

Chapter 3

Stress in Plantation Crops: Adaptation and Management

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Abstract Plantation crops include perennials grown over large areas in monoculture, excepting fruit trees grown in orchards. These crops face both abiotic and biotic stresses, incited by factors those coexist in plantations. Although Plantation crops are well adapted and are grown mostly in the tropics, where innumerable stress factors operate. Historical significance of few stress havocs in plantation species is remarkable. A wide range of anatomical, physiological and biochemical features contribute to various stress adaptation in plantation crops. Notwithstanding, improvement of stress resistance in plantation species has been mandated to combat unfriendly factors that jeopardize intensive and extensive cultivation. Conventional breeding is cumbersome in plantation crops, where in the process has to involve many generations running for decades, and expensive in terms of time, space and large volume of individuals handled. Recent developments in molecular genetics and biotechnology are aiding acceleration of breeding process in plantation species. Integration of proper crop management strategies with improved cultivars is essential to meet the goals of stress management. This review presents a comprehensive coverage of various adaptive mechanisms and mitigation strategies for several biotic and abiotic stresses affecting major plantation crops like cardamom, cashew, cocoa, coconut, coffee, date, eucalyptus, oil palm, rubber and tea.

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3.1 Introduction

Although the term “plantation” is loosely defined, it generally includes perennial crops, grown in larger areas in monoculture, producing a wide array of products such as spices, condiments, beverages, oilseeds, other allied materials, industrial and medicinal products, but does not ordinarily include fruit trees grown in larger orchards. They essentially differ from field crops for size of the holding, size of the individual plants, perennial nature and vegetative propagation. Plantation crops are remarkably well adapted plant species grown mostly in tropical regions of the world. These crops are predominantly cross-pollinated and produce heterozygous and heterogeneous population. Inherent genetic variability in the cultivated gene pool of these crops is generally very narrow (Simmonds 1989; Motamayor et al. 2000; Bandyopadhyay 2011). This chapter covers common plantation crops (Table 3.1) having various growth forms (trees, palms or shrubs) and grown for various purposes (oil nuts, industrial raw materials, spices, beverages and in timber industry).

The tropical regions harbor oldest ecosystems on earth, which are diverse, highly evolved, but poorly understood (Ploetz 2007), where plant stress is a common feature. Stress is a disadvantageous influence on a plant, exerted by external factors and stress adaptation or tolerance is the plant’s fitness to cope with an unfavorable environment or an invasion (Taiz and Zeiger 2006; Mittler 2006; Li et al. 2008). When exposed to unfavorable environments, plants show departures from its normal growth and metabolism, which collectively contribute to crop performance and productivity (Blum 2011). Like any other crops of the domesticated environment, plantation crops too are affected by various stress factors.

Stresses faced by plantation crops are either abiotic or biotic (Fig 3.1), originated from factors that coexist in the plantation environment. Abiotic stresses are the most common stress causing physical factors, which occur in all stages of crops’ lifespan. It is estimated that up to 82% of potential crop yields are lost to abiotic stress annually (Bray et al. 2000). Among the biotic factors, diseases are predominant than pests. In some species like cocoa (*Theobroma cacao*), pests and fungal diseases are responsible for more than 40% yield losses (Argout et al. 2008), of which pod rot caused by *Phytophthora* spp. (*P. palmivora* and *P. megakarya*) claims 30-90% of the total global crop loss (Bowers et al. 2001). A great deal of geographic variation exists among various forms of stresses that affect plantation crops, as well as in the adaptation of crops. Stresses can occur from single factor, or from combination of factors in annual cycles. Furthermore, because of perennial nature, accumulated stress effects often act detrimental in plantation crops. Predictions for the global agrarian future warn of rising temperature and humidity fluctuations, water logging, salinity and other problems that can adversely affect crop plants. In addition, these factors may affect diversity and virulence of agricultural pests and diseases leading to epidemics (Gregory et al. 2009). Fortunately, in plantation crops, very few stress factors are known to cause serious concerns in the industry and some are historically documented. During second half of 19th century, coffee plantations of Ceylon was devastated by leaf rust disease caused by *Hemileia vastatrix*, leading to the

Table 3.1 Details of major plantation crops

| Crop | Botanical name | Family | 2n ^a | Center of diversity | Geographic distribution | Economic produce | Reference |
|--------------|----------------------------------------|---------------|-----------------|-----------------------------------|-------------------------|---------------------|------------------------------------|
| Cardamom | <i>Elettaria cardamomum</i> (L.) Maton | Zingiberaceae | 48 | Indian center | Tropical | Spice | Ravindran and Madhusoodanan (2002) |
| Cashew | <i>Anacardium occidentale</i> L. | Anacardiaceae | 42 | Tropical Americas | Tropical | Culinary nut | Ohler (1979) |
| Cocoa | <i>Theobroma cacao</i> L. | Sterculiaceae | 20 | Amazon | Tropical | Chocolate, cocoa | Wood and Lass (2001) |
| Coconut palm | <i>Cocos nucifera</i> L. | Arecaceae | 32 | South America, Southeast Asia (?) | Tropical | Oil nut | Thampan (1993) |
| Coffee | <i>Coffea arabica</i> L. | Rubiaceae | 44 | East Africa | Subtropical, tropical | Beverage | Wrigley (1988) |
| | <i>C. canephora</i> Pierre. | | 22 | Central and West Africa | | | |
| Date palm | <i>Phoenix dactylifera</i> L. | Arecaceae | 36 | Iran and Arabian region | Arid tropical | Oil nut | Zaid and Jimenez (2002) |
| Eucalyptus | <i>Eucalyptus</i> sp. | Myrtaceae | 22 | Australia | Subtropical, tropical | Wood, medicinal oil | Coppen (2002) |
| Oil palm | <i>Elaeis guineensis</i> Jacq. | Arecaceae | 32 | West Africa | Tropical | Oil nut | Hartley (1988) |
| Rubber tree | <i>Hevea brasiliensis</i> Muell. Arg. | Euphorbiaceae | 36 | Amazon basin | Tropical | Natural rubber | Webster and Baukwill (1989) |
| Tea | <i>Camellia sinensis</i> | Camelliaceae | 30 | Indo-china | Subtropical, tropical | Beverage | Eden (1976) |

^a2n Diploid chromosome number

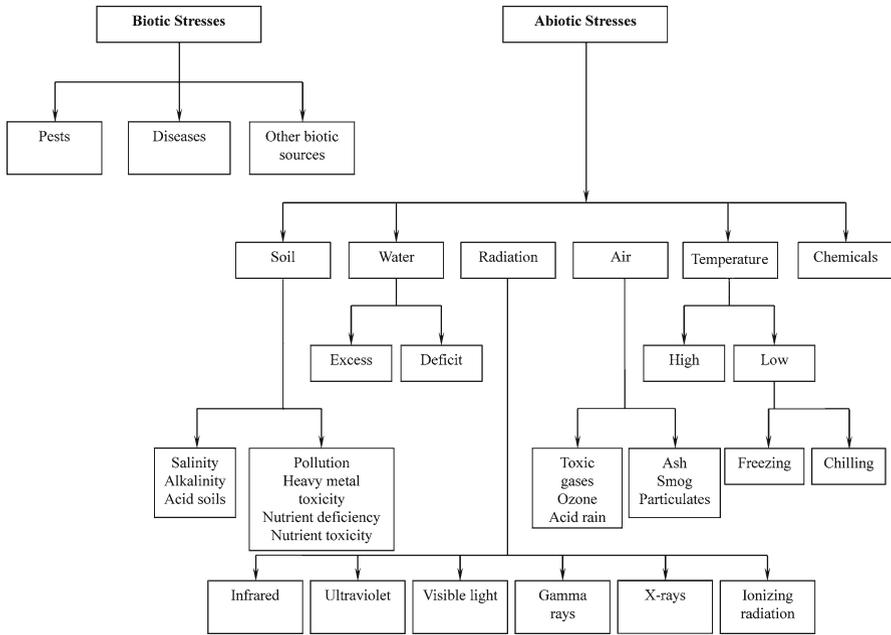


Fig. 3.1 Environmental stresses in plantation crops

closure of entire coffee plantation industry, paving way to the development of tea industry (Ward 1882a, b). Similarly, entire natural rubber plantations were shifted to South and Southeast Asia from Brazil in the late 19th century due the epidemics of South American leaf blight (SALB) disease caused by *Microcyclus ulei* (Labroy and Cayla 1913; Leiberei 2007). In cocoa, two serious diseases (witches’ broom by *Crinipellis pernicioso* and frosty pod rot caused by *Moniliophthora roreri*) devastated cocoa production in South and Central Americas (Pereira et al. 1996; Borrone et al. 2004). Recently, during 1980s, a leaf spot disease caused by *Corynespora cassicola* caused total replanting of high yielding rubber clones in Sri Lanka (Silva et al. 1998; Manju et al. 2001; Fernando et al. 2009). Among these, serious threat of SALB to the world economy has led to the decision to include *M. ulei* as a potential biological weapon by the U.S. National Research Council (Madden and Wheelis 2003) and by the United Nations Office on Drugs and Crime (Lieberei 2007).

3.2 Adaptation to Abiotic Stresses

Abiotic stress occurs from the factors of physical environment and plays a major role in survival and reproduction in plants. Survival under abiotic stress requires specific adaptation that takes place at two levels (a) individual and (b) population.

Table 3.2 Natural adaptation and sensitiveness of plantation crops to abiotic stresses

| Crop | Adaptation | Sensitivity | Reference |
|------------|----------------------------------------------------------------|-----------------------------------------------------------------|----------------------------------------------------------------------------------------------|
| Cardamom | Low temperature >10°C | High rainfall Wind Drought | Murugan et al. (2007) |
| Cashew | Drought Well drained acid soils | Water logging Low temperature, Frost | Paiva et al. (2009) |
| Cocoa | Shade Warm humid climate High rainfall | Drought Low temperature | Herzog (1994) Amanor (1996) Nair (2010) |
| Coconut | Warm humid climate High rainfall Salinity Strong wind | Water logging Drought Tropical storms | Lakmini et al. (2006) Batugal et al. (2009) Nair (2010) Remison and Iremiren (1990) |
| Coffee | Cool mountain climate to Warm humid climate Shade | Drought | Van der Vossen (2001) Lashermes et al. (2008) Klein et al. (2002) |
| Date palm | Drought High temperature Low temperature Salinity | Rain and humidity UV radiation | Zaid and Jimenez (2002) |
| Eucalyptus | Low temperature | Drought Frost Wind | Grattapaglia (2008) |
| Oil palm | High rainfall Long photoperiod | Drought Salinity Heavy metal toxicity High temperature | Jalani et al. (1997) Henson et al. (2005) Cha-um et al. (2010) Nair (2010) |
| Rubber | Long photoperiod Acid soils | Water logging Low temperature Wind Hailstorm | Bolton (1964) Vinod et al. (1996b) |
| Tea | Low temperature | Wind Frost Drought Flooding Hailstorm | Mondal (2009) Singh (1980) |

Individual phenotypic adaptation (phenotypic plasticity) softens the impact of natural selection among genotypes (Bradshaw 1965; Schlichting 1986; Sultan 1987) and by itself forms the chief objective of natural selection (Wright 1931). However, at population level, adaptive plasticity of a plantation species (Table 3.2) will reflect on the environmental stresses it had faced repeatedly in its evolutionary history. One of the best examples for adaptive response is the deciduous nature of rubber trees in the native evergreen rainforests of Amazon, which remains warm and wet throughout the year. Apart from the popular understanding that deciduous trees shed leaves

in order to avoid a winter or a tropical dry season, it is postulated that trees might also shed leaves to have a break in their parasitism, and to resuscitate their biochemical locks. This possibly explains why the rubber tree became deciduous, owing to continuous parasitism by *M. ulei*, the SALB pathogen (Robinson 1995).

