cold tolerant (Sonali) and cold susceptible (Amethyst) genotypes during cultivation.
Figure 4.2 The plants of cold tolerant (Sonali) and cold susceptible (Amethyst) genotypes before commencement of the cold stress treatment.
4.3.2 Analysis of cold stress response

The cold tolerant and susceptible genotypes used in the first group were Sonali and Amethyst, respectively. The second group had ILC-01276 and Dooen as tolerant and susceptible genotypes, respectively. The leaves and flower tissues were collected after the stress treatment and used for microarray analysis of gene expression.

Six microarrays were hybridised for each of the 48 genotype x treatment/control x tissue-type x biological replication conditions, producing 288 microarray images for analysis of DE ESTs. The analysis consisted of a two-way comparison to finally identify ESTs that were consistently DE in both the tolerant/susceptible genotypes.

The number of microarray probes that were undetected (mean fluorescence intensity less than two times the mean local background intensity in all tissue-types and replications) in each cold tolerant and susceptible genotype varied according to the source of the probes. As seen for drought stress, the levels of undetected features for *L. sativus* probes were higher than the *C. arietinum* probes. All lentil RGA sequence probes were undetected in all genotypes assessed.

Overall, 210 transcripts were >2-fold DE in all the genotypes and tissue-types examined. The Venn diagram shown in Figure 4.3 illustrates one of the many ways in which this large data set can be sorted to reveal potential insights. This diagram provides an important overview showing the distribution of changes into genotype-specific responses. The tolerant and susceptible genotypes varied in the number of transcripts DE. However, two transcripts were commonly DE in all the cold tolerant and susceptible genotypes. The expression data for the cold stress response has been
deposited in Minimum Information about a Microarray Experiment (MIAME) compliant format in the Gene Expression Omnibus, National Center for Biotechnology Information (Series number GSE7417).

**Figure 4.3** The number of transcripts DE by the cold tolerant and susceptible genotypes assessed.
*Tolerant-1 is Sonali; Tolerant-2 is ILC-01276; Susceptible-1 is Amethyst; Susceptible-2 is Dooen.

The cold tolerant and susceptible genotypes did not show any genotype-specific pattern for the number of DE ESTs (Figure 4.4). The susceptible-1 (Amethyst) had the highest number of induced ESTs (60) whilst tolerant-2 (ILC-01276) had the highest number of repressed ESTs (59). The susceptible-1 genotype showed an unusual
expression profile compared to the remaining genotypes. It induced more ESTs (60) whilst repressing relatively few ESTs (43) in response to the cold stress. Further, the tolerant-1 (Sonali) genotype induced more ESTs and repressed fewer ESTs than the tolerant-2 (ILC-01276). As reported for drought stress, it is believed that these differences may be the result of genotype × environmental interaction because the background for stress application (glasshouse temperature – 15 to 25°C, light intensity, humidity, etc) was very similar but not exactly the same. However, because the stressed plants were compared with unstressed plants, which only differed to unstressed plants in the treatment condition (4°C at night), the differences may be more due to the varied response of the cold tolerant and susceptible genotypes to the cold stress condition.

Figure 4.4 The number of ESTs DE between the cold stressed and unstressed plants of the tolerant and susceptible genotypes assessed.
The ESTs that were more than 2-fold DE (between treatment and control plants of all genotypes) included genes related to cell cycle, cell rescue, cellular metabolism, signalling and communication, transport facilitation, defence, energy metabolism and protein synthesis (Table 4.1). Most of the DE ESTs belonged to the cellular metabolism category followed by those related to defence, unknown function, signalling, cell rescue, etc. The ESTs expressed from various functional categories did not show any consistent pattern related to the tolerant and susceptible genotypes.

The list of transcripts that were >2-fold DE between cold-stressed and unstressed plants in all genotypes was extensive and therefore presented in Appendix 7. However, a list of transcripts that were highly DE (>5-fold) is presented in Table 4.2. These included genes from all different functional categories indicating a broad response. The important transcripts included a membrane-related protein CP5 (DY475119) that was highly (>5-fold) repressed in the leaves of both susceptible genotypes, whilst being >2-fold repressed in the leaves of tolerant genotypes. Cold stress is known to cause change in fluidity of plasma membrane at the micro-domain leading to stress perception (Chinnusamy et al., 2006). The significant variation in repression of this protein between the tolerant and susceptible genotypes may be a feature determining tolerance/susceptibility to cold stress.

Further, a Ca-binding mitochondrial carrier (DY396262) was repressed only in the leaves of tolerant genotypes. Rapid temperature drop has been shown to cause increase in cytosolic Ca\(^{2+}\) (Plieth et al., 1999) derived from either influx from apoplastic space or release from internal stores (Sanders et al., 1999; Knight, 2000) leading to signalling of downstream genes for stress adaptation (Xiong et al., 2002).
Table 4.1 Classification of cold regulated ESTs into functional categories based on sequence similarity to known genes.

<table>
<thead>
<tr>
<th>Functional Category</th>
<th>Genotype*</th>
<th>Induced</th>
<th>Repressed</th>
<th>Total</th>
<th>Total% of Genotype^</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cell cycle &amp; DNA processing</td>
<td>T1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.0</td>
</tr>
<tr>
<td></td>
<td>S1</td>
<td>2</td>
<td>0</td>
<td>2</td>
<td>1.9</td>
</tr>
<tr>
<td></td>
<td>T2</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.0</td>
</tr>
<tr>
<td></td>
<td>S2</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>2.0</td>
</tr>
<tr>
<td>Cell rescue, death/ageing</td>
<td>T1</td>
<td>5</td>
<td>3</td>
<td>8</td>
<td>12.9</td>
</tr>
<tr>
<td></td>
<td>S1</td>
<td>7</td>
<td>3</td>
<td>10</td>
<td>9.7</td>
</tr>
<tr>
<td></td>
<td>T2</td>
<td>2</td>
<td>5</td>
<td>7</td>
<td>10.0</td>
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<tr>
<td></td>
<td>S2</td>
<td>6</td>
<td>3</td>
<td>9</td>
<td>17.7</td>
</tr>
<tr>
<td>Cellular communication and signalling</td>
<td>T1</td>
<td>1</td>
<td>4</td>
<td>5</td>
<td>8.1</td>
</tr>
<tr>
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<td>S1</td>
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<td>17</td>
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<td>S2</td>
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<td>3</td>
<td>3</td>
<td>5.9</td>
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<td>Cellular metabolism</td>
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<td>2</td>
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<td>17.1</td>
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<td>S2</td>
<td>2</td>
<td>6</td>
<td>8</td>
<td>15.7</td>
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<td>4</td>
<td>5</td>
<td>8.1</td>
</tr>
<tr>
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<td>6</td>
<td>7</td>
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<td>2</td>
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<td>1.9</td>
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<td>3</td>
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<tr>
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<td>0</td>
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<tr>
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<td>4</td>
<td>7</td>
<td>11</td>
<td>21.6</td>
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</tbody>
</table>

*T1 is tolerant-1, T2 is tolerant-2, S1 is susceptible-1, and S2 is susceptible-2.

^Total% of Genotype is the percentage of ESTs DE for the particular Functional Category from the total ESTs DE in the genotype.
Table 4.2 The ESTs that were >5-fold differentially expressed in the cold tolerant and susceptible genotypes of Group I and Group II

<table>
<thead>
<tr>
<th>GenBank Accession</th>
<th>Category</th>
<th>Group I* (Log ratio)</th>
<th>Group II* (Log ratio)</th>
<th>Putative Function</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Tolerant leaves</td>
<td>Susceptible leaves</td>
<td>Tolerant flowers</td>
</tr>
<tr>
<td>DY396414</td>
<td>Cell cycle/DNA processing</td>
<td></td>
<td></td>
<td>2.34</td>
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<td>Cell rescue/death/ageing</td>
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<td>DY396363</td>
<td>Cell rescue/death/ageing</td>
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<td>Cell rescue/death/ageing</td>
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<td>DY475076</td>
<td>Cell rescue/death/ageing</td>
<td></td>
<td></td>
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</tr>
<tr>
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<td>Cell rescue/death/ageing</td>
<td></td>
<td>-3.65</td>
<td></td>
</tr>
<tr>
<td>DY396383</td>
<td>Signalling/communication</td>
<td>-2.51</td>
<td></td>
<td></td>
</tr>
<tr>
<td>DY475119</td>
<td>Signalling/communication</td>
<td></td>
<td></td>
<td>-2.39</td>
</tr>
<tr>
<td>DY475384</td>
<td>Signalling/communication</td>
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<td>-3.27</td>
<td></td>
</tr>
<tr>
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</tr>
<tr>
<td>DY396306</td>
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</tr>
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<td></td>
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</tr>
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<td></td>
</tr>
<tr>
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</tr>
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<td>Category</td>
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<td>Group II*</td>
<td>Putative Function</td>
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<td>----------</td>
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<td>-----------------------------------------------------------------------------------</td>
</tr>
<tr>
<td>CV793610</td>
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<td>3.87</td>
<td></td>
<td>Class 10 pathogenesis related protein induced by pathogen infection</td>
</tr>
<tr>
<td>CV793603</td>
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<td></td>
<td>Nematode Resistance Protein Hs1pro-1 homolog</td>
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<td></td>
<td>Gamma-thionien type defensin/protease inhibitor</td>
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<td>2.66</td>
<td></td>
<td>Thioredoxin</td>
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<tr>
<td>DY475287</td>
<td>Energy</td>
<td>-3.81</td>
<td></td>
<td>NADH-plastoquinone oxidoreductase subunit I (EC 1.6.5.3)</td>
</tr>
<tr>
<td>DY475423</td>
<td>Energy</td>
<td>-3.55</td>
<td></td>
<td>ATP synthase (EC 3.6.1.34)</td>
</tr>
<tr>
<td>DY475542</td>
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<td>-3.34</td>
<td></td>
<td>18S rRNA</td>
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<tr>
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<td>-5.16</td>
<td></td>
<td>18S nuclear rRNA</td>
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<tr>
<td>DY475406</td>
<td>Protein synthesis/fate</td>
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<td></td>
<td>FKBP-type peptidyl-prolyl cis-trans isomerase</td>
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<td>DY475479</td>
<td>Protein synthesis/fate</td>
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<td></td>
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<tr>
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<td>DY475390</td>
<td>Unknown</td>
<td>-2.79</td>
<td></td>
<td>Unknown</td>
</tr>
</tbody>
</table>

* Group I had Sonali (ATC 48113) and Amethyst (ATC 42331) as tolerant and susceptible genotypes, respectively. Group II had ILC-01276 (ATC 40021) and Dooen (ATC 40874) as tolerant and susceptible genotypes, respectively.
The cytosolic Ca\textsuperscript{2+} concentration is controlled by binding and chelation of various substances and by transport across plasma and intracellular membranes (Saris and Carafoli, 2005). Hence, the repression of the Ca-binding mitochondrial carrier only in the tolerant genotypes may be related to regulation of cytosolic Ca\textsuperscript{2+} leading to cold acclimation/tolerance.