Adaptation to environmental stress in plants is determined by their genetic make up. The difference in regulatory mechanisms of defense related genes decide whether a plant is resistant or susceptible. These differences are ubiquitous arsenals that help plants to combat stresses of various kinds.

3.2.1 Drought

Drought ranks foremost among the abiotic constraints for production in plantation crops because most of them are grown in tropical semi-arid conditions. Generally, plants adapt themselves to survive drought through two different ways viz., drought escape and drought tolerance. Perennial plantation crops have no scope for drought escape (Kozłowski and Pallardy 1997), while they withstand water stress by drought tolerance. Drought tolerance is manifested either through desiccation avoidance or desiccation tolerance. Desiccation or dehydration avoidance is achieved by maintaining high water potential within plants. In plants, primary mechanisms that maintain high water potential are reduction in transpiration through stomatal regulation, reduction in transpiring area, reduction in radiation absorption and maintaining water uptake by increasing root growth and root hydraulic conductivity. These mechanisms operate through morphological adaptations involving roots, stem and leaves and physiological regulation of transpiration; thereby plants increase internal water storage and prevent tissue dehydration during drought. Reduction in tissue hydration is primarily achieved by maintaining turgor through osmotic adjustment by accumulating solutes and inducing stomatal closure by increasing abscisic acid (ABA) content in leaf tissues, while maintaining near normal physiological activities (Repellin et al. 1994). Maintenance of low water potential primarily requires maintenance of turgor achieved through osmotic adjustments. Desiccation tolerance is rather a limited choice for majority of woody plants (Kozłowski and Pallardy 1997).

Crop adaptation depends on the degree of plant sensitivity to drought. The degree of drought sensitivity varies among plantation crops at species, genotype, phenological and organ levels. For example, at species level, crops like rubber and cashew are very sensitive to water logging; and at organ level, leaves are found to be more vulnerable than stem in evergreen trees (Chen et al. 2009).

Systematic investigations on drought tolerance in plantation crops reveal that a wide range of anatomical, physiological and biochemical adaptability contributes to the level of tolerance (Rajagopal et al. 1990). Therefore, many physiological parameters such as pre-dawn and midday leaf water potential, net photosynthesis, stomatal conductance, transpiration and intercellular CO₂ concentration and biochemical attributes like ascorbic acid, glutathions, tocopherols, chlorophylls, carotenoids, free amino acids and soluble carbohydrates have been used to assess drought stress

in these crops. Physiological and morphological characteristics, such as stomatal conductance, crown architecture, root depth and water use efficiency may be used as potential traits for selecting coffee genotypes with superior performance under drought conditions.

3.2.1.1 Anatomical Adaptations

Majority of the anatomical adaptations to drought are modifications to reduce water loss from plants during dehydrating conditions. This is mainly achieved by controlling transpiration loss through stomatal regulation. Stomatal response is probably one of the most complex behaviors in plants. External factors like light, air humidity, soil water content, nutrient status etc. and internal factors like ABA concentration, leaf water status etc. are known to exert direct influence on stomatal behavior. Stomatal behavior is a key indicator in assessment of drought tolerance in plantation crops. Striking differences in stomatal function during drought has been reported in rubber (Sangsing et al. 2004a), cocoa (Gomes et al. 1987; Willson 1999), coconut (Prado et al. 2001; Passos et al. 2005; Gomes et al. 2008) and many other woody plant species (Kozłowski and Pallardy 1997).

Cavitation Resistance

Under drought situations, xylem cavitation occurs when sap pressure within the vessels fall below a threshold resulting in irreversible collapse of the xylem conduits. In cavitation resistance, stomatal closure takes place well in advance as a response to increase in plant hydraulic resistance that prevents water loss, thereby maintaining sap pressure above the threshold (Sperry and Tyree 1988). Sangsing et al. (2004b) have found (i) relatively high vulnerability of xylem conduits to cavitation, (ii) associated responses between stomatal behavior and occurrence of cavitation and (iii) substantial genotypic variation in vulnerability to cavitation suggesting that whole plant level drought adaptive mechanisms are in force in rubber trees. Cavitation resistance therefore is a parameter that pertains more to drought survival. Analysis of xylem embolism, especially in the petioles, may provide a sound criterion for evaluation of genotype behavior under drought conditions.

As that of rubber tree, coffee can also adapt to drought by regulation of hydraulic conductance. Hydraulic conductance in coffee is found to be directly associated with transpiration rate, that may help in regulation of water loss though transpiration and to maintain the sap pressure above threshold to avoid xylem cavitation (Tausend et al. 2000). A drought tolerant genotype therefore must be able to maintain high relative water content (RWC) under moisture stress conditions. It has been reported that by efficient stomatal control on transpiration coupled with low cell-wall elasticity (Pinheiro et al. 2004) coffee plants could retain high leaf RWC (DaMatta et al. 1993) under drought. A slight shift in turgor due to the loss of little water from ensuing drought can signal leaves to maintain a high RWC and retain a

high symplast volume. Further, conservation of a high symplast volume may be crucial for maintaining gas exchange under drought as seen in arabica coffee (Meinzer et al. 1990), and hence maintenance of a high RWC is crucial in conferring drought tolerance in coffee (DaMatta 2004).

Foliar Abscission

Leaf abscission occurs in deciduous plantation crops like rubber when they approach annual period of water deficit. Leaf abscission may be considered as a whole-plant mechanism to limit water loss through transpiration in these plants. Leaf shedding was reported in field grown robusta coffee in response to water deficit (DaMatta and Rena (2001) occurring sequentially from older to younger leaves; and more drought-sensitive the genotype is, greater would be the extent of leaf shedding. However, DaMatta (2004) suggested that at least in robusta coffee senescence might be merely a consequence of and not a defense against stress since drought-sensitive clones, which considerably lose their foliage, also show most impaired water status in the remaining leaves.

Leaf Anatomy

Leaf anatomical adaptations such as cell size and number, stomatal frequency, stomatal resistance and epicuticular wax content have been described as essential anatomical indicators for assessing moisture stress in coconut (Gomes and Prado 2007). Waxes are involved in plant's first defense against abiotic stress of which hydrophobic waxes play an important role in water retention by limiting non-stomatal water loss (Kerstiens 1996; Riederer and Schreiber 2001; Jenks 2002). Drought adaptive anatomical features in coconut includes leaflets with upper epidermal waxy cuticle two-times thicker than the lower epidermis, thicker cuticular edges, xylem tracheids with thick lignification and tracheids with scalariform thickening. Further, water tissue with thin-walled cells at the upper and lower angles of straightened leaflet margin and fibrous sheet encircling seven to eight large vascular bundles in a strong midrib are also seen in leaflet lamina. Presence of two layers of large hypodermal cells below the upper epidermis and a multi-layered and closely packed palisade tissue also seen in contrast to scanty spongy parenchyma exist between the upper and lower hypodermis. Drought tolerant coconut cultivars had more scalariform thickening on tracheids and large sub-stomatal cavities (Kumar et al. 2000). A negative relationship between the epicuticular wax content of coconut leaves and transpiration rate has been reported by Kurup et al. (1993) substantiating the presence of high epicuticular wax content among drought tolerant than susceptible genotypes (Riedel et al. 2009).

Stem Vascular Systems

Palms like coconut, oil palm and date have tall singular stems developed from the apical meristem. Being monocotyledons, vascular bundles of xylem and phloem

appear scattered throughout the ground parenchyma, and there is no distinction between cortex and pith in these plants. Vascular bundles have an anastomosing or weaving pattern running longitudinally throughout the length of the stem. Stem anatomy is organized in such a way to minimize isolated functional sectors of mass flux from roots to canopy. The transport capacity of this massive hydrosystem increases with the stem diameter, and is functional throughout the lifespan of the palm that can extend well above a century. Hence, the ability to withstand water stress in palms like coconut is presumably coordinated by stem processes (Tomlinson 2006) as well. This complex process may contribute to higher drought adaptation of tall coconut varieties than the dwarf ones. Passos and Silva (1991) found that stem girth of tall coconut decreases between dawn and midday before increasing again during afternoon suggesting stem organized control of water transport. Variation in stem diameter as a response to drought stress also has been described in coconut. Stresses due to drought, flooding, mineral deficiency and some diseases can cause decreases in stem diameter, which reverses to normal when environmental conditions improve. Therefore, stem girth and form make a good record of palms' stress history. Phenological variations in drought sensitivity in oil palm indicate that young palms are more susceptible since they do not possess extensive root system and voluminous stem as in adult palms (Villalobos et al. 1992).

3.2.1.2 Physiological Adaptations

Behavioral Adaptations

Rubber as a deciduous tree has a different phenological adaptation than the evergreen trees. Annual natural defoliation known as 'wintering' occurs at the onset of winter and extends roughly for 4-6 weeks through the season (Vinod et al. 1996a). Leaf flushing occurs at the end of wintering period and well before the arrival of the rains that coincides with dry months. Flushing process requires large quantity of water for leaf development and expansion (Elliot et al. 2006; Williams et al. 2008). Root zone activities show significant deep root water uptake during wintering and flushing of rubber trees (Guardiola-Claramonte et al. 2008). Significant reduction in transpiration (Priyadarshan and Clément-Demange 2004) and increase in root water uptake helps trees to maintain stem water potential required for subsequent leaf flushing. Rubber trees can conserve extracted water without being released to atmosphere until the new foliage is grown (Guardiola-Claramonte et al. 2010).

Differential adaptation to drought among major sub-types of coffee, arabica and robusta appears to be governed by changes in rates of water use and/or efficiency of extraction of soil water (Meinzer et al. 1990; DaMatta et al. 2003; Pinheiro et al. 2004). During prolonged drought, reduction in leaf area and alternate assimilate partitioning new foliage the major adaptive mechanism for survival in arabica coffee (DaMatta 2003). Behavioral difference among the tolerant and susceptible genotypes was reflected in relative drought tolerance, governed by adaptation in root depth, plant hydraulic conductance and stomatal control of water loss (Pinheiro et al. 2005). Accordingly, better drought adaptation among genotypes with deeper

root systems is reported among robusta coffee (Pinheiro et al. 2004). Similarly rooting depth influenced drought tolerance has been reported in tea wherein shallow rooted clones were found drought susceptible than the deep-rooted clones. Moreover, drought tolerance was found to increase with rooting depth in shallow rooted clones, whereas no much variation was found in deep-rooted clones (Nagarajah and Ratnasuriya 1981).

Canopy Architecture

Canopy architecture has been found to play a significant role in drought adaptation in trees. Canopy structure partially determines the hydraulic architecture of a tree (Herzog et al. 1998). In coffee, dwarf cultivars with dense crowns are better able to withstand drought by delaying dehydration than cultivars with open crowns. Canopy compactness is also achieved by reducing the size of the leaves and altering the crown shape, that result in better energy dissipation with reduced transpiration (Kozłowski and Pallardy 1997). In rubber trees, adaptation to prolonged drought has been reported to produce compact canopy. This prevents high light intensity (which can be photoinhibitory) from reaching the lower canopy leaves and blocks penetrating radiation from reaching the plantation floor that can heat up surface soil, change vapor pressure deficit (VPD) and alter microclimate leading to evapotranspiration loss. Compact canopy has been implied as an ideal phenotypic feature for drought tolerance in rubber clones (Devakumar et al. 1999). DaMatta (2004) has suggested microclimate associated transpiration loss as one of the probable reasons of crop failure, in spite of sufficient supplemental irrigation, at locations with high evaporative demands planted with coffee cultivars with open crowns.

Stomatal Control – Hydraulic Signaling

Stomatal regulation takes place in plants as a response to signals arising primarily from roots. These signals trigger a cascade of events such as induction of differential gene expression, changes in cell metabolism and development of defensive systems in the above ground organs (Jackson 2002; Kholodova et al. 2006). Primarily systemic signals are hydraulic in nature spreading along the xylem that coordinates physiological responses (Jackson 2002) especially in leaves. As available soil moisture falls, a gradual reduction ensues in shoot water status, initiating direct hydraulic signals to leaves. Several studies suggest ABA accumulation as the primary candidate for hydraulic signaling in plants (Davies and Zhang 1991; Comstock 2002; Kholodova et al. 2006). Root tissues synthesize ABA as an initial response to diminishing soil moisture availability. Hydraulic signals are instantaneously spread through the continuous water phase within plants culminating in foliar stomatal regulation.

As a reliable indicator of stomatal performance, stomatal conductance has been used in plantation crops for assessing drought sensitivity (Rajagopal and Ramadasan 1999; Nainanayake and Morison 2007; Lakmini et al. 2006; Carr 2011), because

stomatal conductance is highly correlated with transpiration rate and photosynthetic health. Stomatal conductance has been used as an early indicator of stress in arabica coffee, because decline in stomatal conductance is found to occur even at one-third depletion of available soil water. Evidences suggest that during short-term water deficit, yield reduction in coffee genotypes may be associated with stomatal conductance and net carbon assimilation (Nunes 1976). Although poor stomatal control was found during drought (DaMatta et al. 1997) the mechanisms leading to clonal tolerance to drought in robusta coffee still remain largely unknown (Pinheiro et al. 2005). In coconut, strong evidence of stomatal regulation of plant water status has been documented at mild to moderate drought (Prado et al. 2001; Passos et al. 2005; Gomes et al. 2008) making it a useful parameter to differentiate drought sensitive and tolerant genotypes in association with tissue water potential (Lakmini et al. 2006). VPD sensitive stomatal regulation was reported in cocoa (Willson 1999), wherein leaves exhibit reduced water use efficiency at high VPD (Gomes et al. 1987), leading to tissue water deficit under conditions of limited soil water supply.

Stomatal Control – Non-hydraulic Signaling

Several studies have shown that signals of moisture depletion reaches leaves from roots, unassisted by shoot water status, indicating the existence of a non-hydraulic route of signal transport (Crocker et al. 1998). Although perceived as an important component of plant responses to drought, exact mechanisms involved in non-hydraulic root to shoot signaling still remain unclear (Davies et al. 1994). Recently, a non-hydraulic chemical mediated signaling has been reported in coconut, in which chloride ions are involved in sensing soil water depletion in the root zone and sending stomata-closing signals to the leaves. In coconut, chloride ions are found to play two important functions in regulating water balance; first, they regulate stomatal closure by coordinating water flow between six neighboring cells (two guard cells and four subsidiary cells) of the stomatal apparatus, and secondly, chloride ions improve osmoregulation capacity under water stress (Gomes and Prado 2007).

Photosynthesis

Variation in photosynthesis and associated systems has also been used as indicators of drought tolerance in plantation crops. Largely, photosynthetic performance of plants is determined by environmental variables under field conditions. Photosynthesis is closely associated with stomatal function since gas exchange in plants takes place through stomata. Drought-induced stomatal closure limits CO₂ diffusion from the atmosphere to the intercellular spaces resulting in reduced photosynthetic activity (Repellin et al. 1994, 1997). Genotypic variations have been reported in coconut in rates of gas exchange recovery and internal dehydration on exposure to drought. In dwarf coconut varieties, photosynthetic acclimation was observed after repeated drying and recovery cycles (Gomes et al. 2008). Use of rate of photosynthesis and

instantaneous water use efficiency as reference parameters has been reported promising in coconut (Nainanayake and Morison 2007). Chlorophyll fluorescence transients have been implicated in differentiating and screening of coconut seedlings that can adapt to water stress condition (Bai et al. 2008)

3.2.1.3 Biochemical Adaptations

Osmoregulation

Osmotic adjustment (OA) has been found associated with maintenance of gas exchange under drought (Turner 1997) in plants. OA occurs in cells in response to drought stress signals, where in osmolyte accumulation takes place to prevent cellular dehydration. Osmolytes are low molecular weight metabolites that are able to compensate high osmotic pressure without interfering with plant metabolism, even at elevated concentrations. They include sugars, polyols, amino acids and quaternary ammonium compounds. Proline is a typical osmolyte, synthesized in plants under different stress conditions. Although drought sensitive, cocoa plants exhibit active osmotic adjustments when exposed to dehydrating environments (de Almeida and Valle 2007), but suffer yield loss under stress (Moser et al. 2010). Osmotic adjustments and stomatal regulation have been reported as one of the mechanisms operating in drought tolerant coconut varieties (Rajagopal and Ramadasan 1999).

Other Biochemical Indicators

The plant hormones, ABA and ethylene play significant role in plant adaptation to environmental stress. Two key multigene families, 9-cis-epoxycarotenoid dioxygenase (NCED) genes (Seo and Koshiba 2002) and 1-aminocyclopropane-1-carboxylate synthase (ACC synthase) genes (Yang and Hoffman 1984) respectively regulate the biosynthesis of these hormones. Late embryogenesis abundant (LEA) proteins are a distinct group of proteins that are induced during dehydration stress caused by extreme temperatures, drought, salinity and certain developmental events such as seed maturation (Close 1996, 1997). LEA proteins are believed to be a subgroup of dehydrins that have extreme hydrophilic nature and are soluble at high temperature. LEA proteins are believed to act as a novel form of molecular chaperone to help prevent the formation of damaging protein aggregates during water stress (Goyal et al. 2005). Dehydrins in general are structural stabilizers, that protect nuclear, cytoplasmic, and membrane macromolecules from dehydration-induced damage, thus maintaining cell structure and integrity. In plantation crops, dehydrin like proteins have been identified in coffee (CcDH1, CcDH2 and CcDH3; Hinniger et al. 2006) and eucalyptus (Bocca et al. 2005). Another important and highly diverse set of proteins implicated in dehydration stress are heat shock proteins (HSPs). HSPs too functions as molecular chaperons minimizing the aggregation of proteins and targeting aggregated proteins for degradation, while assisting in protein folding, assembly and transport.

Various adaptations to drought include a stress-induced cascade of reactions in plants, including scavenging of reactive oxygen species (ROS) produced during oxidative stress. To prevent oxidative damage, cells contain antioxidants that scavenge the free radicals (Yamasaki et al. 1997). Phenolic compounds are cellular compounds with antioxidant properties (Rice-Evans et al. 1997); and several studies have shown that production of compounds with efficient antioxidant structures, such as additional hydroxyl groups on ring B of the flavonoid skeleton is accelerated (Ryan et al. 1998) during drought stress. Plant cells also contain enzymes, such as superoxide dismutase (SOD) and catalase that protect them by scavenging superoxide radicals and hydrogen peroxide respectively (Takeuchi et al. 1996). Transcriptome profile of the rubber tree latex contains many genes related to water stress in abundance, whose actual role in stress defense is not yet known. Transcripts of two genes encoding for *Hevea brasiliensis* ASR (abscisic acid, stress and ripening) like proteins, HbASRLP1 and HbASRLP2 were the most abundant next to those of rubber elongation factor (REF) and small rubber particle protein (SRPP) in the latex. These genes are homologous to tomato ASR gene family (Rossi et al. 1996) and the putative proteins coded by these genes have a domain similar to those proteins induced by water deficit stress, ABA stress and ripening. Further, a gene family of HbRLPs (REF like proteins) was also found expressed at higher levels in rubber latex. Both HbRLPs and SRPP are structurally closer to stress related proteins (Ko et al. 2003).

In tea, elevated polyphenol content has been reported as an indicator for drought tolerance (Hernández et al. 2006; Cheruiyot et al. 2007). Drought tolerant tea clones had higher catalase activity for scavenging hydrogen peroxide formed in the photorespiratory pathway (Jeyaramraja et al. 2003a). Furthermore, drought induced reduction in catechin content has been reported in tea clones (Singh et al. 2009a, b). This behavior is attributable either to an instability of the catechins under drought (Jeyaramraja et al. 2003b) or to possible loss of catechins due to enhanced cellular injury or to down-regulated pathways leading to limitation in the availability of precursor molecules (Singh et al. 2008, 2009a, b; Jeyaramraja et al. 2003b; Sharma and Kumar 2005).

Although mechanisms are many, each plantation crop has its own combination of adaptive mechanisms to counter drought stress. Overall strategy appears to be to reduction or cessation of leaf-area development, maintenance of good water use efficiency with stomatal regulation, maintenance of efficient photosynthesis and tolerance of additional stress with osmotic adjustment of mature leaves, fruits and roots. Foliar abscission appears to be the choice during severe stress. Osmotic adjustment of the functional leaves is effectively carried out to maintain the overall canopy function and leaf longevity is maintained for a considerably long period.