The ubiquitin (DY396366) and polyubiquitin (DY396371, DY396410) transcripts were repressed only in the leaves of the tolerant genotypes. Cold acclimation induces the expression of C-repeat binding factors (CBF), which subsequently activate the downstream genes that confer chilling tolerance (Chinnusamy \textit{et al}., 2006). The transcription of CBFs and other cold-induced regulons is regulated by a constitutively expressed transcription factor, inducer of CBF expression 1 (ICE1), which is supposed to be negatively regulated by ubiquitination (Chinnusamy \textit{et al}., 2006). Hence, the repression of ubiquitins in the leaves of cold tolerant plants may be related to activation of ICE1 leading to cold acclimation. Conversely, two ubiquitin-specific protease transcripts (DY396408, DY396274) and a polyubiquitin transcript (DY396354) were induced in the leaves and flowers of a susceptible genotype. The induction of ubiquitins in susceptible genotype may possibly hinder cold acclimation and adaptation.

An interesting pattern was observed in relation to transcripts associated with synthesis/accumulation of osmolytes in the tolerant and susceptible genotypes. Firstly, the S-adenosylmethionine decarboxylase transcript (DY475170) involved in the synthesis of polyamines was induced in the flowers/leaves of tolerant and susceptible genotypes. Polyamines are known to act as osmolytes/compatible solutes and
accumulate under drought/osmotic stress (Mitra, 2001). Secondly, a trehalose phosphatase transcript (DY475282) was repressed only in the leaves of tolerant genotypes. Trehalose phosphatase catalyses the reaction leading to trehalose synthesis and therefore, its repression may mean that tolerant genotypes did not prefer to use trehalose as osmolyte under cold stress. Finally, the transcripts associated with β-glucosidase (DY475415) and β-galactosidase (EB085056, DY475141) were >3-fold repressed only in the leaves of tolerant genotypes. Both these enzymes are hydrolases that catalyse the reactions associated with hydrolysis of disaccharides (sucrose, lactose, maltose, etc.) into monosaccharides (glucose, galactose, etc.). Thus, the tolerant genotypes appeared to retain disaccharides under cold stress. Importantly, microorganisms like Escherichia coli and Bacillus thuringiensis showed increased tolerance to freeze drying in the presence of disaccharides such as sucrose, and it has been proposed that they protect membranes and proteins in intact bacteria while drying (Leslie et al., 1995). Potentially, these molecules may perform a similar role in the plant cells and provide protection against cold-stress. Further, a sucrose synthase transcript (DY475105) was induced in the leaves of a tolerant genotype, which supports the hypothesis of sucrose accumulation. Since this feature was only observed in the tolerant genotypes, it may contribute towards overall cold-tolerance.

Whilst sucrose accumulation in the leaves may be beneficial under cold-stress, it is detrimental for the flowers. In rice, low temperature at the most sensitive stage of pollen development resulted in accumulation of sucrose in the anthers, accompanied by a decrease in starch in mature pollen grains. This has been proposed to be linked to pollen sterility (Oliver et al., 2005). Interestingly, the α-amylase precursor (DY396337) and α-amylase (DY396402) transcripts were induced in the flowers of a
susceptible genotype. The $\alpha$-amylase is involved in breakdown of starch to sucrose. Hence, the induction of genes associated with starch breakdown in the flowers of the susceptible genotype may contribute towards its susceptibility.

Further, the auxin-repressed protein (DY475078) and auxin responsive protein IAA9 (DY396315) transcripts were $\geq$3-fold induced in the flowers and leaves of the susceptible genotypes. The plant hormone auxin regulates its growth and development. The induction of auxin-repressible protein is negatively correlated with shoot elongation (Park and Han, 2003). This observation may indicate that the growth and development of cold susceptible genotypes was suppressed due to cold-stress.

The wound-induced protein (DY475220), involved in cell rescue, was induced in flowers and leaves of susceptible-2, while it was repressed in the leaves of tolerant-1 and susceptible-1. Another wound-induced protein (DY475254) was induced in the flowers and leaves of tolerant-1, and leaves of susceptible-2. Although the function of wound-induced proteins in abiotic stress tolerance is not clear, interaction between wounding, pathogen infection, abiotic stress and hormonal responses has been reported (Cheong et al., 2002).

Subsequently, a glutathione S-transferase (GST) transcript (DY396404) was induced in the leaves of susceptible-1, while another GST (DY475250) was repressed in the leaves of tolerant-2. The GST is believed to act as an antioxidant to help scavenge reactive oxygen species produced during stress. In *Arabidopsis*, two GST transcripts were induced and three were repressed in response to drought, cold and salinity (Seki
et al., 2002), which indicated the variable activity of these transcripts under stress perhaps providing an array of functions in the response.

Interestingly, transcripts associated with superoxide dismutase (DY475397) were highly repressed in the flowers and leaves of susceptible genotypes and leaves of a tolerant genotype. Superoxide dismutase is involved in the programmed cell death pathway where its repression allows the accumulation of reactive oxygen species that signal and contribute to cell death (Neill et al., 2002). Subsequently, this result suggests that cold stress may lead to the promotion of cell death pathways.

Almost all of the transcripts involved in energy metabolism/photosynthesis were repressed in the leaves and flowers of tolerant and susceptible genotypes (e.g. DY475423, DY475554, DY475555, DY475487, DY475316, DY475556, DY475287, DY475434 and DY475305). This observation is not surprising since low temperature is known to cause reduced enzyme activity that leads to impairment of photosynthesis and respiration (Wolk and Herner, 1982; van Heerden and Kruger, 2000).

Besides these, many proteins involved in pathogen defence were induced/repressed in the leaves and flowers of tolerant and susceptible genotypes (e.g. CV793610, DY396305, DY396390, DY475397, DY396269 and DY396359). Although defence related genes were shown to be expressed in response to abiotic stresses (Seki et al., 2002) and a significant crosstalk between biotic and abiotic stresses was reported (Fujita et al., 2006), their actual role still remains unclear.
Finally, the proteins with unknown and unclear functions that were DE in the leaves and flowers of tolerant/susceptible genotypes need further investigation to confirm their involvement and role in the stress response. For instance, the repression of genes related to DY475203 and DY475323 only in the tolerant genotypes may impart cold tolerance to chickpea leaves.

4.3.3 ESTs consistently DE in cold tolerant/susceptible genotypes

The main objective of this study was to find a suite of ESTs/genes that are consistently DE in both the tolerant/susceptible genotypes in response to the cold-stress condition. The ESTs that were uniquely DE between the tolerant-1 and susceptible-1 genotypes were compared with those uniquely DE between tolerant-2 and susceptible-2. This was followed by a two-way comparison where, the genes uniquely DE between tolerant-1 and susceptible-2 were compared with those of tolerant-2 and susceptible-1. This led to identification of ESTs that were consistently DE only in the tolerant/susceptible genotypes.

Fifteen out of the 210 DE transcripts identified in the cold tolerant and susceptible genotypes were consistently expressed, all of which were repressed. Most of these were identified in the leaves of the tolerant genotypes, and included a beta-galactosidase (DY475141) transcript that was described earlier as possibly indicative of disaccharide (e.g. sucrose) retention with the effect of protecting cell membranes during cold stress. Several protein synthesis/modification and energy/metabolism transcripts were also repressed (e.g. DY475282, DY396371 and DY475555), which was likely due to the impairment of photosynthesis and respiration at low temperature (Wolk and Herner, 1982; van Heerden and Kruger, 2000). Other consistently
repressed transcripts in tolerant genotypes included putative signalling (DY396262, DY475384 and DY396307) and defence-related proteins (CV793589 and DY396343), which may be involved in the cold tolerance mechanisms as discussed in section 4.3.2. In susceptible genotypes, a superoxide dismutase (DY475397) and sorting nexin protein (DY475523) that controls trafficking of membrane/secretory proteins were the only transcripts to be consistently repressed. The repression of superoxide dismutase may lead to flower abortion, whilst repression of sorting nexin protein may affect solute transportation, contributing towards susceptibility.

4.3.4 qRT-PCR confirmation

Two transcripts that were DE in both the tolerant/susceptible genotypes were selected for qRT-PCR validation. The PCR amplification efficiency was verified by a validation experiment. The $C_T$ values were automatically generated by the MyiQ™ instrument (Bio-Rad, Hercules, CA). The melt curve analysis showing single peak and gel electrophoresis indicated specific amplification of single product. The comparative $C_T$ method ($\Delta\Delta C_T$ method) was used to determine fold change values (as described in section 2.2.4). The fold-change values obtained through qRT-PCR show similar expression pattern to those obtained using microarray analysis (Table 4.3). As observed in Chapter 2, the qRT-PCR fold-change values were generally exaggerated compared to the corresponding microarray values.
Table 4.3 Expression ratios of selected transcripts assessed by microarray and qRT-PCR. Array values indicate mean log2 fold change (FC) ratio relative to untreated controls and qRT-PCR values indicate log2 ratios of $2^{\Delta\text{Ct}_{\text{control}}/\Delta\text{Ct}_{\text{treatment}}}$. A set of DE genes that were expressed in both the tolerant/susceptible genotypes were chosen for qRT-PCR confirmation of expression.

<table>
<thead>
<tr>
<th>Treatment/ Genotype/ Tissue-type</th>
<th>GenBank Accession</th>
<th>Putative Function</th>
<th>Group I*</th>
<th>Group II*</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Array</td>
<td>qRT-PCR</td>
</tr>
<tr>
<td>Cold tolerant leaves</td>
<td>DY475384</td>
<td>Similar to serine/threonine protein kinase</td>
<td>-2.43</td>
<td>-2.95</td>
</tr>
<tr>
<td>Cold susceptible flowers</td>
<td>DY475397</td>
<td>Superoxide dismutase copper chaperone precursor involved in oxidative stress</td>
<td>-4.16</td>
<td>-4.53</td>
</tr>
</tbody>
</table>

* Group I had Sonali (ATC 48113) and Amethyst (ATC 42331) as tolerant and susceptible genotypes, respectively. Group II had ILC-01276 (ATC 40021) and Dooen (ATC 40874) as tolerant and susceptible genotypes, respectively.

4.4 Conclusions

In précis, this is the first document revealing the use of cDNA microarrays in chickpea to study cold stress response in tolerant and susceptible genotypes. Expression profiles in conferring tolerance/susceptibility to cold stress were generated for 756 probes including chickpea unigenes, Lathyrus ESTs, and lentil RGAs. The results indicated that significant differences exist between the response of the cold tolerant and susceptible genotypes. This highlights the multiple gene control and complexity of the cold tolerance mechanism. Only 15 transcripts were found to be consistently DE from the 210 transcripts expressed in all genotypes and tissue types studied. Although no phenotypic differences were seen among cold stressed and unstressed plants at the time of tissue sampling, changes at the transcript level indicated a stress response. Importantly, a membrane related protein CP5 associated with signalling was 2.5 times
more repressed in leaves of the susceptible genotypes compared to the tolerant ones. Since membrane related proteins are thought to be involved in the perception of cold stress, a further investigation of their role is warranted. Further, the repression of the Ca-binding mitochondrial carrier may be related to causing a Ca\(^{2+}\) influx, which is known to act as a sensor and activate downstream genes leading to cold adaptation. Subsequently, the repression of ubiquitins and polyubiquitins leading to induction of ICE1 that activates downstream genes resulting in cold adaptation may confer cold tolerance in chickpea plants. Moreover, the accumulation of disaccharides, especially sucrose, in the leaves of chickpeas by suppression of β-glucosidase and β-galactosidase, and induction of sucrose synthase, may impart cold tolerance. Whilst, accumulation of sucrose in chickpea flowers by induction of an α-amylase precursor and α-amylase genes may cause flower abortion and thus result in cold susceptibility.