3.2.2 Temperature

Most of the plant processes are temperature dependent. In plantation crops, apart from growth and establishment, significant temperature influence may be seen on reproductive growth such as floral initiation, release of bud dormancy, anthesis,

fruit-set and fruit development. Thermal adaptation varies widely among tropical, subtropical and temperate plantation crops, since the temperature plays a leading role in limiting plant distribution between tropical and temperate regions. In general, flowers and fruits are injured by extremely low or high temperatures. When temperature falls, molecular activity gets decreased and essential biochemical processes involved in sustaining growth are arrested. Low temperatures also decrease the permeability of membranes and increase protoplasmic viscosity. On the other hand, when temperatures goes excessively high, molecular activity may get impaired and the enzymes controlling metabolic processes are denatured or inactivated.

3.2.2.1 Low Temperature

Plant stress occurring due to lowering ambient temperature has been a common phenomenon in all the crops. Degree of variation in plant responses to low temperature depends primarily on the basic adaptation pattern of the crops. Temperate species can tolerate very low temperature, which are fatal to tropical crops. This is the reason why tropical and sub-tropical species fail to establish under temperate climates. In temperate species, low temperature favors shoot growth through its effects on bud formation, bud dormancy and bud expansion. Low temperature is an essential requirement for these crops to break bud dormancy, and elevated temperature during mild winter impairs bud break resulting in crop failures (Weinberger 1950).

However, excessive freezing causes various stress reactions in temperate plantation species. Freezing injury occurs mainly during autumn (winter) season, while frost injury inflicts damages to flowers, buds and young fruits during spring season. Furthermore, rootstocks are more susceptible to freezing injury than scion. Freezing injury occurs when low temperature spells are followed by a period of mild weather that permitted growth to start and caused loss of cold resistance. Hence, repeated mild freezing spells are more deleterious than a single spell of deep freezing. In addition, a few temperate zone plants are susceptible to chilling injury that occurs when they are exposed to temperatures a few degrees above freezing. Freezing injury can be caused either directly by intracellular freezing or indirectly by dehydration of tissues resulting from extracellular freezing. Plants are usually killed by ice crystal formation within the cells, but formation of ice crystals within the intercellular spaces is not necessarily fatal. In frost hardy plants, cellular freezing is prevented through a cell sap concentration mechanism. Concentrated cell sap has lower freezing point than water, and hence ice formation is prevented. Although, slower cooling causes ice to form initially in the intercellular spaces, and as the temperature decreases gradually, water moves out of the cells to the intercellular ice nuclei, making the cell sap thicker. However, rapid cooling is normally fatal because there is little time for water to move out leading to a sudden intracellular freezing resulting in mechanical disruption of protoplasm. In tree species, whole plant level freezing damage occurs when crown and roots are affected; of this, crown damage is usually irrecoverable and fatal. In *Eucalyptus globulus*, it was reported that freezing tolerance of provenances occurred due to their ability to evade the formation of

ice in their leaves, suggesting that supercooling is the most probable mechanism conferring resistance in these plants. In addition, accumulation of soluble carbohydrates in the leaves provides cryoprotective mechanisms (Moraga et al. 2006) as soluble sugars are known to function as cryoprotectants in plant tissues, especially at membrane level (Tinus et al. 2000).

Frost cracks can develop on tree trunks when alternating freezing and thawing occur during the winter and early spring. These cracks occur with a loud bang and can be of several feet long. The bark at the affected region occasionally peels off exposing the underlying wood, which becomes site for secondary infection. Since these lesions damage phloem, downward translocation of organic solutes is impeded. Although less hardy, root tissues are relatively less injured than stems during winter, because soil and snow cover protect them from exposure to freezing air temperature. However, freeze damage occurs in roots, when dry soil sucks moisture out of roots during winter, and if the soil is wet, no damage is found to occur.

Spring frost during growing season often injures cambium, causing the formation of abnormal stem frost rings. These rings usually have an inner part of frost-killed cells and an outer layer of abnormal xylem cells produced after the frost. In forest plantations of eucalypts, frost injury is a common problem in temperate regions throughout the world making most of the eucalypt species unsuitable for commercial plantings. *E. nitens* is a fast-growing species widely adapted for planting in high altitudes where occurrence of severe frost is a common occurrence (Turnbull and Eldridge 1984) in contrast to *E. grandis*, use of which is limited due to its lesser frost tolerance (Eldridge et al. 1994).

On the contrary, tropical species are vulnerable to sub-optimal temperature due to intrinsic oxidative stress occurring from the exposure to low temperature. Cold susceptibility occurs from reduction in photosynthetic efficiency and increased photoinhibition of photosystem (Fryer et al. 1998). Reduction in photosynthetic functions is observed in rubber trees grown under cold climate (Alam et al. 2005). Moreover, rubber is reported to have potential for acclimation of photosynthesis to temperature in the growing environs (Kositsup et al. 2009). This photosynthetic plasticity at a reference temperature is associated with flexible response in net CO₂ assimilation rate. Although rubber trees grown at 18°C were not able to maintain net CO₂ assimilation rate, photosynthetic capacity and leaf nitrogen status close to those of trees grown at 28°C, they had potential to survive low temperature stress. Metabolic flexibility of rubber was reported to confer less intrinsic oxidative damage in plants grown under elevated CO₂ in encountering low temperature stress (Alam et al. 2005). Some rubber varieties were found to have greater resilience to chilling up to 96 hours without any damage to photosynthetic apparatus (Mai et al. 2009). Moreover, variation in membrane injury caused by low temperature has also been reported in rubber clones (Ray et al. 2004). Phenological adaptations for low temperature tolerance in rubber clones include shorter reflushing time and faster wintering (Vinod et al. 2010). Abundance of stress responsive proteins, like low temperature- and salt-responsive protein and low-temperature-induced protein has been identified in latex transcriptome (Ko et al. 2003).

Most of the palm species are acclimatized to tropical rain forests and are grown in wide range of habitats outside freezing environments (Gomes and Prado 2007). An exception is the date palm that is cultivated in arid and semi-arid regions characterized by long, hot and dry summers and winters with sub-freezing temperatures. Date palm can withstand wide temperature fluctuations up to its zero vegetation point of 7°C, below which growth stops and plants enters into a resting stage. Freezing injury occurs when the temperature fall below 0°C resulting in metabolic disarrays, leading to partial or total damage of leaves. Inflorescences are also heavily damaged by frost. Pinnae margins turn yellow and dry out at -6° C and exposed leaves of the canopy dry out from -9 to -15°C. If freeze occurs for a long period (12 hours to 5 days), entire palm looks burnt with all leaves showing frost damage (Mason 1925; Nixon 1937). Even if the entire crown is damaged, palms survive and grow after normal conditions are returned, because the meristematic area of a date palm is well protected against frost.

3.2.2.2 High Temperature

Exposure to relatively high temperatures causes heat injury in plantation crops that reduces growth and diminishes chance of survival. Heat injuries may be direct or indirect. Direct injury is the immediate plant response during the exposure of elevated temperature or immediately thereafter. Direct heat injury is relatively rare when compared to indirect injury in planation crops. Indirect heat injury in plants occurs slowly and may not be apparent for many hours or even days after exposure to high temperature. High temperature causes rapid decline in apparent photosynthesis beyond a critical high temperature, while continuing to increase respiration resulting in rapid depletion of carbohydrate reserves and sometimes death. Formation of toxic compounds, production of biochemical lesions, and breakdown of protoplasmic proteins (Levitt 1972) are also common.

Most common direct heat injury observed in rubber is severe sun scorching (Vinod et al. 2003) that occurs when the collar region of young plants is damaged by sun exposed surface soil layer heated well in excess of 55-60°C. In grown-up rubber plants, excessive heating up of stems facing afternoon sun develops cracks and lesions called heat canker. Rubber plants are damaged due to sun scorch mostly when they are very young. After three years of growth expanding crown provides shade protection from scorching. Generally, sun scorch at the collar region results in girdling and death of the plants, while bark lesions results in partial drying up of the bark exposing the stem underneath. Since cambial cells are sensitive to high temperature, they die due to desiccation and oxidative stress. Exposed bark becomes brittle and cracks develop resulting in oozing of latex from crack wounds. This enhances internal drying and secondary pathogen damage ultimately resulting in complete death of the affected bark region. Among the palms grown in plantation sector, betel-nut palm (*Areca catechu* L.) is highly prone to sun scorch (Staples and Bevacqua 2006).

Of the tropical plantation crops, cashew is a hardy tree (Purseglove 1986) that is adapted to a wide range of environmental constraints. It grows well in areas of high

temperature, where diurnal temperature can exceed 40°C and can survive seasons of drought. Cashew has an extensive root system with which it can forage for moisture and nutrients and can thrive in poor and marginal soils (Kembo and Hornung 1999).

3.2.3 Salinity

Salinity is a common problem in all parts of the world, especially secondary land salinization that occurs mainly due to clearing of forests and shrub lands for agriculture and excessive irrigation (Cramer et al. 2004). Plant stress due to salinity occurs when soluble salt concentration in soil and water exceeds limits of plant tolerance. Salt affected areas can be of two types, sodic and saline. They have excess sodium and high concentration of carbonate or bicarbonate anions with greater pH ranging from 8.5 to 10.8. They have very poor structure and their sodium absorption ratio (SAR) is high. Saline soils are rich in sodium ions, but with chloride and sulfate as dominant anions; pH and SAR are much lower than sodic soils, but have higher electrical conductivity ($>4 \text{ dS m}^{-1}$). Salt-affected soils contain high concentrations of soluble salts that reduce growth in most of the plant species (Flowers and Flowers 2005).

Plants that are sensitive to natural salinity are called glycophytes, and those resistant are called halophytes. Some halophytes can tolerate extreme salinity because of their anatomical, physiological and morphological features or avoidance mechanisms (Flowers et al. 1986).

Salinity induces stress in plants in many ways. It affects numerous physiological or biochemical processes, many of which are seen at cellular level. Primarily high salt concentration reduces osmotic potential of the soil solution creating water stress to root cells even under sufficient soil water availability. Salts interact with nutrient ions and make them unavailable to plants. Further, ions such as sodium cause internal toxicity in plants and they are not readily sequestered into vacuoles in glycophytes (Sairam and Tyagi 2004).

Plant adaptation to salt varies among plantation species in the degree of tolerance to a range of salt concentration that is achieved through one or more different mechanisms. The most important mechanisms are the exclusion of ions at root zone and suppression of ionic translocation to the shoot that help plants to keep levels of ions in growing meristem and young shoots low. Sequestering of salt ions into vacuoles or deposition into bark, ray cells, tracheid walls and lumens, or older senescent leaves, also help tolerant species to prevent salts from interfering with normal metabolic activity in the cells. Some plants show ability to maintain ion exclusion from young shoots under hypoxic conditions of waterlogging and maintain the ability to uptake water continuously in presence of high salt concentrations (Niknam and McComb 2000). Leaf and root Na/K ratio as well as stomatal resistance of plants exposed to salinity proved appropriate indexes of whole plant response to salt stress. Among the eucalypts, *E. grandis* tolerates low to medium levels of soil salinity through salt exclusion mechanism, until a threshold concentration, above which the tolerance fails. Once broken, tissues become very sensitive to salt. On the other hand, *E. maculata*

shows less tolerance than *E. grandis* at the lower salt levels, but survives higher salt levels at which *E. grandis* becomes susceptible (Sun and Dickinson 1993).