One of the limitations of this study is that the cold stress response at different time-points could not be assessed due to lack of resources. The study of more genotypes and transcriptional changes at several time points may provide a better picture of involvement of the genes being interrogated here in cold tolerance/susceptibility. Subsequently, the functionality of candidate tolerance genes detected through this approach could be validated by overexpressing the genes through transgenics or silencing them using knockout-mutants/antisense/RNAi. Nevertheless, this study shall serve as a basis for further investigation of cold stress response in chickpea.
Chapter 5

Comparative transcriptional profiling of salt tolerant and susceptible genotypes to reveal potential gene candidates for high-salinity tolerance/susceptibility

5.1 Introduction

Saline soils are defined as those that have a high concentration of soluble salts (Ecₑ is ≥ 4 dS/m) (Munns, 2005). This Ecₑ would inhibit the root and shoot growth of most of the crops and resulting stress is known as salt-stress. Worldwide, increasing use of irrigation is exacerbating the problem of soil-salinity (Munns, 2005) and it has been predicted that by 2050, 50% of all the arable land would be salinized (Wang et al., 2003). Legumes in general are sensitive to salinity, and within legumes, chickpea, faba bean, and field pea are more sensitive than other grain legumes (Ahmad et al., 2005). In a field where salinity rises to 100 mM NaCl (about 10 dS/m), most of the legumes would die before maturity (Munns et al., 2002). The impact of salt-stress on chickpea has been reviewed in section 1.2.3.2.

Salt tolerance is the ability of a crop to grow and produce its economic product without major yield loss in saline versus normal soils. The mechanisms of salt tolerance include control of salt at whole plant level, control at cellular level, and control at molecular level (refer to section 1.2.3.3). Breeding for salt tolerance involves selection for percent biomass production and yield, both of which have a different pattern of response under salt stress (Munns et al., 2002). The screening for salt tolerance is limited by its enormous potential for interaction with other
environmental stresses, which makes it difficult to separate genetic and environmental variations (Flowers, 2004; Toker et al., 2007). Molecular breeding for salt tolerance in chickpea is in its infancy (refer to section 1.2.3.5). However, QTLs for salt tolerance have been identified in barley, citrus, and rice, and have been associated with ion transport under saline conditions (Flowers, 2004). These QTLs have been known to differ with genotypes and different stages of plant growth (Flowers, 2004). Therefore, a thorough investigation into molecular mechanisms for salt tolerance is needed to understand the genetic basis of tolerance.

Salinity stressed plants suffer from ionic imbalance in addition to osmotic stress. Salinity tolerance thus involves genes that regulate the uptake and transport of salt throughout the plant, maintain ionic and osmotic balance in roots and shoots, and regulate the development of senescence (Munns, 2005). Salt stress is thought to be perceived by the salt overly sensitive-3 (SOS3) protein. The SOS3, along with SOS2, is known to activate SOS1 (a Na⁺/H⁺ antiporter on plasma membrane) (Chinnusamy and Zhu, 2003). The SOS1 gene expression results in Na⁺ efflux and ion homeostasis. Besides, the mitogen activated protein kinase (MAPK) cascade is putatively involved in osmotic homeostasis and reactive oxygen species (ROS) scavenging (Chinnusamy and Zhu, 2003). Additionally, genes associated with synthesis of osmoprotectants like pyrroline-5-carboxylate synthetase (Atienza et al., 2004; Udea et al., 2004), myo-inositol 1-phosphate synthase (Kreps et al., 2002) and betaine aldehyde dehydrogenase (Udea et al., 2004) have been known to be induced upon salt stress. However, there is lack of information in the published literature about the actual number of genes involved in salt tolerance and how they interact for effective tolerance.
Transcriptional profiling using microarrays has been largely employed in the discovery of genes and pathways important for salt tolerance (as reviewed by Munns, 2005). Apart from studying the response of a particular genotype to different abiotic stresses, some studies have focused on comparative response of stress tolerant and susceptible genotypes to the particular stress. One such study by Kawasaki et al. (2001) compared the genes expressed by a salt tolerant genotype (Pokkali) and a salt susceptible genotype (IR29) of rice in response to salt stress. They concluded that the two genotypes differed in the timing of gene expression upon stress. The delayed gene expression by the salt susceptible genotype (IR29) was assumed to be responsible for salt sensitivity (Kawasaki et al., 2001). In yet another study in rice, the transcriptome of a salt tolerant genotype (FL478) and a salt sensitive genotype (IR29) differed significantly upon salt stress. The larger number of genes expressed by FL478 compared with IR29 was believed to be associated with FL478 being able to maintain low Na\(^+\) to K\(^+\) ratio (Walia et al., 2005). Taji et al. (2004) extended this concept of comparative transcriptomics to the species level by comparing the expression profiles of Arabidopsis with a halophyte (Thellungiella halophila) that share 90-95% microsynteny at cDNA level. The main difference in gene expression was that T. halophila expressed a higher level of stress responsive genes even before the stress was imposed, again revealing the importance of the timing of gene expression for stress tolerance. The comparison of gene expression profiling between contrasting genotypes thus has potential of lending us to a major breakthrough in understanding the spatial and temporal pattern of gene expression required for salt stress tolerance.
Hence, the aims of the experiments described in the current chapter were to:

1. Challenge two groups of salt tolerant and susceptible genotypes with high-salinity stress and compare the transcripts that are differentially expressed in them. Perform a two-way comparison of the differentially expressed transcripts in the two groups of tolerant and susceptible genotypes. This study shall help determine if a particular set of genes are expressed only in the tolerant/susceptible genotypes, which may mean they are associated with stress tolerance/susceptibility. Additionally, it may reveal how the genes being interrogated behave in different tolerant and susceptible genotypes under the stress condition.

2. Interpret the results from transcriptional profiling in the context of putative gene functions and genotypes in which they were expressed to try and uncover the mechanism and pathways involved in high-salinity tolerance in chickpeas.

### 5.2 Materials and methods

#### 5.2.1 Selection of genotypes

The salt tolerant and susceptible genotypes were selected after consultation with Moses Maliro (Joint Centre for Crop Innovation, University of Melbourne) and Dr. Bob Redden (Curator, Australian Temperate Fields Crop Collection, Horsham, Victoria, Australia). The salt tolerant genotypes used in the present study were CPI 060546 (ATC 40586) and ICC 06474 (ATC 40171), where ATC is Australian Temperate Crop identification number. The salt susceptible genotypes used in the present study were CPI 60527 (ATC 40033) and ICC 08161 (ATC 40707). The
characters of these genotypes as obtained from Moses Maliro (pers. comm., 2005; Maliro et al., 2007) are presented in Table 5.1.

Table 5.1 Results on necrosis score, shoot biomass (g), % biomass reduction at 42 days after sowing (DAS) for the genotypes used in current study. The plants were grown in pots in a polyhouse and salt stress applied by watering them on alternate days with salt solution (6 dS/m). The salt stress treatment commenced 21 DAS and plants analysed for salt tolerance at 42 DAS (Courtesy: Moses Maliro).

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<tr>
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<td>S1-85</td>
<td>CPI 060546</td>
<td>Turkey</td>
<td>1.7</td>
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<td>2.44</td>
<td>36</td>
<td>Highly tolerant</td>
</tr>
<tr>
<td>S1-22</td>
<td>ICC 06474</td>
<td>Iran</td>
<td>3.0</td>
<td>1.44</td>
<td>2.04</td>
<td>36</td>
<td>Highly tolerant</td>
</tr>
<tr>
<td>S1-81</td>
<td>CPI 60527</td>
<td>Turkey</td>
<td>9.7</td>
<td>0.36</td>
<td>5.61</td>
<td>87</td>
<td>Highly susceptible</td>
</tr>
<tr>
<td>S1-93</td>
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<td>Iran</td>
<td>10.0</td>
<td>0.31</td>
<td>3.11</td>
<td>84</td>
<td>Highly susceptible</td>
</tr>
</tbody>
</table>

5.2.2 Experimental design, stress treatment and analysis of differentially expressed genes

The first group of salt tolerant and susceptible genotypes used was CPI 060546 and CPI 60527, respectively. The second group of salt tolerant and susceptible genotypes used was ICC 06474 and ICC 08161, respectively. Ten treatment and ten control plants per genotype were cultivated and high-salinity stressed as described in section 2.2.2.3. The shoot and root tissues were harvested from five treatment and control plants per genotype at 24 and 48 hours post treatment (hpt). The tissues were snap frozen and stored at −80°C until RNA extraction. The high-salinity stress treatments for all the genotypes were performed with three biological replications. The tissues from five experimental replicate plants per biological replication were pooled together.
before RNA extraction. The shoot and root tissues were pooled separately. This RNA was used to prepare cDNA targets for expression analysis using microarray and quantitative real-time PCR (qRT-PCR). The total RNA extraction, preparation of targets, labelling and hybridisation were conducted as described in section 2.2.3. The experimental design for high-salinity stress treatments was same as shown in Figure 3.1 except that the shoot and root tissues were harvested at 24 and 48 hpt and used individually for analysis. The ESTs DE in all the tolerant and susceptible genotypes were identified as described in section 3.2.2.

A list of DE ESTs for each genotype and tissue-type was then compiled and sorted according to their putative functions. The ESTs DE in the first group of tolerant and susceptible genotypes were compared to identify the ESTs uniquely DE in the tolerant/susceptible genotype. The ESTs found to be uniquely DE in the first group of salt tolerant and susceptible genotypes were validated by comparing the expression of these ESTs in the second group of tolerant and susceptible genotypes. Finally, a two-way comparison of genes that were DE in both the tolerant and susceptible genotypes was conducted (see Figure 3.2) to identify genes that were consistently DE only in the salt tolerant/susceptible genotypes. The differential expression of couple of genes was further validated using qRT-PCR. The qRT-PCR was conducted by comparative C_T method as described in section 2.2.4. Subsequently, the ESTs DE in the two groups of salt tolerant and susceptible genotypes were analysed based on their putative functions and genotypes in which they were expressed to reveal the possible mechanisms of high-salinity tolerance/susceptibility in chickpea.
5.3 Results and discussion

5.3.1 High-salinity stress treatment

The tolerant and susceptible genotypes were grown hydroponically and high-salinity stressed as described in 2.2.2.3. Figure 5.1 shows 18-day-old chickpea plants ready to be salt stressed. The salt stress was visible as senescence/yellowing of older leaves at 24 hpt (Figure 5.2). The symptoms of salt-stress progressively advanced up the plants as evidenced by appearance of water-soaked lesions on the leaves moving upwards from the crown region on the second day after stress (Figure 5.3). To avoid sampling severely stressed and dying leaves, only the topmost growing leaves along with the corresponding shoot were harvested for analysis of salt stress response. However, the complete root system was harvested for microarray analysis. As expected, the tolerant plants showed delayed senescence compared to the susceptible ones. One more visible difference after high-salinity stress imposition was that the shoot and the root growth in treatment plants were suppressed while the unstressed (control) plants continued to grow. This was evidenced by higher canopy area and denser root mass of control plants at the time of tissue collection.

5.3.2 Analysis of high-salinity stress response

The salt tolerant and susceptible genotypes used in the first group were CPI 060546 and CPI 60527, respectively. The leaves/shoot and root samples were collected 24 and 48 hpt treatment, as described earlier. The second group of salt tolerant and susceptible genotypes used was ICC 06474 and ICC 08161, respectively.

Six microarrays were hybridised for each of the 96 genotype x treatment/control x tissue-type x time-points x biological replication conditions producing 576 microarray
Figure 5.1 A photograph showing 18-day-old hydroponically grown chickpea plants before commencement of the high-salinity stress treatment.

Figure 5.2 A close-up view of senescence/yellowing of older leaves caused by high-salinity stress treatment.
Figure 5.3 Close-up view of water-soaked lesions on the leaves of chickpea plants caused by high-salinity stress. ‘A’ shows upper leaf surface, whilst ‘B’ the lower leaf.
images for analysis of DE ESTs. The analysis consisted of a two-way comparison to finally identify transcripts that were consistently DE in both tolerant/susceptible genotypes. The tissues from 24 and 48 hpt were analysed separately. The number of microarray probes that were undetected (mean fluorescence intensity less than two times the mean local background intensity in all tissue-types and replications) in each chickpea genotype (tolerant and susceptible) varied according to the source of the probes. As observed for drought and cold stress response, the levels of undetected features for *L. sativus* probes were higher than the *C. arietinum* probes. All lentil RGA sequence probes were undetected in all the genotypes.

Overall, 386 transcripts were >2-fold DE in all the genotypes and tissue-types examined. The Venn diagram shown in Figure 5.4 illustrates one of the many ways in which this large data set can be sorted to reveal potential insights. This diagram provides an important overview showing the distribution of changes into genotype-specific responses. Globally, the salt tolerant and susceptible genotypes varied in their response to salt stress. However, twelve transcripts were commonly DE in all the tolerant and susceptible genotypes. The expression data for high-salinity stress response has been deposited in Minimum Information about a Microarray Experiment (MIAME) compliant format at Gene Expression Omnibus, National Center for Biotechnology Information (Series number GSE7418).

The number of transcripts induced and repressed by high-salinity stress in the tolerant and susceptible genotypes are presented in Figure 5.5. The number of ESTs repressed were two to 10 times the induced ESTs for the all genotypes, tissue-types and time-points studied. Tolerant-1 (CPI 060546) had the highest number of repressed ESTs.
Figure 5.4 The number of transcripts DE by the salt tolerant and susceptible genotypes assessed.
* Tolerant-1 is CPI 060546; Tolerant-2 is ICC 06474; Susceptible-1 is CPI 60527; Susceptible-2 is ICC 08161.

![Figure 5.4 Diagram](image)

Figure 5.5 The number of ESTs DE between the high-salinity stressed and unstressed plants of the tolerant and susceptible genotypes assessed.
(102) at 24 hpt, while susceptible-1 (CPI 60527) and tolerant-2 (ICC 06474) had highest number of induced ESTs (23). At 48 hpt, the susceptible-1 genotype had highest number of induced and repressed ESTs (50 and 111).

The number of transcripts DE at least in one genotype under high-salinity stress (386) was approximately two and four times of those DE in response to cold (210) and drought (109), respectively. These included transcripts related to cell cycle, cell rescue, cellular metabolism, signalling and communication, transport facilitation, defence, energy metabolism, transcription, protein synthesis and genes with unknown/unclear functions (Table 5.2). Most of the DE transcripts were from genes with unknown functions followed by genes involved in cellular metabolism, defence, energy metabolism, protein synthesis, cell rescue, etc. The transcripts expressed from various functional categories did not show any particular pattern related to the tolerant and susceptible genotypes.

The transcriptional changes in shoots and roots of the salt tolerant and susceptible genotypes were documented after 24 and 48 hours of high-salinity stress. The high-salinity stress induced/repressed 57% of the total (715) chickpea and grasspea ESTs at least once in all the genotypes, time-points and tissue-types studied. The list of ESTs DE between high-salinity-stressed and unstressed plants of all genotypes is extensive and therefore presented in Appendix 8. However, a list of ESTs highly DE (>5-fold) is presented in Table 5.3. From the 386 ESTs DE in the tolerant and susceptible genotypes, only those thought to be functionally important or with interesting expression profiles are discussed.
Table 5.2 Classification of high-salinity regulated transcripts into functional categories based on sequence similarity to known genes.

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<th>Repressed 24 hpt</th>
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*T1 is tolerant-1, T2 is tolerant-2, S1 is susceptible-1, and S2 is susceptible-2.
^Total% of Genotype is the percentage of ESTs DE for the particular Functional Category from the total ESTs DE in the genotype.
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- DY475248: Polymorphic antigen membrane protein
- DY475320: Serine/threonine protein kinase
- DY475550: WD repeat protein (trp-asp domains)
- DY475478: Hypothetical transmembrane protein
- DY396270: Deoxycytidylate deaminase
- DY396308: Xyloglucan endotransglycosylase LEXET2
- DY396435: L-ascorbate peroxidase, cytosolic
- DY396401: Ubiquitin-carboxyl extension
- DY475543: Fructose-1,6-bisphosphatase
- DY475108: Asparagine synthetase (EC 6.3.5.4)
- DY475113: Cytochrome C oxidase subunit
- DY475152: Cytidine deaminase enzyme
- DY475155: Superoxide dismutase
- DY475213: Carbonic anhydrase (EC 4.2.1.1)
- DY475240: Ribose 5-phosphate isomerase
- DY475242: Thiazole biosynthetic enzyme involved in thiamine biosynthesis
- DY475548: Fructose 1,6-bisphosphatase
- DY475393: Cytochrome c biogenesis protein
- DY475403: Carbonic anhydrase
- DY475408: Xylosidase
- DY475443: Succinate dehydrogenase subunit 3
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**Putative Function**

- Photosystem II reaction centre I protein
- Photosystem II D2 protein
- Chloroplast genome DNA
- NADH-plastoquinone oxidoreductase subunit I
- NADH-ubiquinone oxidoreductase
- NADH dehydrogenase
- Photosystem I assembly protein ycf3
- Ferredoxin (electron transfer protein)
- Chloroplast DNA for P700 chlorophyll a-apoproteins
- Chloroplast DNA between the RUBISCO large subunit and ATPase (beta) genes
- 5.8S, 18S and 25S rRNA
- 60S ribosomal protein L17
- 50S ribosomal protein L12
- Chloroplast 16S rRNA
- 26S ribosomal RNA
- Aquaporin-like transmembrane channel protein
- Aquaporin membrane protein
- DNAJ like protein involved in intracellular protein transport increased during heat shock
- Unclear
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* Group I had CPI 060546 (ATC 40586) and CPI 60527 (ATC 40033) as tolerant and susceptible genotypes, respectively. Group II had ICC 06474 (ATC 40171) and ICC 08161 (ATC 40707) as tolerant and susceptible genotypes, respectively.

TS = Tolerant Shoots; SS = Susceptible Shoots; TR = Tolerant Roots; SR = Susceptible Roots; 24 hpt = 24 hours post treatment; 48 hpt = 48 hours post treatment.
Interestingly, the transcript associated with Ca-binding mitochondrial carrier (DY396262) was repressed in roots of tolerant genotypes at 24 and 48 hpt, and in shoots of only one susceptible genotype at 48 hpt. Drought, cold and high-salinity stresses have been shown to induce transient Ca$^{2+}$ influx into the cell cytoplasm (as reviewed by Sanders et al., 1999; Knight, 2000) that causes signalling of downstream genes responsible for stress adaptation (Xiong et al., 2002). The cytosolic Ca$^{2+}$ concentration is controlled by transport across plasma and intracellular membranes (Saris and Carafoli, 2005) and therefore the repression of Ca-binding mitochondrial carrier in roots of only tolerant genotypes at both time points might be related to achieving Ca$^{2+}$ influx required for stress adaptation/tolerance. Alternatively, the Ca$^{2+}$ influx may be necessary to regain ionic balance after exclusion of Na$^+$ from the cells. This was observed only in one susceptible genotype at later time point, which might contribute towards susceptibility.

The poly (A) binding protein transcripts (DY396360 and DY396412) were 2- to 5-fold repressed in roots of both the tolerant genotypes at 24 hpt, whereas at 48 hpt, they were induced in roots and repressed in shoots of susceptible-1. Poly (A) binding proteins are a family of eukaryotic, cytoplasmic proteins thought to bind to the poly (A) tails of mRNAs and play a role in translational regulation (Yohn et al., 1998). In Arabidopsis, one RNA-binding protein was induced and three RNA-binding proteins were repressed in response to drought, cold and salinity (Seki et al., 2002).

Interestingly, a splicing factor-like protein (DY396290) involved in DNA processing was repressed in roots of both tolerant genotypes at 24 hpt, and also repressed in shoots and roots of both the susceptible genotypes at this time. However, at 48 hpt, it
was repressed only in roots of both susceptible genotypes. Subsequently, at 24 hpt, RNA production/processing may be suppressed in roots/shoots of all the genotypes but is repressed only in roots of susceptible genotypes at 48 hpt.

A putative heat shock protein and heat shock factor binding protein (DY396361 and DY475474) were repressed in roots and shoots of tolerant genotypes at 24 hpt. On the contrary, heat shock protein DNA-J homolog (DY396397) was induced in roots of susceptible-1 at 24 hpt. Further, these transcripts were repressed in roots of all tolerant and susceptible genotypes at 48 hpt. Heat shock proteins are molecular chaperones for protein molecules and play an important role in protein-protein interactions such as folding, assisting in the establishment of proper protein shape and prevention of unwanted protein aggregation. In other plants, these proteins were induced by abiotic stresses like drought, cold and salinity (Kreps et al., 2002; Seki et al., 2002). However, several heat shock proteins studied by Seki et al. (2002) like, HSP 90 and HSP 81-2, were repressed at 10- and 24- hpt after being induced in the first hour. Subsequently, the heat-shock proteins in this study may have been induced very early after high-salinity treatment and then repressed at tissue sampling times.

Interestingly, proline oxidase transcript (DY475225) involved in the conversion of proline to glutamate was repressed only in roots of the susceptible genotypes at 24 hpt, and repressed in shoots and roots of susceptible-2 and in shoots of tolerant-2 at 48 hpt. Osmolytes such as proline accumulate under salt stress to prevent wilting and toxicity in the presence of high internal salt concentration and possibly aid in salt tolerance (Munns, 2005). These osmolytes accumulate if the plants cannot maintain turgor by regulating ion exchange. Subsequently, the early repression of proline
oxidase in susceptible genotypes may indicate a reaction to osmotic stress through the retention of proline, which was only observed later in one tolerant genotype.