Coconut palms are moderately tolerant to salinity (Remison and Iremiren 1990). Although grown in wide range of ecological conditions, coconut is considered to possess halophytic properties (Purseglove 1975). Traditionally planters apply sea salt in coconut groves in India, Java and Columbia (Child 1964; Manciot et al. 1979), and it is experimentally proved that sodium chloride (NaCl) application improved development of inflorescence, number of female flowers and nut yield (Fremond et al. 1966; Roperos and Bangoy 1967). Coconut is naturally adapted to maritime shores and is capable of absorbing chloride ions rather easily (Magat et al. 1975; Manciot et al. 1979; Remison and Iremiren 1990). In coastal areas, chloride accumulation in coconut leaves is a common phenomenon. Until recently, importance of chloride ions in coconut physiology was not understood. Evidences indicate that chloride ions play a significant role in non-hydraulic signaling of stomatal control in palms. It is now found that palms deficient in chloride had impaired stomatal function. The physiological role of chloride in coconut nutrition was earlier suspected to be associated with the water economy of the plant. Coconut belongs to a group of plants that lack chloroplasts and starch in their guard cells. For stomatal movements, such plants require chloride ions (Von Uexkull 1985).

3.2.4 Radiation

Adaptations of plantation species to local environments include the efficiency to harvest radiation for optimal growth and development. Most of the radiation in the atmosphere is infrared radiation (700-3000 nm, 67% of the photons) and visible light (400-700 nm, 28%; Nobel 1983). Ultraviolet (UV) radiation (200-400 nm), on the other hand, reaches the atmosphere in smaller amounts (5% of the photons). Biologically most hazardous part of UV radiation, i.e. UV-C (200-280 nm) and UV-B (280-320 nm) are completely absorbed by the stratospheric ozone layer and by other oxygen molecules in the atmosphere (Frederick 1993). In addition, ozone layer absorbs some of the longer-wave UV-B and UV-A radiations (320-400 nm). Therefore, of the photons reaching earth's surface, only about 2% are in the ultraviolet range (Nobel 1983). However, of the total solar energy, UV-B comprises about 1.5% and UV-A radiation about 6.4% (Frederick et al. 1989). Infrared region is responsible for the thermal stress in plants discussed in the previous section. Effect of other types of radiations such as X-rays, gamma rays and other ionizing radiation are negligible in plantation crops.

3.2.4.1 Visible Light

Plants use radiation in the regions approximately from 400 to 700 nm for photosynthesis, the region from 660 to 730nm has important qualitative, photo-morphogenic

effects on growth. Physically, effects of light on plant growth depend on irradiant quality and duration (photoperiod) of which the former depends on the intensity and quantum of light exposure. Hence, high and low light exposures can make different effects on plants.

Plantation crops such as cocoa, cardamom, coffee and tea are heliophobes, which prefer low light. Heliophobes are naturally adapted to shade and does not tolerate heavy sunlight. Shade tolerance in trees varies with the age of the tree and with environmental conditions. Trees and shrubs vary widely in their capacity to grow in shade and this often becomes a decisive factor in their success under low light conditions. Trees tend to show higher degree of shade tolerance in their youth, and those growing on nutrient rich soils are more tolerant (Daniel et al. 1979). Shade effect is a complex mechanism in cocoa and is often associated with tree nutrition. Notwithstanding, young cocoa leaves grow well under shade than under full exposure (Wessel 1985). Furthermore, cocoa trees grown under shade have a bushy appearance with small leaves, shorter internodes and dense crown, which is desirable for commercial cultivation.

Coconut and rubber prefer good light, and low light interception showed adverse stress effect in growth of rubber (Khasanah et al. 2006). Shade grown young rubber plants had asynchronous variation in growth between roots and leaves that was attributed to competition for photosynthate between secondary roots and leaves (Thaler and Pagès 1996). On contrary, in its natural habitats, young rubber plants grow and establish under the shades of overstorey canopy of rain forests. Rubber plants are found to show differential adaptation to light intensities at different phenological stages. They show natural adaptation to shade only when they are young, and lose this trait when the tree crown brushes overstorey canopy. Under commercial planting, rubber seedlings grown on cleared lands are found to show better growth when put under shades of intercrops (Rodrigo et al. 1997, 2001), possibly because of reduced thermal and/or photooxidative stresses. Senevirathna et al. (2003) have concluded that shade adaptation and shade-induced reductions in dynamic photoinhibition account for the enhanced early growth of rubber under light shade. Shade provides greater protection against diseases and weeds in coffee, cocoa and cardamom than under exposed conditions. There are many reports to suggest that shade increases fruit weight and bean size in coffee, but not quality and fruit-bean ratio (Muschler 2004).

Extensive efforts have been made to understand the factors responsible for shade tolerance in plants. Stomata of shade tolerant species were found to open more rapidly in sun flecks than those of intolerant species (Woods and Turner 1971; Davies and Kozlowski 1974), allowing the former to carry out photosynthesis during short periods of illumination. However, significant relation between stomatal response and shade tolerance could not be established (Pereira and Kozlowski 1976), because stomatal response not only varied with fluctuations in light intensity, but also was greatly modified by water stress preconditioning, temperature and mineral deficiency (Davies and Kozlowski 1974). This implies that many other factors like anatomical changes in leaves (Jackson 1967), changes in chlorophyll-protein ratio, enzyme activity of chloroplasts (Holmgren et al. 1965), rate of respiration

(Loach 1967), rate of photosynthesis (Kozlowski and Keller 1966) and various metabolic changes (Durzan 1971) influence shade tolerance.

Most of the tropical plantation species are adapted to high light exposure. For instance, radiation requirement of rubber (Ong et al. 1998) and coconut (Ochs 1977; Ohler 1999) ranges from 6 to 9 hours per day and exceed 2000 hours annually. Even though cocoa and coffee are heliophobes naturally, in cultivated conditions high productivity is recorded in coffee when grown under sunshine duration of 1900-2200 hours per annum (Descroix and Snoeck 2004; Wintgens 2004). In cocoa, mature trees yield well under full exposure but only in fertile soils. In poor soils, higher yield is obtained only under shade. In rubber, high irradiance especially in association with drought, high or low temperature can cause depression of photosynthetic productivity due to induction of photooxidative stress (Jacob et al. 1999). Oxidative stress induced chlorophyll degradation was also reported in rubber under high irradiance (Ray et al. 2004).

Apart from light intensity, photoperiod variations influence both vegetative and reproductive phases of plant growth (Garner and Allard 1920). At equator, days are of equal length during the entire year, but as we move away, large seasonal differences occur in the length of the daylight period. In temperate species, short days arrest shoot expansion and trigger a dormant state, whereas long days delay or prevent dormancy. Progressive slowing down of shoot elongation takes place under short-day conditions, successively producing shorter internodes until growth eventually ceases. Nevertheless, tropical plantation crops also show varied responses to day length. Experiments under controlled environments show greatly increased shoot growth during days longer than normal in coffee, cocoa and many other woody species (Longman and Jenfk 1987).

3.2.4.2 UV Radiation

One of the growing concerns of present day is that the quantum of UV-B radiation reaching earth is increasing. Predictions based on stratospheric chemistry and climate-change models estimate that maximum springtime UV-B radiation will increase dramatically by 2020 (Shindell et al. 1998; Taalas et al. 2000). The intensity of UV-B radiation, in particular, is regulated by the thickness of the ozone layer that is rapidly being depleted by alarming concentration of anthropogenic atmospheric contaminants like chlorofluorocarbons and nitrogen oxides (Crutzen, 1972; Molina and Rowland, 1974).

Plants have several mechanisms for UV-B evasion, which include many UV-B absorptive pigments, reflective modifications and leaf thickness (Caldwell et al. 1983; Beggs et al. 1986). Thicker leaves may have an internal protective influence (Johanson et al. 1995; Newsham et al. 1996) by slight increase in the thickness of upper epidermis, spongy parenchyma and spongy intercellular space (Kostina et al. 2001). This feature is common in most of the plantation tree species. In addition, scattering and reflection of UV-B radiation is achieved through epidermal (epicuticular) wax and leaf hairs (Karabourniotis et al. 1999; Kinnunen et al. 2001). High level of cuticular wax content is a common feature in plantation crops. Changes in

crystalline structure of the epicuticular wax with concomitant changes in light reflection may protect plants from damaging effects of UV light or aid them in the adaptation to different light intensities (Riedel et al. 2009). Protective role of epicuticular wax under abiotic stress is reported in coconut (Kurup et al. 1993).

Notwithstanding, most efficient mechanism of UV-B evasion is the accumulation of UV-B absorbing compounds in the epidermal cells of leaves (Burchard et al. 2000). Plants contain many phenolic compounds with anti-oxidant properties. Phenolics like light absorbing flavonoid compounds have been implicated in protecting plants from the damaging effects of UV-B radiation (Li et al. 1993). Flavonoid compounds are a group of phenylalanine derived aromatic secondary products, synthesized via phenylpropanoid pathway. Anthocyanins are the most common flavonoid compounds in higher plants. Temporary reddening of mature leaves seen on exposure to UV-B radiation has been attributed to anthocyanin accumulation (Steyn et al. 2002; Close and Beadle 2003; Gould 2004; Kytridis and Manetas 2006). Although not many studies have been reported on the effects of UV-B radiation in plantation crops, still it is prudent to believe that they have natural adaptation to this kind of stress. Leaves of tropical plantation crops like cashew, rubber and cocoa appear copper brown when young, and often turn reddish in the event of stress due to the accumulation of flavonoid pigments. Phenolic accumulation under photooxidative stress is a common feature in tea (Hernández et al. 2006) and coffee.

3.2.5 Nutrient Stress

Even in the presence of adequate levels of nutrients, crops might not reach optimal growth and productivity when grown in soils that contain phytotoxic levels of some metals / nutrients. Some of the micronutrients that can be potentially toxic at higher concentrations are copper, cobalt, iron, molybdenum, nickel and zinc. Even essential elements at excess levels can reduce plant growth. Plants therefore experience two types of stress in presence of soil elements, (i) deficiency and (ii) toxicity.