Transcripts representing a senescence-associated protein (DY396273) and ripening related protein (DY396347) were repressed in the roots and shoots of tolerant-1, respectively, at 24 hpt. On the other hand, a senescence-associated protein DIN 1 (DY396338) was >3-fold induced in roots of susceptible-1 at this time. Further, DY396273 was >3-fold induced in shoots of susceptible-1 at 48 hpt. These results may indicate that whilst, the tolerant-1 genotype was avoiding ageing/death related genes, the susceptible-1 genotype was already undergoing cell death due to high-salinity stress at 24 hpt in roots and 48 hpt in shoots. In fact, it has been appraised that one of the mechanisms of salt tolerance involves delay of senescence (Munns, 2005).

Amongst the transcripts related to cellular metabolism, carbonic anhydrase transcripts (DY475213 and DY475403) were repressed in roots of the tolerant/susceptible genotypes at 24 and 48 hpt. Carbonic anhydrase (CA) is involved in diverse biological processes including pH regulation, ion exchange, CO₂ transfer, respiration and photosynthetic CO₂ fixation (Tiwari et al., 2005). Biosynthesis of CA is dependent upon photon flux density, CO₂ concentration and Zn availability. Hence, the repression of CA in roots may be an adaptive mechanism to regain ionic homeostasis and/or balance pH. Alternatively, it might be just because of suppression of respiration and CO₂ transfer under high-salinity stress.

Further, two cytosolic fructose 1,6-bisphosphatase transcripts (DY475548 and DY475543) were repressed only in roots of the tolerant genotypes at 24 hpt, while
DY475543 was repressed only in roots of susceptible-2 at 48 hpt. The fructose 1,6-bisphosphatase is involved in gluconeogenesis and is under indirect regulation of ATP. When the concentration of ATP in the cell is low, AMP would then be high resulting in inhibition of fructose 1,6-bisphosphatase and thus gluconeogenesis. This may imply that at low ATP concentration, cell does not expend energy in synthesizing glucose. Thus, the roots of tolerant genotypes may be trying to conserve energy by repressing fructose 1,6-bisphosphatase as early as 24 hpt, which did not occur in susceptible genotypes until 48 hpt and may contribute towards susceptibility.

Amongst the defence related transcripts, caffeoyl-CoA O-methyltransferase 4 (DY396415), which is associated with lignification (Martz et al., 1998), was repressed in shoots and roots of susceptible genotypes at 24 hpt, and repressed only in shoots of susceptible-1 at 48 hpt. On the other hand, a putative glycine-rich cell wall protein GRP 1.8 (DY396342) was repressed only in the roots of the tolerant genotypes at 24 hpt. The GRPs are also closely associated with lignification of cell walls in response to wounding or pathogen attack (Keller and Baumgartner, 1991). Lignin biosynthesis is involved in the reinforcement of the plant cell wall in the response to wounding or pathogen challenge by the increased formation of cell-wall-bound ferulic acid polymers. The repression of genes related to lignification may indicate direction of cellular resources toward other processes. The important observation is that the tolerant and susceptible genotypes appear to repress different genes for lignification.

Interestingly, several pathogenesis related protein 4A transcripts (DY396281, DY396372, DY396384, DY396388, CV793597) were highly induced in roots of all the tolerant and susceptible genotypes at 24 hpt, and again in all genotypes except
susceptible-2 at 48 hpt. This transcript was not expressed in response to drought-stress and only repressed in response to cold-stress. The plant defence related genes have been known to be induced in response to abiotic stresses (Seki et al., 2002). In fact, many genes identified in expression studies in response to salt stress include those in common with pathogen infection (Munns, 2005). Considering the pathogenesis related protein 4A was highly induced only in response to high-salinity stress in this study, further investigation of their involvement in salt stress may be warranted.

Amongst the transcripts related to signalling and communication, a histidine-containing phospho-transfer protein ATHP3 (DY396300) was repressed only in roots of tolerant genotypes at 24 and 48 hpt. The ATHPs (or AHPs) are thought to be involved in stress sensing and relay signal transduction, where ATHP1 is thought to sense osmotic stress and transfer the signal via ATHP2/ATHP3 to the Arabidopsis Response Regulators (ARRs) (Urao et al., 2000). The amino acid sequences of ATHP2 and ATHP3 show 81% identity, suggesting possible functional redundancy (Hwang et al., 2002). Moreover, overexpression of ATHP2 has been shown to cause cytokinin hypersensitiveness affecting root and hypocotyl elongation (Suzuki et al., 2002). Hence, the repression of ATHP3 only in roots of tolerant genotypes at both time-points may be important to sustain root growth under high-salinity stress.

The auxin-repressed protein transcripts (DY396269, DY396289, DY396292 and DY396359) were induced in roots of tolerant-1, tolerant-2 and susceptible-1 whilst they were repressed in shoots of tolerant-2 and susceptible-1 at 48 hpt. The plant hormone auxin regulates its growth and development. The induction of auxin-repressible protein is negatively correlated with growth and shoot elongation (Park
and Han, 2003). This observation suggests that the roots of all the genotypes ceased to develop at 48 hpt, but the shoots were still undergoing growth, which supports the hypothesis that genes regulating cell division and elongation might be affected by salt stress (Munns, 2005). Moreover the terminal parts of the plant are known to be the last affected by salt stress (Munns et al., 2002).

Importantly, the transcripts associated with transport facilitation like aquaporin (DY475124) and aquaporin-like transmembrane protein (DY396334) were repressed in roots of the tolerant genotypes at 24 hpt. Also, aquaporin 2 (integral tonoplast water channel protein; DY475512), aquaporin membrane protein (DY475174) and aquaporin-like transmembrane channel protein (DY396334) were repressed in roots of susceptible-1 at 48 hpt. At the same time only DY475174 was repressed in roots of tolerant-1. The study of all putative membrane transporters in Arabidopsis revealed a coordinated down-regulation of all aquaporin forms early after high-salinity stress imposition (Maathuis et al., 2003). The suppression of root hydraulic conductivity under salt stress is observed in many plants and represents one of the best characterised examples of stress-induced regulation of water transport in plants (Luu and Maurel, 2005). Hence, the early repression of aquaporins in roots of both tolerant genotypes, which takes place only in one susceptible genotype at later time-point (48 hpt) might be a feature determining tolerance/susceptibility.

Finally, the role/involvement of the genes with unknown/unclear functions will become clear only after subsequent studies. However, the high-induction (up to 10-fold) of EB085058 in all genotypes, high-repression (up to 56-fold) of DY475357 only in tolerant genotypes, and repression of DY475416 only in the roots of tolerant
genotypes at all times, indicates that these genes may possibly contribute towards salt-tolerance in chickpea.

5.3.3 ESTs consistently DE in salt tolerant/susceptible genotypes

The main objective of this study was to find a suite of ESTs/genes that are consistently DE in both the tolerant/susceptible genotypes in response to the high-salinity stress condition. The ESTs that were uniquely DE between the tolerant-1 and susceptible-1 genotypes were compared with those uniquely DE between tolerant-2 and susceptible-2. This was followed by a two-way comparison where the ESTs uniquely DE between tolerant-1 and susceptible-2 were compared with those of tolerant-2 and susceptible-1. This led to identification of ESTs that were consistently DE only in the tolerant/susceptible genotypes.

The interesting transcripts consistently DE under high-salinity stress include histidine-containing phosphotransfer protein (ATHP3) (DY3963000), glycine-rich protein GRP 1.8 (DY396342) and protein kinase (DY475077) involved in signalling were repressed in roots of tolerant genotypes at 24 hpt. Further, chloroplast DNA for P700 chlorophyll a-apoproteins (DY475501) and NADH-plastoquinone oxidoreductase subunit I (DY475287) transcripts associated with energy metabolism were repressed in the shoots of tolerant genotypes at 24 hpt. Also, aquaporin (DY475124) associated with transport facilitation was repressed in the roots of tolerant genotypes at 24 hpt. On the other hand, proline oxidase transcript (DY475225) and a transcript with unclear function (DY475186) were repressed in the roots of susceptible genotypes at 24 hpt. At 48 hpt, the pathogenesis-related protein transcript (DY396301) was repressed in shoots of both the tolerant genotypes. Interestingly, a transcript with
unclear function (DY475205) was induced in shoots of the susceptible genotypes at 48 hpt. Further, a probable Ca-binding mitochondrial carrier transcript (DY396262) involved in signalling was repressed in roots of the tolerant genotypes at 48 hpt. Also, carbonic anhydrase transcript (DY475403) and thiazole biosynthetic enzyme transcript (DY475242) were repressed in roots of both the tolerant genotypes, whilst xlyosidase (DY475408) was induced in roots of susceptible genotypes at 48 hpt. More importantly, the pathogenesis-related protein 4A transcript (DY396281) involved in defence was >6-fold induced in roots of both the tolerant genotypes at 48 hpt. The possible involvement of these transcripts in conferring salt tolerance/susceptibility to chickpea has been discussed in section 5.3.2.

5.3.4 qRT-PCR confirmation

Five transcripts that were consistently DE in both the tolerant/susceptible genotypes were selected for qRT-PCR validation. The PCR amplification efficiency was verified using a validation curve analysis. The \( C_T \) values were automatically generated by the MyiQ™ instrument (Bio-Rad, Hercules, CA). The melt curve analysis showing single peak and gel electrophoresis indicated specific amplification of single product. The comparative \( C_T \) method (\( \Delta\Delta C_T \) method) was used to determine fold change values (as described in section 2.2.4). The fold-change values obtained through qRT-PCR show similar expression pattern to those obtained using microarray (Table 5.4). As observed in Chapter 2, the qRT-PCR fold-change values were generally exaggerated than the corresponding microarray values.
Table 5.4 Expression ratios of selected transcripts assessed by microarray and qRT-PCR. Array values indicate mean log$_2$ fold change (FC) ratio relative to untreated controls and qRT-PCR values indicate log$_2$ ratios of $2^{\Delta C_{\text{control}}/\Delta C_{\text{treatment}}}$. A set of DE genes that were expressed in both the tolerant/susceptible genotypes were chosen for qRT-PCR confirmation of expression.

<table>
<thead>
<tr>
<th>Treatment/ Genotype/ Tissue-type/ Time-point</th>
<th>GenBank Accession</th>
<th>Putative Function</th>
<th>Group I*</th>
<th>Group II*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Salt tolerant shoots 24 hpt</td>
<td>DY475501</td>
<td>Chloroplast DNA for P700 chlorophyll a-apoproteins</td>
<td>-1.06</td>
<td>-2.43</td>
</tr>
<tr>
<td>Salt tolerant roots 24 hpt</td>
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<td>Aquaporin</td>
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<tr>
<td>Salt susceptible roots 24 hpt</td>
<td>DY475225</td>
<td>Proline oxidase involved in the conversion of proline to glutamate</td>
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<tr>
<td>Salt tolerant roots 48 hpt</td>
<td>DY475403</td>
<td>Carbonic anhydrase</td>
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</tr>
<tr>
<td>Salt susceptible roots 48 hpt</td>
<td>DY475408</td>
<td>Xylosidase</td>
<td>2.48</td>
<td>2.73</td>
</tr>
</tbody>
</table>

* Group I had CPI 060546 (ATC 40586) and CPI 60527 (ATC 40033) as tolerant and susceptible genotypes, respectively. Group II had ICC 06474 (ATC 40171) and ICC 08161 (ATC 40707) as tolerant and susceptible genotypes, respectively.