3.2.5.1 Nutrient Deficiency

Most of the plantation crops are adapted to nutrient deficient situations of marginal lands, a notable exception being coffee. Annual nutrient requirements of these crops are lower than many of the annual field crops. Plantation crops are large plants with extensive root system, which capacitate them to forage for nutrients from a larger soil volume. However, severe nutrient deficiency can be deleterious to these crops. Among the major nutrients, potassium is required for physiological development of trees, while phosphorus is required for adequate development of root system, meristem growth and wood formation. Magnesium is of particular importance for latex production in rubber trees. Plants under nutrient deficient stress exhibit characteristic external symptoms of starvation.

Plantation crops like rubber, cocoa, oil palm (Fageria and Baligar 2008), and cardamom (Krishnakumar and Potty 2002) are suitable for acid soils. Low pH or acidity favors complex interactions of plant growth-limiting factors involving physical, chemical and biological properties of soil. Calcium, magnesium and phosphorous deficiencies are considered major nutrient constraints that limit plant growth in acidic soils. Phosphorus limitation occurs due to fixation by oxides of iron and aluminum found in abundance in acidic soils. Young plants may require addition of fertilizers when grown in poor soils, but for established trees, there are many reports of adequate growth and cropping without any additional fertilization. The absolute phosphorus requirements of trees are small and deficiency symptoms are seldom found in fields. However, low availability of potassium can be serious and severe deficiency can induce compensatory uptake of other positively charged (especially magnesium and calcium) ions. Therefore, potassium deficient trees are therefore often characterized by unusually high leaf magnesium concentrations. Among plantation crops coffee, tea and cardamom are sensitive to low nutrient levels, resulting in low yields, poor quality and predisposal to pathogen damage.

3.2.5.2 Nutrient Toxicity

Direct nutrient toxicity due to high availability of major nutrients is not common in plantation crops. However, excess quantities of micronutrients and beneficial elements can result in serious toxic stresses limiting crop yield and profitability. Excess levels of nitrogen, phosphorus and potassium may boost vegetative growth, favoring pest and pathogen attacks, and the additional vegetative growth often occurs at the expense of reproductive phase. Sulfur toxicity occurs when sulfur dioxide adsorbed by leaves reacts with water to form bisulfate, inhibiting photosynthesis and degrading chlorophyll (Marschner 1995). Excess application of copper fertilizers or copper-based fungicides can result in copper toxicity, while high zinc fertilization causes zinc toxicity. Boron toxicity was reported to cause serious leaf damage in many crops. Aluminum toxicity is a common problem in acid soils. Tea plants show aluminum tolerance and have high internal tolerance to aluminum which is directly associated with aluminum accumulation (Rout et al. 2001).

3.2.6 Pollution

Pollution stress occurs in plants when pollutants such as toxic substances, gases, particulate matter, acids and radioactive substances contaminate their primary-growing environments (air, water and soil). Pollutants interfere with photosynthesis and respiration, enzyme activity and metabolic processes and causes membrane damage and cell death. Pollution stress is a growing problem in populated and industrialized regions of the world today. Natural pollution does however occur, due

to seismic and volcanic activities and acid rains. Pollution being not a regular natural process and mostly of anthropogenic origin, natural adaptation to pollutants is seldom found in plantation crops. However, being large plants they do tolerate moderate and short period pollutions without much damaging effects. However, continuous and heavy exposure may not be tolerated.

3.2.6.1 Air Pollution

Air pollution is a major cause of concern in plantation crops in the recent times. Major air pollutants are carbon oxides, nitrogen oxides, sulfur oxides, ozone, fluorides, ammonia and particulate matter. Ozone, nitrogen oxides, sulfur dioxide and peroxy acetyl nitrates (PANs) can cause direct damage to leaves when they enter stomata. Chronic exposure of leaves to air pollutants can also break down waxy layer that protects plants from excessive water loss, diseases, pests, drought and frost (Miller 1990).

Ozone is produced in the atmosphere during a complex reaction involving nitrogen oxides and reactive hydrocarbons in the presence of sunlight. Reactive hydrocarbons are components of automobile exhausts, fossil fuel combustion and volatile organic compounds emitted by biosphere. Ozone is a main component in the oxidant smog complex (Thomas 1961) and is regarded as a serious air pollutant that affects crop productivity, climate change, human and animal health (Royal Society 2008). Many species of tropical rain forests and plantation crops like oil palm are known to emit isoprene (2-methyl-1, 3-butadiene), a potential reactive volatile organic compound. Emission of isoprene by oil palm is a biological phenomenon that is believed to be under strong circadian control (Wilkinson et al. 2006). In addition, oil palm plantations emit oxides of nitrogen from fertilized soils in significant quantities. Therefore biological emission of volatile organic compound and non-biological emission of nitrogen oxides aid ground level ozone build-up in and around oil palm plantations (Hewitt et al. 2009). Regional ozone pollution (Pierce et al. 1998) can cause vegetation injury in plantation surroundings due to oxidant build-up in the air.

Other major air pollutants are sulfur dioxide and fluorides. Major sources of these pollutants are coal-burning operations, burning of petroleum and the smelting of sulfur containing ores. Sulfur dioxide is converted to bisulfate, which is oxidized to sulfuric acid by the reaction with water and form acid rain. Fluorides are dissolved readily in atmospheric moisture that turns acidic. Sulfur and fluoride toxicity occurs on leaves however, species, varietal and phenological level differences in sensitivity are observed in plants (Griffiths 2003). Nevertheless, scientific information on sulfur dioxide or fluoride toxicity in plantation crops is hardly available.

Other air pollutants like ammonia, chlorine, hydrogen chloride, hydrogen cyanide etc. does not contaminate atmosphere unless in the event of accidents involving the storage, transportation or application of these materials. Release large quantities of these compounds into the atmosphere for brief periods can cause severe injury to vegetation in the immediate vicinity. In rubber plantations, gaseous ammonia is

used as an anticoagulant for long-term latex preservation, but no adverse effect of exposure has been reported.

Particulate air pollutants such as cement dust, magnesium-lime dust and carbon soot is deposited on plantations near such industries. Particle deposits on the leaves inhibit normal respiration and photosynthesis. Cement dust can cause chlorosis, necrosis and death of leaves by the combined effect of a thick crust and alkaline toxicity produced in wet weather (Griffiths 2003). Similar stress effects can also happen when volcanic ash is deposited on the leaves in the event of volcanic activity.

3.2.6.2 Water and Soil Pollution

Water pollution occurs when industrial and domestic effluents are mixed with surface and/or ground water or when the effluents are used directly for irrigation. Effluents may contain a wide variety of toxic elements in varying concentrations. Prolonged usage of contaminated water causes elements to accumulate in the soil to levels toxic to plants. Common toxic elements are boron, chloride, copper, nickel, zinc, mercury, arsenic or cadmium. In addition, agricultural soils gets polluted by heavy metals by the soil addition of industrial and urban wastes, sewage sludge, fertilizers and pesticides and products from burning of fossil fuels. Studies show that toxic elements can incite almost all kinds of stress responses in plants, from altered respiration and photosynthesis, oxidative damage, membrane damage, impairment of enzyme activity and metabolism, anatomical and ultrastructural changes, poor growth and quality (Setia et al. 2008).

Limited studies are now available on natural adaptation of plantation crops to water and soil pollution, especially for heavy metal contamination. Arsenic accumulation in oil palm has been reported when grown in arsenic rich soils (Amonoo-Neizer and Amekor 1993) apparently without any stress symptoms. No direct stress was found in crops like coffee, rubber, coconut, eucalyptus and tea grown in soils with high content of lead, chromium, cadmium and nickel, except for the presence of these ions in elevated quantities (Abreu et al. 2005). There are very few evidences of heavy metal sequestration in plantation species so far. Metallothionein like genes (Abdullah et al. 2002) and stress inducible metallothionein promoters have been reported in oil palm, which may play a role in heavy metal detoxification. Metallothioneins are cysteine-rich low molecular weight proteins capable of sequestering metallic ions by binding (Omidvar et al. 2010). Similarly, metallothionein proteins have been isolated from rubber, which have been induced under oxidative stress situations (Zhu et al. 2010). Another low molecular weight protein family, small cysteine rich ligands called phytochelatins, which are involved in accumulation, detoxification and metabolism of heavy metal ions in plants (Maiti et al. 2004) have been identified in tea (Yadav and Mohanpuria 2009) and oil palm (Teoh et al. 2003). Radical scavenging proteins such as dehydrins that binds metals using a histidine-rich domain have been suggested to reduce metal toxicity in plant cells under water-stressed conditions (Hara et al. 2005).

3.2.7 Flooding

Flooding can be accumulation of water at the site of plant growth either by submerging the plants, fully (inundation) or partially (waterlogging), or for a shorter (flash flood) or longer (submergence) period. During waterlogging soil is saturated and root zone is affected, while during inundation stems are affected in addition to roots (Mullan and Barrett-Lennard 2010). Generally, inundation is not a problem in plantation species, but water logging can affect plantations grown at low-lying areas. Depletion of oxygen from soil (hypoxia) results in reduction in aerobic soil activities and anaerobic decomposition of organic matter is induced resulting in accumulation of carbon dioxide. Although rubber tree is sensitive to waterlogging, genotypic variations in adaptive as well as responsive behavior were recorded in rubber seedlings subjected to flooding (Gomes and Kozlowski 1988) ranging from downward curving of leaves (epinasty), reduced chlorophyll content, accelerated ethylene production, inhibited growth, induced decay of roots and stimulated production of lenticels and adventitious roots with large cells (hypertrophy). These adventitious roots contain extensive aerenchymatous cells that would facilitate diffusion of atmospheric oxygen to reduce root zone hypoxia, conferring flooding tolerance. Alternatively, these new roots may restore root to shoot communication and export essential mineral ions and hormones to the shoot system. Therefore it was suggested that, in rubber, flood adapted genotypes can be used as rootstocks in flood affected areas. In cocoa, although trees can withstand flash floods of mild intensity, they are particularly sensitive to water logging, but genotype variation in survival rate has been observed (Bertolde et al. 2010).

3.2.8 Fire

Fire occurrence in plantations is either anthropogenic or natural. Fire damage is a common occurrence in rubber and oil palm plantations, when people set fire to clear the undergrowth or deliberately to settle disputes. Oil palm plantation floors of South East Asia are infested with obnoxious weeds like cogon grass (*Imperata cylindrica*), which are generally cleared by burning (Yassir et al. 2010) occasionally causing fire accidents in plantations. In rubber, during wintering, plantation floors are carpeted by dry leaves that aid the fires to rage through plantations. Oil palms generally survive fire damage (Friday et al. 1999; Hairiah et al. 2000), but rubber trees suffer severe damage, rendering affected bark unusable for latex extraction.

3.2.9 Wind

Wind and hailstorms are natural phenomena that can affect agricultural crops adversely. Perhaps plantation crops are most affected by wind among agricultural crops. Degree of damage depends on the force at which wind blows through the

plantations. Although storms and tornados can destroy entire plantation, mild to severe winds can result in branch snaps, trunk snaps and uprooting. Steady winds can give constant strain on the trees. In rubber plantations, when trees are exposed to steady winds from one direction, trees develop a leaning appearance with trunk bent along the direction of wind. Constant strain on the wood tissues leads to tension wood formation on the upper (windward) side (Savill 1983; Reghu et al. 1989). In spite of being susceptible to strong winds, rubber clones show a great degree of variation in wind tolerance (Vinod et al. 1996b; Priyadarshan et al. 1998). Some clones achieve wind fastness by the help of altered crown structure and branching pattern (Cilas et al. 2004) that allow wind to pass through the plantation without inflicting much damage. Palms are more adapted to wind than the trees. In some palms as the root system develops, stem base enlarges giving additional stability to withstand strong winds, storms and hurricanes (Tomlinson 1961). When grown under optimum environments, coconut palms develop enlarged base in tall as well as in dwarf genotypes (Satyabalan 1997).

Hails occurs commonly in tropics, at higher altitudes and latitudes with the onset of summer. There are reports of hailstorm damage to plantation crops like rubber, coffee, tea, cardamom and coconut. In northeast India where rubber is grown extensively, hail shower is a normal annual occurrence during summer. Although mild hail showers do not pose any problem to mature rubber trees, they are capable of inflicting damage in young plants. Notwithstanding, hailstorm of severe intensity can cause severe damage to rubber trees, by shattering the bark by falling hailstones (Meenattoor et al. 1995). Trees that survive damage take a longer time to recoup and it is reported that even after eight years affected bark has not returned to full anatomical features required for commercial latex collection (Vinod and Thomas 2006).

3.2.10 *Lightning*

Lightning is a spectacular natural phenomenon, occurs commonly along with thunderstorms, volcanic eruptions and dust wind. A lightning is most likely to hit a tall green tree, with an upward stroke of current in excess of 100,000 A (Ahrens 2007) passing through the tree, causing excessive internal heating, resulting in splitting up of vascular tissues and cracking of trunk (Thomas et al. 1995). Extensive observations of lightning damages are reported in crops like coconut and rubber. In rubber, direct lightning strikes cause trees to wilt within few hours of the incident. In partial strikes die-back of branches occur after few days, and in few cases, bark on one side of the trunk is seen damaged on entire length of the tree. Direct lightning strike on rubber trees are normally fatal, and those survive partial strikes remain unsuitable for tapping (Steinmann 1925). Direct fatality may occur only on one or more trees however, many trees around are subsequently killed, from secondary infections of pathogens and more conspicuously from wood boring ambrosia beetles (*Xyleborus* sp., *Xylosandrus* sp., *Platypus* sp). Wood of the affected trees generally shows dark streaks of vascular burning. However, in coconut palms, lightning leaves no palm to

survive. Depending on the degree of electrical discharge, the death may occur instantly or after few days. In severe direct strikes, the treetop may be burnt, or decapitated, but such occurrences are relatively rare (Ohler 1999).

3.2.11 Soil Erosion

Soil erosion is a serious problem in plantation crops, since these crops are grown on cleared lands, and are generally planted in wider spacing. Soil disturbances during planting activity and removal of natural ground cover enhance steady depletion of soil layers either by run-off, landslides and wind erosion. Erosion causes loss of fertility that result in poor development of roots in addition to susceptibility to pest and diseases. Poor root anchorage affects absorption of soil water and nutrients and increases susceptibility to wind damage. It is reported that eroded soils under coffee were more acidic than non-eroded soils, with considerable loss of fertility (Hartemink 2006). Plantation crops like rubber grown in sloppy areas are more susceptible to run off and landslides during rainy seasons. In mature oil palm plantations, soil erosion depends chiefly on slope of the site and soil management practices. Intercropping with soil disturbing crops increases the chance of erosion, while those require minimal soil disturbance may help to prevent erosion. In young oil palm and rubber tree, the practice of growing cover crops helps to limit erosion. As the trees mature, cover crop disappears due to canopy or crown closure, resulting in increase of run off and erosion (Chew et al. 1999). Furthermore, the risk of soil erosion is more in surface feeders like rubber and oil palm wherein top soil erosion exposes most of the feeding roots that subsequently dry up and die, resulting in poor uptake of water and nutrients (Ferwerda 1977; Howell et al. 2005). Plant stress attributable to soil erosion can be seen in coffee plantation without adequate shade, having low planting density and grown on slopes. Erosion occurs in tea plantations after pruning.

3.2.12 Climate Change

Climate change is a matter of concern of twenty-first century that warns of rising temperature, unprecedented drought, flood, desertification, radiation, cyclones, forest fires, extreme low temperature that can adversely affect agriculture and human life. Predictions for the first three decades indicate that developing nations will be affected most because of following three reasons. Firstly, most of the developing nations are in tropical and sub-tropical regions where the negative impacts of climate change are expected to be more. Secondly, a large proportion of the global population growth will be happening in the developing world, and the third, more than half of the population in developing nations is dependent on agriculture (Reynolds and Ortiz 2010). This is of particular concern to plantation crops, because most of them are cultivated in the tropics. Being perennial crops, adverse effect on

these crops will have long-term repercussions - the production decline and commodity price escalation.

Counting on natural adaptations to climate change in plantation crops is a difficult task. Being perennials, long-term survival can be the best index of adaptation. Fortunately, there are no reports of serious influence of climate change on plantation crops so far. However, one recent report from Ethiopia suggests of a shift in cropping pattern attributable to climate change, which reports of conversion some marginal coffee areas for cultivation of khat (*Catha edulis*), a hardy drought resistant plant, due to prolonged dry periods (Labouisse et al. 2008). A comprehensive review on current knowledge and future perspectives on diseases in tropical and plantation crops as affected by climate changes can be found in Ghini et al. (2011).

3.3 Adaptation to Biotic Stresses

Like abiotic stresses, most of the biotic stresses are seasonal in nature. Therefore, perennial crops are subjected to all kinds of biotic stress irrespective of the seasons. These crops undergo *in situ* natural selection against recurring factors, years after, and become capable of buffering the damage and only the fittest is carried forward to future generations. In practice, most of the biotic factors co-exist in cropping environments in this fashion, but the limit of buffering become apparent when varieties are tested in different environments or when a 'new' disease or pest arrives.

3.3.1 Defense Against Pathogenesis

Pathogenesis is associated with onset of favorable weather conditions, and therefore is limited to certain locations and seasons. Plants have active surveillance mechanisms either constitutive or induced against pathogens that are genetically programmed into every species (Bittel and Robatzek 2007). Basal resistance or innate immunity is the primary level of plant adaptation against diseases, triggered when microbe-associated molecular patterns (MAMPs) are recognized by pattern recognition receptors (PRRs) of host plant cells. MAMPs include specific proteins, lipopolysaccharides and cell wall components of pathogens. Activation of PRRs leads to active defense responses, both in basal and non-host resistance (Jones and Dangl 2006).

3.3.1.1 Constitutive Defense

Constitutive defense in plantation crops are manifested through morphological, physiological and biochemical adaptations involving cuticular modifications, accumulation of wax and other organic compounds, production of specialized secretions and stomatal, bark or lenticel adaptations. Most of the morphological modifications also provide structural rigidity and strength to the plants (Freeman and Beattie 2008).

Structural defense

Cuticle acts as the primary physical barrier of plant's defense against pathogens. Recent evidences indicate cuticular modifications that confer disease resistance by release of fungitoxic substances as well as changes in gene expression that form a multifactorial defense response (Chassot et al. 2008). In plantation crops, cuticular defense against *Colletotrichum kahawae*, the coffee berry disease (CBD) pathogen has been known for a long (Nutman and Roberts 1960) in resistant varieties. Cuticular extracts (Nutman and Roberts 1960), wax extracts (Steiner 1972; Lampard and Carter 1973) and hypocotyl extracts (Masaba and Helderma 1985) of resistant varieties have shown clear suppression in conidial germination and mycelial growth of *C. kahawae*, however the exact components responsible for resistance have not been identified yet.

Waxes form a part of the preformed plant defense system against biotic stresses such as fungi, bacteria and insects (Gülz et al. 1991; Yoon et al. 1998; Marcell and Beattie 2002). Epicuticular wax of coconut predominantly contains lupeol methyl ether, isoskimmiwallin and skimmwallin (Escalante et al. 2002) and other compounds such as lupeol, 3- β -methoxy lupane (lupane methyl ether) and acetates of lupeol, skimmwallinol and isoskimmiwallinol. Epicuticular wax constitute 95% of the total wax content in coconut, while the remaining 5% include triterpenoids, sterols, primary alcohols, fatty acids and unidentified compounds (Riedel et al. 2009). However, significant genotype variation in epicuticular wax content is found in coconut as well as in rubber (Rao et al. 1998).

Biochemical defense

Majority of the phytochemicals belongs to three major classes of terpenoids, alkaloids and phenolics, and all of them are secondary metabolites. The basic terpene is isoprene, and depending on the number of isoprene units present in the molecules, terpenoids are classified as mono-, sesqui-, di-, tri-, tetra- and polyterpenes. One of the most versatile and abstruse compound produced by the rubber tree, the elastomer called rubber is a polyterpene known as *cis*-poly isoprene. Why rubber tree and many other species produce this compound expending so much of energy remains a mystery. Further, rubber is said to be at the metabolic dead-end since no enzymes are capable of breaking it down (Bonner and Galston 1947). Rubber particles are produced in latex, the cytoplasm of a specialized anastomosing network of laticifer cells. Notwithstanding, there seems to be a general agreement on the role of latex in plant defense against diseases and pests (Dussourd and Eisner 1987; Farrell et al. 1991). In support to this, antifungal activity of latex has been demonstrated *in vitro* (Moulin-Traffort et al. 1990; Giordani et al. 1999).

Alkaloids are nitrogenous compounds, derived from amino acids tryptophan, tyrosine, lysine and aspartates, possessing antibiotic and antifungal properties. Caffeine is a predominant alkaloid found in coffee, tea and cocoa. Highly toxic to fungi and insects, caffeine can even cause allelopathy in other plant species (Freeman

and Beattie 2008). The phenolics are another class of defense-related secondary metabolites commonly found in plantation crops that are produced through shikimic acid - phenylpropanoid pathways. Shikimate pathway converts carbohydrate precursors into phenylalanine and tyrosine. Phenylalanine is the precursor molecule for the phenylpropanoid pathway. The phenylpropanoids commonly found in plants are anthocyanins, flavonoids, furanocoumarins, lignins and tannins (Saltveit 2010).