5.4 Conclusions

cDNA microarrays have not been previously used to study high-salinity stress response in salt tolerant and susceptible genotypes of chickpea. The limited number (756) of chickpea, *Lathyrus*, and lentil probes available were used to generate the expression profiling for conferring tolerance/susceptibility to high-salinity stress. The results indicate how the genes being interrogated behave differently in tolerant and susceptible genotypes assessed. Overall, the number of transcripts expressed in response to high-salinity stress (386) was approximately twice and four times those expressed in response to cold (210) and drought (109) stresses, respectively. This was
partly because salt stress response was studied at two time points (24 hpt and 48 hpt). However, the large transcriptome change highlights the role of multiple genes and pathways in conferring salt tolerance. The key findings include repression of senescence-related transcripts in the tolerant genotypes whilst their induction in susceptible genotypes. Delay in senescence has been associated with salt tolerance in other crops and may be a feature determining salt tolerance in chickpea as well. Interestingly, transcript associated with conversion of proline to glutamate was repressed in susceptible genotypes at 24 hpt. This indicated that susceptible genotypes were feeling the stress early on and appeared to maintain cell turgor by retaining proline. Additionally, the tolerant and susceptible genotypes differed in timing of gene expression (for e.g., Ca-binding mitochondrial carrier, aquaporins and fructose 1,6-bisphosphatase repressed at 24 hpt in tolerant genotypes and 48 hpt in susceptible genotypes). The early repression of these transcripts in the tolerant genotypes might be a feature determining tolerance/susceptibility. In one instance, different genes associated with lignification were repressed by tolerant and susceptible genotypes, which might be important feature and needs further investigation. Moreover, transcripts associated with pathogenesis related protein 4A were highly induced in roots and shoots of all genotypes in both time-points. Since, this reaction was not observed in response to either drought or cold stresses in this study, it might be worth exploring this further. Study of high-salinity stress response in more tolerant and susceptible genotypes may possibly provide a better understanding of the role of these genes in conferring salt tolerance to chickpeas. Subsequently, the functionality of candidate tolerance genes detected through this approach could be validated by overexpressing the genes through transgenics or silencing them using knockout-mutants/antisense/RNAi.
Chapter 6

Summary, conclusions and future directions

6.1 Summary

In Chapter 1, I reviewed the state of our knowledge about chickpea and major abiotic stresses, namely drought, cold and salinity that hinder its productivity. A key finding of this review was that abiotic stress tolerance is governed by multiple genes and we still lack understanding of the overall coordinated tolerance response at the molecular level. The plant stress responses are complex and diverse, and every gene involved in the tolerance response, from perception to signalling to direct involvement, forms part of a coordinated response network.

The availability of a set of ESTs from chickpea and its close relative grasspea, and RGAs from lentil made it possible to construct a boutique ‘Pulse Chip’ array (Chapter 2). The ESTs on this array were mainly derived from pathogen challenged cDNA libraries. However, based on the functional annotation of these ESTs, I decided to explore the ‘Pulse Chip’ array to identify genes and pathways involved in abiotic stress response mechanism in chickpea. Before using the ‘Pulse Chip’ array for extensive studies, I decided to firstly validate the above assumption by studying the response of ICC 3996 (the donor of chickpea ESTs on the array) to the major abiotic stresses: drought, cold and high-salinity (Chapter 2). The stress challenge assays were carefully designed and the experiments were conducted in a reference design, where corresponding tissues from unstressed plants served as controls. A stringent selection criteria for DE genes including a two-fold cut-off combined with Students \( t \) test
(P<0.05) ranking and FDR multiple testing correction was used to keep false positives at a minimum. This study identified 46, 54 and 266 ESTs as DE between stressed and unstressed plants in response to drought, cold and high-salinity stresses, respectively. The putative role of these ESTs and associated pathways in response to drought, cold and high-salinity stresses is detailed in section 2.4. However, the identification of a significant number of DE genes in response to these abiotic stresses provided the necessary impetus to explore the use of ‘Pulse Chip’ array for gene expression profiling of abiotic stress tolerant and susceptible genotypes.

Two groups of drought, cold and high-salinity stress tolerant and susceptible genotypes were challenged with respective stress and gene expression profiles were generated for each one of them (Chapters 3 - 5). The comparison of transcripts DE in the tolerant and susceptible genotypes in response to drought, cold and high-salinity stresses revealed that 477 transcripts were DE in at least one genotype, time-point or tissue-type studied. The number of transcripts DE in response to high-salinity stress (386) was much higher than those expressed in response to cold (210) and drought (109) stresses in all genotypes (Figure 6.1). Considering the differences in the number of transcripts DE in response to these stresses in this and other studies, I propose that the number of DE transcripts in response to a particular stress depends on the method of stress induction and its severity. Overall, 38 transcripts were commonly DE in response to drought, cold and high-salinity stresses. This may be a preliminary indication of crosstalk and shared pathways among these stress responses. However, all of these transcripts except the senescence-associated protein DIN1 showed different expression patterns in the tolerant/susceptible genotypes. The results indicate that significant differences exist between the stress-responses of stress tolerant and
susceptible genotypes in response to these stresses. This highlighted the multiple gene control and complexity of abiotic stress tolerance mechanism. However, the comparison of transcripts DE in response to these stresses allowed the detection of behavioural patterns of related genes in tolerant and susceptible genotypes.

**Figure 6.1** A combined relationship between the number of transcripts DE in response to the three abiotic stress treatments for all genotypes, tissue types and time-points assessed.
For all treatments, the number of undetected microarray probes (mean fluorescence intensity less than two times the mean local background intensity in all tissue-types and replications) in each chickpea genotype varied according to the source of the probes. In general, the levels of undetected features for *L. sativus* probes were higher than the *C. arietinum* probes. This may be due to the weaker homology between *L. sativus* and *C. arietinum*. None of the lentil RGA probes were detected in any treatment or genotype, possibly due to hybridisation interference caused by introns present in these genomic DNA probes. Therefore, it may be ideal to produce more chickpea ESTs that may be used in future studies.

### 6.2 Conclusions

Although this study provided several insights on the genes and pathways involved in abiotic stress tolerance, definitive evidence is still lacking. This is because microarray studies merely provide “guilt by association” inferences. Therefore, functional characterisation of these genes via knockouts/TILLING-mutants/overexpressing-transgenics is still necessary. However, sufficient information has been obtained in this study to formulate hypotheses concerning abiotic stress tolerance mechanisms in chickpea, which can be tested in future studies. The hypotheses for drought, cold and high-salinity stress tolerance mechanisms in chickpea are discussed separately. This discussion is based on the findings of this study and previous reports on the functions of these genes (Chapters 3 - 5).

#### 6.2.1 Drought stress tolerance

The different genes/mechanisms that may possibly confer drought tolerance/susceptibility to chickpea plants are:
Delay of senescence: The delay of senescence or ‘stay green’ phenomenon that has been proposed to confer stress tolerance to other crops may also be a factor contributing towards drought tolerance in chickpeas. This is possibly executed by repression of senescence-associated protein DIN1, auxin-repressed proteins, auxin-responsive protein IAA9, magnesium chelatase, phosphate-induced protein, ubiquitins and polyubiquitins. The repression of ubiquitins and polyubiquitins may also indicate a decreased need of guided protein degradation in the event of stress.

Transport facilitation: The genes that help to control the transport of various solutes within and between the cells may contribute toward drought tolerance in chickpea. The important ones induced in this study include the lipid-transfer protein precursor and protein-transport protein. On the contrary, suppression of aquaporins and the DNA-J like protein may be symptomatic of, or contribute towards, susceptibility (see section 3.3.2; page 144).

Induction of pollen tube growth: The inability of the pollen tube to reach the ovary under stress condition is known to cause flower abortion. Therefore, the induction of the RAC-GTP binding protein in the flowers of a tolerant genotype that facilitates pollen tube growth may contribute towards drought tolerance by promoting successful fertilisation and seed production (see section 3.3.2; page 146).

Closure of stomata, suppression of CO₂ fixation and reduced energy capture: In the event of drought stress, this phenomenon may help to reduce transpiration and free-up cellular resources, thus conferring tolerance. This mechanism possibly involves
repression of ATP synthase, NADH ubiquinone oxidoreductase, NADH dehydrogenase, ferredoxin and thioredoxin (see section 3.3.2; page 146).

*Tolerance via pathogenesis-related genes:* These genes are usually involved in plant defence against pathogens but may also serve in signalling some drought tolerance/susceptibility pathways. The repression of the pathogenesis-related protein may contribute towards drought tolerance in chickpea flowers, whilst that of disease-resistance response protein may contribute toward susceptibility (see section 3.3.2; page 145).

*Unknown mechanisms:* The role/involvement of the genes with unknown/unclear functions may be revealed from e.g. TILLING/overexpression studies. For instance, suppression of the genes related to DY475051 in the flowers of only the susceptible genotypes may contribute towards drought susceptibility in chickpea flowers.

### 6.2.2 Cold stress tolerance

The genes/mechanisms that may contribute towards cold tolerance/susceptibility of chickpea plants are:

*Stress perception:* Cold stress is believed to be perceived through changes in membrane properties and therefore, the high-repression (>5-fold) of membrane-related protein CP5 in the susceptible genotypes may contribute towards cold-susceptibility in chickpeas (see section 4.3.2; page 162).

*Ca$^{2+}$ signalling:* The Ca$^{2+}$ influx is known to act as a sensor and activate downstream genes leading to cold adaptation. One mode of effecting a Ca$^{2+}$ influx and thus cold
tolerance in chickpea may be repression of the Ca-binding mitochondrial carrier (see section 4.3.2; page 162).

**Cold adaptation (regulation of ICE1):** Cold acclimation induces the expression of C-repeat binding factors (CBF); the transcription of which is regulated by the inducer of CBF expression 1 (ICE1). ICE1 is negatively controlled by ubiquitins and therefore, the repression of ubiquitins and polyubiquitins leading to induction of ICE1 that activates downstream genes resulting in cold adaptation may confer cold tolerance to chickpea.

**Cold adaptation (accumulation of osmolytes):** The accumulation of polyamines by induction of S-adenosylmethionine decarboxylase may allow chickpea plants to adapt to cold. However, the accumulation of disaccharides, especially sucrose, in the leaves of chickpeas by suppression of β-glucosidase and β-galactosidase, and induction of sucrose synthase, may impart cold tolerance (see section 4.3.2; page 166).

**Flower abortion (susceptibility):** Whilst sucrose accumulation in the leaves may be beneficial under cold-stress, it is detrimental for the flowers. The accumulation of sucrose in chickpea flowers by induction of α-amylase precursor and α-amylase genes may cause flower abortion and thus result in cold susceptibility (see section 4.3.2; page 167). Further, the repression of superoxide dismutase in the flowers may cause accumulation of reactive oxygen species and cell death, thus leading to flower abortion (see section 4.3.2; page 169).
Delay of senescence: As observed for drought stress, the delay in senescence caused by the repression of senescence-associated protein DIN1 and auxin-repressed protein may confer cold tolerance to chickpea plants.

Suppression of transportation (susceptibility): The suppression of solute transport due to repression of sorting nexin protein that controls trafficking of membrane(secretory proteins only in the susceptible genotypes may contribute toward cold susceptibility in chickpea.

Unknown mechanisms: The role/involvement of the genes with unknown/unclear functions may be revealed from e.g. TILLING/overexpression studies. For instance, repression of the genes related to DY475203 and DY475323 only in the tolerant genotypes may impart cold tolerance to chickpea leaves.

6.2.3 Salt stress tolerance

The genes/pathways that may possibly confer salinity tolerance/susceptibility to chickpea plants are:

Ca\(^{2+}\) influx: Ca\(^{2+}\) influx is known to act as a sensor and activate downstream genes resulting in salt-stress adaptation. Hence, the repression of the Ca-binding mitochondrial carrier in the roots of tolerant genotypes may effect a Ca\(^{2+}\) influx necessary for salt-stress adaptation. Alternatively, the Ca\(^{2+}\) influx may be necessary to regain ionic balance after exclusion of Na\(^+\) from the cells (see section 5.3.2; page 193).
**Ion homeostasis and/or pH balance:** In the event of salt-stress, one of the priorities of the plant cells must be to regain ionic homeostasis and/or pH balance. One key enzyme associated with these roles is carbonic anhydrase that was highly repressed in roots of all the genotypes and may be a feature contributing towards salt-stress adaptation in chickpea (see section 5.3.2; page 195).

**Suppression of aquaporins:** The aquaporins are membrane channel proteins that facilitate water diffusion across membranes and are known to be repressed in the roots under high-salinity stress. In the event of high-salinity stress, the repression of aquaporins in the roots of chickpea is essential to regulate the salt uptake and early repression may be associated with salt tolerance (see section 5.3.2; page 198).

**Suppression of lignification:** The suppression of lignification may be an adaptive mechanism against salt stress or required to free-up cellular resources that can be used in other processes. However, the differential repression of glycine-rich proteins in the tolerant genotypes and caffeoyl-CoA O-methyltransferase in the susceptible genotypes may contribute towards tolerance/susceptibility (see section 5.3.2; page 196).

**Delay of senescence:** The delay of senescence or ‘stay green’ phenomenon may borrow the extra time needed for stress adaptation. Therefore, the repression of senescence-associated proteins, ripening-related protein, ubiquitin-conjugating protein associated with photomorphogenesis, and WD-repeat protein in chickpea may contribute towards salt tolerance. Further, the repression of ubiquitins and polyubiquitins may be essential to suppress protein degradation under salt-stress.
**Accumulation of osmolytes:** The osmolytes are used by plants to maintain cell-turgor under osmotic stress. The chickpea plants accumulate osmolytes like sucrose and proline by repressing β-galactosidase and proline oxidase, respectively, to survive under salt stress (see section 5.3.2; page 194).

**Energy utilisation:** The efficient utilisation of available energy (ATPs) under stress can certainly determine the ability of a plant to cope with stress. In chickpeas, the early repression of fructose 1,6-bisphosphatase (and thus gluconeogenesis) in the roots may be a feature determining salt tolerance (see section 5.3.2; page 195).

**Pathogenesis-related mechanisms:** The plant defence genes have been proposed to be involved in salt tolerance mechanism. The high-induction of pathogenesis-related protein 4A only in response to high-salinity stress may mean it is associated with salt-tolerance in chickpea (see section 5.3.2; page 196).

**Unknown mechanisms:** The role/involvement of the genes with unknown/unclear functions may be revealed from e.g. TILLING/overexpression studies. However, the high-induction (up to 10-fold) of EB085058 in all genotypes, high-repression (up to 56-fold) of DY475357 only in tolerant genotypes, and repression of DY475416 only in roots of tolerant genotypes at all times, signify that these genes may contribute towards salt-tolerance in chickpea.

**6.2.4 Achievements of this study in relation to the original aims**

The major outcomes of this study are:
1. A boutique ‘Pulse Chip’ array was successfully generated from 516 non-redundant chickpea ESTs along with 156 grasspea ESTs, 41 lentil RGAs, 43 chickpea bad reads and 12 controls.

2. The study on expression profiling of ICC 3996 responses to drought, cold and high-salinity stresses revealed 46, 54 and 266 ESTs to be differentially expressed under these stresses, respectively. The significant transcriptional change and annotation of DE transcripts implied the experimental design and downstream analysis employed to be useful for the identification of candidates imparting tolerance to these stresses.

3. Transcriptional profiling of drought, cold and high-salinity tolerant and susceptible genotypes revealed 109, 210, and 386 transcripts to be DE, respectively, in all the genotypes, tissue-types, and time-points assessed.

4. The comparison of transcriptional profiles of drought, cold and high-salinity stress tolerant and susceptible genotypes revealed putative genes and pathways that may possibly confer tolerance/susceptibility to these stresses. It also highlighted the multiple gene control and complexity of abiotic stress tolerance mechanism.

6.2.5 Limitations of this study and possible solutions

Comparable to other studies, the availability of time and resources limited the breadth and scope of the research performed. The limitations to this study and likely solutions are:

1. A ‘closed architecture’ system was used for interrogation that restricted the results to the number of transcripts and associated genes that were present on the array. An alternative approach could be use of techniques like SAGE or
MPSS that allow sampling the whole genome. However, such technologies have their own limitations (see section 1.3.2).

2. It is crucial to emphasise that changes in mRNA accumulation may not necessarily correlate with protein/enzyme activity levels and therefore need further confirmation of participation in stress response using a proteomic or transgenic approach.

3. The drought, cold and high-salinity stress response at more time-points could not be assessed due to the lack of resources. The inclusion of additional time-points could have captured more transcriptional changes and probably revealed difference in timing of gene expression between tolerant and susceptible genotypes.

4. The drought stress response in the roots could not be studied because of poor quality RNA obtained. A possible solution may be growing the plants in ‘sand and gravel’ instead of ‘potting mix’. This may make it easy to wash the roots quickly and thoroughly allowing good quality RNA to be extracted.

5. When applying stress treatments, the response in the plant may be variable due to the nature of treatment, variation in response by plants, or natural variation between plants. It may possibly be ideal therefore to compare expression profiles of recombinant inbred lines (RILs) or near isogenic lines (NILs) that are tolerant and susceptible to these abiotic stresses to reduce background genetic variation amongst the plants.

6. The changes in the physiology of plants in response to the abiotic stresses imposed were not recorded. It might be helpful to record the changes in physiological functions of the plant such as, transpiration ratio, respiration rate, chlorophyll content, relative water content of leaves, and osmotic
potential, to name a few. These observations might be useful to relate the transcriptome to physiological state of the plant under stress, and thus provide more evidence to support involvement of proposed genes/pathways in stress tolerance/susceptibility.

6.3 Future directions

6.3.1 Directly utilising the results from this study

To carry on from the results of the current study, I propose that the first logical step would be to convert the candidate ESTs into molecular markers and map them onto the integrated chickpea genomic linkage map. Subsequently, the quantitative trait loci (QTLs) for drought, cold and high-salinity stresses should be identified to see if any of the candidate ESTs co-localise with the respective QTLs. The co-localisation of the candidate ESTs with the respective QTLs may bolster their case of being possibly associated with stress adaptation/tolerance. Secondly, more in-depth expression studies involving the use of additional genotypes and more time-points supplemented with physiological observations during stress imposition may possibly provide a better insight into the role/involvement of the proposed genes/mechanisms in conferring abiotic stress tolerance/susceptibility in chickpea. Further, it may be useful to identify the copy number and allelic forms of important candidates, which may be executed using genomic Southern blots. The presence of more copy number in either tolerant/susceptible genotypes may possibly explain the difference in expression level leading to tolerance/susceptibility. The identification of allelic forms may involve sequencing of candidate genes from the tolerant and susceptible genotypes and aligning them together to reveal differences, if any. The allelic differences may possibly explain the variation in stress adaptation/tolerance. Finally, important
candidates can be short listed and their proof-of-function established using knockouts/TILLING-mutants/overexpressing-transgenics.

6.3.2 Associating the results of this study to other studies

The major purpose of chickpea breeding is development of elite cultivars with durable and broad-spectrum resistance/tolerance to major abiotic and biotic stresses to boost its productivity. The efforts to produce new elite cultivars with durable resistance to major biotic and abiotic stresses is limited by the fact that stress tolerances are governed by multiple genes involved in multiple mechanisms that may be expressed at different plant growth stages. Hence, the use of molecular and functional genomic tools shall be vital for efficient breeding. To this extent, the current study has used available EST sequences to generate a cDNA microarray and interrogate the role of these genes in tolerance/susceptibility to the major abiotic stresses: drought, cold and, high-salinity. However, these sequences were derived from biotic stress challenged cDNA libraries, and used in absence of purely abiotic stress related cDNA libraries in chickpea. To get a better picture, it would be ideal to use ESTs derived from abiotic stress challenged libraries. Moreover, inclusion of transcripts representing major proportion of the chickpea genome would enhance the power of such a study. The first step in this direction has already been taken by development of an EST library of chickpea root tissue (Jayashree et al., 2005). This library is much larger (>2800 ESTs) and was constructed after subtractive suppressive hybridisation (SSH) of root tissue from two closely related chickpea genotypes contrasting for drought avoidance and tolerance. Although these ESTs are yet to be employed in functional studies, many potential drought responsive transcripts have been identified and many have been developed into molecular markers. Further, in absence of the whole genome sequence
for chickpea, the use of sequence and gene information from related crops should be exploited to understand and improve its stress tolerance. To this end, the gene expression patterns and metabolomic changes induced by various abiotic stresses in pea, chickpea, and *M. truncatula* are being analysed using various genomic approaches to dissect mechanisms of abiotic stress tolerance (Huguet and Crespi, 2005). This is being coupled with detailed genetic mapping of crosses between salt tolerant and sensitive varieties in chickpea and *M. truncatula*. This approach has been proposed to help evaluate control mechanisms exerted by the QTLs on gene expression patterns and identify regulators of gene expression and metabolic adaptation (Huguet and Crespi, 2005). Moreover, the Grain Legumes Integrated Project (GLIP) aims to screen sequences from legumes and develop a ‘LeguStressChip™’ to serve as a diagnostic tool to screen legume germplasm for stress tolerance. Another GLIP project is using a genomics approach to develop tools to transfer the information gained from model plants (including *M. truncatula*, *Lotus japonicus*, and *Arabidopsis thaliana*) to grain legume crops like chickpea, pea, faba bean, alfalfa, and clover (Denarie, 2005; Ellis and Perez de la Vega, 2005). Such large-scale coordinated research projects shall accelerate our effort to understand stress tolerance in chickpea and other legumes, and boost the technology transfer from model crops to cultivable species. Very recently, another transcriptional profiling technique, SuperSAGE was used in chickpea to investigate salt, drought and cold stress (Kahl *et al.*, 2007). The authors exploited the high power approach to analyse 40,000 unique mRNAs, and identified >3,000 genes responding to the stresses applied. The identification of large sets of candidate genes responding to a certain abiotic stress shall enable the construction of specialised microarrays that could be used to confirm gene functions by co-expression with other known genes.
Consequently, the functionality of candidate tolerance genes detected through all of the above approaches could be validated by overexpressing the genes through transgenics or silencing them using knockout-mutants/antisense/RNAi. In one such study, the dehydration responsive element binding (DREB) gene, DREB1A, has been transformed into chickpea and placed under the control of a stress-inducible promoter from the rd29A gene via Agrobacterium-mediated genetic transformation (Sharma, 2006; URL: http://iscb.epfl.ch/3_sci_prog/second_phase/3_project_ps4_2_2.html). Another construct using P5CSF129A gene driven by a CaMV 35S promoter has been transformed into chickpea for proline accumulation (Sharma, 2006; URL: http://iscb.epfl.ch/3_sci_prog/second_phase/3_project_ps4_2_2.html). The study of transgenic events of rd29A:DREB1A and 35S:P5CSF129A in T3 generation under dry-down experiments revealed that the transgenic events showed decline in transpiration at lower FTSW values (drier soils), an indication of drought tolerance, and are being further characterised.

The identification of novel genes, determination of their expression patterns in response to different stress conditions, and an improved understanding of their functions in stress adaptation will provide basic knowledge to design effective engineering strategies for enhancement of stress tolerances. The current study is the first documentation of transcriptional profiling of chickpea responses to drought, cold and high-salinity stresses. The results of this study shall help the ongoing and future investigation of abiotic stress response in chickpea that aim to develop broad-spectrum and durable stress tolerance.


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## Appendix 1. Characteristics of the 768 microarray features.

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<td>cDNA clone</td>
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<td>Row Column</td>
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<td>13</td>
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<td>cDNA clone</td>
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<td>14</td>
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<td>cDNA clone</td>
<td>Experimental</td>
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### Appendix 2. Composition of modified Hoagland’s nutrient medium* (adapted from Taiz and Zeiger 2002)

<table>
<thead>
<tr>
<th>Compound</th>
<th>Molecular weight</th>
<th>Concentration of stock solution</th>
<th>Concentration of stock solution</th>
<th>Volume of stock solution per litre of final solution</th>
<th>Element</th>
<th>Final concentration of element</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>g mol(^{-1})</td>
<td>mM</td>
<td>g L(^{-1})</td>
<td>mL</td>
<td>μM</td>
<td>ppm</td>
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<td><strong>Macronutrients</strong></td>
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<td></td>
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<td></td>
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<tr>
<td>KNO(_3)</td>
<td>101.10</td>
<td>1,000</td>
<td>101.10</td>
<td>6.0</td>
<td>N</td>
<td>16,000</td>
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<tr>
<td>Ca(NO(_3))(_2).4H(_2)O</td>
<td>236.16</td>
<td>1,000</td>
<td>236.16</td>
<td>4.0</td>
<td>K</td>
<td>6,000</td>
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<tr>
<td>NH(_4)H(_2)PO(_4)</td>
<td>115.08</td>
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<td>115.08</td>
<td>2.0</td>
<td>Ca</td>
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<tr>
<td>MgSO(_4).7H(_2)O</td>
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<td>1,000</td>
<td>246.48</td>
<td>1.0</td>
<td>P</td>
<td>2,000</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>S</td>
<td>1,000</td>
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<tr>
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<td></td>
<td></td>
<td></td>
<td></td>
<td>Mg</td>
<td>1,000</td>
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<tr>
<td><strong>Micronutrients</strong></td>
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<td></td>
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<td></td>
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<td>H(_3)BO(_3)</td>
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<td>12.5</td>
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<td></td>
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<td>MnSO(_4).H(_2)O</td>
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<td>CuSO(_4).5H(_2)O</td>
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<td>Cu</td>
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<td>H(_2)MoO(_4)</td>
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<td>Mo</td>
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<td>NaFeDTPA</td>
<td>468.20</td>
<td>64</td>
<td>30.0</td>
<td>0.3-1.0</td>
<td>Fe</td>
<td>16.1-53.7</td>
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</tbody>
</table>

* Adjust to pH 6.5 using 1 M NaOH.
Appendix 3. Composition of gel electrophoresis buffers

**5X RNA loading buffer (10 mL)**

- 16 µL saturated bromophenol blue
- 80 µL 500 mM EDTA, pH 8.0
- 720 µL 37% (= 12.3% M) formaldehyde
- 2 mL 100% glycerol
- 3084 µL formamide
- 4 mL 10X FA gel buffer

Add RNase-free water to 10 mL.

**1.2% FA gel**

- 1.2 g agarose
- 10 mL 10X FA gel buffer

Add RNase-free water to 100 mL.
Microwave to melt agarose, cool to 65°C in waterbath.
Add 1.8 mL of 37% (12.3 M) formaldehyde and 1 µL of ethidium bromide (10 mg/mL). Mix well and pour into gel mould.

**10X FA gel buffer**

- 200 mM 3-[N-Morpholino]propanesulfonic acid (MOPS) (free acid)
- 50 mM sodium acetate
- 10 mM EDTA
- Adjust to pH 7.0 using 1 M NaOH.

**1X FA gel running buffer (1 L)**

- 100 mL 10X FA gel buffer
- 20 mL 37% (=12.3 M) formaldehyde
- 880 mL RNase-free water

**5X TBE buffer (1 L)**

- 54 g Tris base
- 27.5 g boric acid
- 20 mL 0.5 M EDTA

Add Milli-Q water to 1 L.
Appendix 4. Recipes for hybridisation reagents.

**DEPC water:**

Add 1 mL of 0.1% Diethylpyrocarbonate (DEPC) to 1000 mL sterile water. Mix well and let set at room temperature for one hour. Sterilise by autoclaving. Let cool to room temperature before use.

**20X SSC (pH 7.0)**

Dissolve the following in 750 mL sterile water:
- Sodium chloride – 175.3 gm
- Sodium citrate – 88.2 gm

Adjust pH to 7.0 with 1.0M HCl and make up to 1000 mL with sterile water.

Sterilise by autoclaving.

**10% SDS (pH 7.2)**

Dissolve the following in 800 mL sterile water by heating at 68°C:
- Sodium-dodecyl-sulphate (SDS) – 100 gm

Adjust pH to 7.2 using 1.0M HCl and make up to 1000 mL with sterile water.
Appendix 5. Ranking method for identification of DE ESTs.

The Microsoft® Excel (Redmond, WA) software was used for the following:

1. Apply FC cut-off of 2 (Log₂ of >1 or <-1)

2. Import dataset into Microsoft Excel and determine equal/unequal variances for each array feature by comparing sample variances (control and treatment) using the F distribution;

Calculate the F statistic \( F = \frac{s^2_1}{s^2_2} \) using:

\[
F = \frac{(\text{cv}_{\text{control}} \times \text{sample mean}_{\text{control}})^2}{(\text{cv}_{\text{test}} \times \text{sample mean}_{\text{test}})^2}
\]

Calculate the degrees of freedom for each variable \((n_1 - 1, n_2 - 1)\). Considering that for each array feature there were 6 technical replicates and 3 biological replicates, \( n = 18 \) for both control and treatment.

\[
df_{\text{control}} = 18-1 = 17
\]
\[
df_{\text{test}} = 18-1 = 17
\]

Calculate F statistic probability using the F distribution tables. This was a two-tailed test so calculated F at \( P=0.025 \) for each tail to give a total \( P=0.05 \). Using these parameters the F statistic must be between 0.32 and 2.72 to assume equal variance between control and treatment means at \( P=0.05 \).

\[
F_{0.975} (17,17) = 2.72
\]
\[
F_{0.025} (17,17) = 1 / F_{0.975} (17,17) = 1 / 2.72 = 0.35
\]

Calculate the F statistic for each array feature using the ‘FDIST’ function.

Use the ‘IF’ function to determine if the F statistic probabilities are within the 0.35 – 2.72 interval. If the result is ‘TRUE’ then variance is equal.

Assuming equal sample variances, pool the sample variances according to

\[
s^2_p = \frac{(n_1 - 1)*s^2_1 + (n_2 - 1)*s^2_2}{n_1 + n_2 - 2}
\]

Considering that both control \((n_1)\) and treatment \((n_2)\) are 18, use the ‘AVERAGE’ function to pool variances.

\[
\text{AVERAGE} (\text{cv}_{\text{control}} \times \text{sample mean}_{\text{control}})^2 + (\text{cv}_{\text{test}} \times \text{sample mean}_{\text{test}})^2
\]

3. Calculate the \( t \) statistic for each sample using a two-sample \( t \) test assuming equal variances;
\[
    t = \frac{\text{sample mean}_{\text{control}} - \text{sample mean}_{\text{test}}}{\sqrt{s_p^2 \times (1/n_1 + 1/n_2)}}
\]

Convert each \( t \) statistic value into a positive number by squaring and the taking the square root.

Calculate the \( P \) value for each \( t \) statistic using the ‘TDIST’ function where \( x = \text{sample} \ t \) statistic, \( df = 18 + 18 - 2 = 34 \), and \( \text{tails} = 2 \).

**Selection method for identification of DE ESTs using Microsoft® Excel (Redmond, WA)**

1. For each dataset, sort the ESTs in ascending order according to \( P \) value.

2. Apply a FDR multiple testing correction;

Number the ranked ESTs from 1 to \( R \).

Use arbitrary \( P \) value cut-off for DE of \( P<0.05 \).

Compare the \( P \) value of each EST to a threshold that depends on the position of the gene in the list. The thresholds are \((1/R \times \alpha)\) for the first gene, then \((2/R \times \alpha)\) for the second and so on, where \( R \) is the number of genes in the list and \( \alpha \) is the desired significance level \((0.05)\).

To pass the threshold and be accepted as DE, the observed \( P \) value must be less than the individual threshold for each EST.

*e.g.* \( p_1 < (1/R) \times \alpha \), \( p_2 < (2/R) \times \alpha \)
### Appendix 6. ESTs >2-fold differentially expressed between drought stressed and unstressed plants (sorted with respect to their putative function)

<table>
<thead>
<tr>
<th>GenBank Accession</th>
<th>Category</th>
<th>Genotype*/Tissue-type</th>
<th>Log2 Ratio</th>
<th>P value</th>
<th>Putative Function</th>
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<td>DY396268</td>
<td>Cell cycle &amp; DNA processing</td>
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* Tolerant-1: BG1103 (ATC 48111); Tolerant-2: BG 362 (ATC48104); Susceptible-1: Kaniva (ATC 40030); Susceptible-2: Genesis 508 (ATC 45226)
Appendix 7. ESTs >2-fold differentially expressed between cold stressed and unstressed plants (sorted with respect to their putative function)

<table>
<thead>
<tr>
<th>GenBank Accession</th>
<th>Category</th>
<th>Genotype*/Tissue-type</th>
<th>Log₂ Ratio</th>
<th>P value</th>
<th>Putative Function</th>
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*Tolerant-1: Sonali (ATC 48113); Tolerant-2: ILC 01276 (ATC 40021); Susceptible-1: Amethyst (ATC 42331); Susceptible-2: Dooen (ATC 40874)
### Appendix 8. ESTs >2-fold differentially expressed between high-salinity stressed and unstressed plants (sorted with respect to their putative function)

<table>
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<td>S-adenosylmethionine decarboxylase (EC 4.1.1.50) involved in the synthesis of polyamines</td>
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<td>P value</td>
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*Tolerant-1: CPI 060546 (ATC 40586); Tolerant-2: ICC 06474 (ATC 40171); Susceptible-1: CPI 60527 (ATC 40033); Susceptible-2: ICC 08161 (ATC 40707)