Polypeptide defense

Passive polypeptide defense is achieved in plants through preformed proteins and enzymes. They include defensins, protease inhibitors, amylase inhibitors and lectins. Defensins are cysteine-rich cationic proteins showing antipathogenic activity that are believed to form multimeric pores in the plasma membrane of pathogens leading to membrane disruption and depolarization by affecting ion-channels resulting in cellular ion imbalance (Thomma et al. 2002; Ganz 2003). Plant defensins are of three types, hevein type, thionin type and knotting type of which hevein and thionin types have eight cysteine residues while knotting type has six. Further, hevein and knotting type have continuous sequence of cysteines at the center while thionone type has cysteine sequences at the N-terminal end (Fujimura et al. 2005). Among the defensins, thionines show high affinity to chitin, the major cell wall component of pathogenic fungi (Oita et al. 2000).

The rubber tree latex contains hevein, a single-chain serine protease that has been described as an antifungal protein (Koo et al. 1998, Ko et al. 2003). It is an acidic protein with a chitin-binding domain belonging to lectin super family and is encoded by a multigene family consisting of at least five members (Pujade-Renaud et al. 2005). 50-70% of the total soluble proteins in rubber tree latex are composed of hevein (Van Parijs et al. 1991). Hevein contains 18% cysteine in its amino acid sequence (Lucas et al. 1985) and are found in two forms viz., prohevein (Hev b 6.01) and hevein (Hev b 6.02). Prohevien is actually the hevein preprotein that matures to hevein. Although hevein promoter is constitutively expressed in rubber (Montoro et al 2008), induced production also has been reported during wound related stress (Broekaert et al. 1990). Therefore, hevein is believed to play an important role in plant defense (d'Auzac et al. 1995). Besides heveins, rubber latex contain many proteins that belong to the class of pathogenesis related (PR) proteins. They are Hev b 2 (endoglucanase), Hev b 11 (*Hevea* endochitinase), Hev b 12 *Hevea* Lipid transfer protein (LTP) and hevamine (Hoffmann-Sommergruber 2002). Unlike that of all known class I chitinases, which are vacuolar proteins Hev b 11 is identified to be a cytosolic (C-serum) protein (Beintema 2007). Hevamine is another chitinase from rubber tree belonging to the family 18-glycosyl hydrolases. This enzyme has a unique property of cleaving the chitin molecule, and the sugar moiety of peptidoglycan (Bokma et al. 1997). Hevamine was the first enzyme found with chitin cleavage specificity (Bokma et al. 2000). Apart from rubber tree, expression and characterization of a putative defensin (EGAD1) in oil palm inflorescences has also been reported (Tregear et al. 2002).

3.3.1.2 Inducible Defense

Successful pathogens overcome primary defense systems and establish contact with the host. From this point onwards, inducible defense decides how plants survive the attack. Induction of defense does not occur until imminence, perhaps to conserve high energy and nutrient required in production and maintenance of defense mechanisms.

Structural fortification

Pathogen induced structural reinforcement of cell wall has been implicated in defense, accomplished through accumulation of glucan polymers such as (1-3)- β -glucan callose (Aist 1976), lignins, suberins (Guest and Brown 1997) or through cross linking of cell wall proteins (Bradley et al. 1992). Induction of callose and other defense related transcripts has been observed in coconut calli as a suitable alternative to characterize both biochemical and molecular interactions that occur between the coconut and its biotic stress factors (Uc et al. 2007). Callose rich haustorial encasements are induced in resistant coffee genotypes in incompatible reaction with leaf rust pathogen, *Hemileia vastatrix*. This encasement is less permeable thus preventing the flow of nutrients to the fungal pegs, thereby arresting the pathogen entry (Silva et al. 2006).

Root rot infection by *Rigidoporus lignosus* and *Phellinus noxius* in rubber tree starts with an increase of cell layers below the point of penetration resulting from a stimulated activity of cork cambium. Cell walls thicken concomitantly due to the accumulation of suberin or lignin. Callose formation occurs in young cork cells as well as in the phloem, obstructing pores of sieve tubes. Heterogeneous lignification takes place in xylem vessels. Tyloses resembling cell islands are formed in the young phloem in order to slow down the progression of invading hyphae (Nicole et al. 1985).

Rapid cork formation below the site of infection has been attributed for the resistant reaction in coffee to berry disease pathogen, *C. kahawae* (Masaba and van der Vossen 1982). Phellogen is formed in few cell layers rapidly, and the fungal invasion is arrested by development of suberized cells (Gichuru 1997).

Secondary metabolites

Many phenolic compounds are induced following pathogenesis. Phytoalexin accumulation in coffee genotypes resistant to *Hemileia vastatrix* and *Pseudomonas syringae* has been implicated in resistance reaction (Rodrigues et al. 1975; Guedes et al. 1994).

A fluorescent blue phytoalexin identified as scopoletin (7-hydroxy-6-methoxy coumarin; Giesemann et al. 1986) is produced in rubber trees during resistant reaction with *Colletotrichum gloeosporioides* (Tan and Low 1975), *Microcyclus ulei*

(Garcia et al. 1995) and *Phytophthora palmivora* (Churugchow and Rattarasarn 2001). MAMPs from *P. palmivora* induced production of scopoletin, *o*-dianisidine (a peroxidase) and accumulation of phenolic compounds in rubber seedlings and in cell suspensions under resistance reaction (Dutsadee and Nunta 2008). Scopoletin was also isolated from leaves of mature rubber trees uninfected with *Corynespora cassiicola* and was found at elevated levels in young leaves post infection. Further, it was demonstrated that scopoletin could fully suppress conidial germination of many rubber tree pathogens viz., *Corynespora cassiicola*, *Cylindrocladium quinqueseptatum*, *Phytophthora* spp., *Colletotrichum acutatum* and *Helminthosporium heveae* (Churugchow and Rattarasarn 2001; Silva et al. 2001). On the contrary, cyanogenesis, the liberation of high amounts of hydrocyanic acid (HCN), is observed from leaves of susceptible in rubber clones, following infections with *M. ulei* while resistant clones released only very little HCN. This indicated that cyanogenesis *per se* does not lead to defense against fungal pathogen but impair resistance reaction (Lieberei 1986).

Lignins are polymers of phenolic monomers commonly found in cell wall, especially in the secondary cell wall. In woody plants, cell wall lignification takes place as cells mature. Lignification provides rigidity to the cell, thereby imparting structural strength to the woody stem. Furthermore, lignins act as versatile defense compounds during pathogen attack. High level of lignin accumulation is a common phenomenon in the renewed bark of the rubber tree, following tapping and other wound induced reactions (Thomas et al. 1995). Gum exudations containing phenolic components occur in coconut and cashew following wounding possibly as a defense against imminent pathogen attack. Apart from lignins, plantation crops such as tea contain water-soluble polymers of flavonoids known as tannins. Tannins are commonly found stored in vacuoles and are toxic to pests rather than pathogens.

Inducible polypeptide defense

Evidences suggest that stress signaling in plants is modulated by multiple hormone-signaling pathways of jasmonic acid, salicylic acid, ethylene and ROS (Fujita et al. 2006) under the regulatory control of transcription factors (TFs) and *cis*-acting elements. TFs are proteins that regulate gene expression by recognizing and binding to the *cis*-elements in the promoter regions of the upstream target genes. Major plant TFs involved in biotic defense belong to five major gene families. Among these, ethylene responsive element binding factors (ERF) zinc finger proteins are involved in ROS signaling, while MYB (myeloblastosis) and MYC (myelocytomatosis) proteins are involved in jasmonic acid signaling. Further, WRKY (tryptophan, W; arginine, R; lysine, K; tyrosine, Y) TFs with zinc finger motifs are active in salicylic acid signaling, whereas, NAC (no apical meristem, NAM; Arabidopsis transcription activation factor, ATAF; cup-shaped cotyledon, CUC) factors activate jasmonic acid signaling and basic-domain leucine-zipper (bZIP) proteins. However, regulatory activity of TFs depends on plant specific adaptation to stress as well as on the types

of stresses plants may experience. Recent developments in functional genomics have revealed presence of these gene families in some of the plantation crops. In coffee, most of the isolated genes showed homology to known plant genes suggesting cross-genome conservation of signaling pathways and pathogen resistance mechanisms (Silva et al. 2006).

The WRKY TFs are now known to play key regulatory functions in plant defense against salinity, mechanical damage, drought, cold, pest and diseases as well as in development of seeds, trichome and in the biosynthesis of secondary metabolites. Gene expression studies in *C. arabica* plants challenged with the rust fungus (*Hemileia vastatrix*), the root-knot nematode (*Meloidogyne exigua*) and abiotic treatments showed concomitant expression of *CaWRKY1a* and *CaWRKY1b* with same altered patterns in both biotic and abiotic treatments (Petitot et al. 2008). WRKY gene based markers have been found useful in delineating genetic diversity in coconut germplasm, indicating genome wide ubiquity and variation of these genes (Mauro-Herrera et al. 2007). In cocoa, *TcWRKY* markers have been developed for genome scanning for stress resistant genes (Borrone et al. 2004). Recently, a set of five WRKY TF members have been described in coffee as possible regulators of defense responses (Ramiro et al. 2010).

The rubber tree latex accumulates high levels of induced plant defense gene transcripts and hydrolytic enzymes such as cellulases, polygalacturanses (Kush et al. 1990), β -1,3 glucanase (Chye and Cheung 1995) and peroxidases (Dutsadee and Nunta 2008) suggesting a functional role for the latex in defense (Dussourd and Eisner 1987; Farrell et al. 1991). A detailed transcriptome profiling (Ko et al. 2003) reveals latex abundance of a gene, HbPII (*H. brasiliensis* protease inhibitor 1) that share conserved domain with potato inhibitor 1 family and share high level sequence homologies with serine proteinase inhibitor, protease inhibitor and PR protein. Other putative plant defense genes highly expressed in latex included LTI6B (low temperature Induced 6B - a low temperature and salt responsive protein, Blt101 (barley low temperature induced protein), and RTM1 (restricted TEV movement - disease resistance protein).

Increased activities of phenylalanine ammonialyase (PAL), NADPH oxidases and peroxidases were reported in coffee (Silva et al. 2008) during incompatible (resistant) reaction with *H. vastatrix*. Presence of PAL, the key enzyme in the phenylpropanoid pathway indicates phenolic production, while rise in lipoxxygenase (LOX) activity (Rojas et al. 1993) indicate peroxide synthesis. However, LOX activity remained constant in a compatible interaction leading to disease. LOX are believed to provide hydroperoxide substrates that can be metabolized to compounds that play important roles in plant defense (Baysal and Demirdöven 2007). Peroxidase production is also reported in defense reaction against *C. kahawae* (Gichuru et al. 1997).

Hypersensitive response

Pathogenesis occurs when successful pathogens break down induced defense systems of the plant and inject a range of effector molecules that suppress host

responses at different defense levels of perception, signaling and suppression. Notwithstanding, plants have evolved a sophisticated immune system to detect these effectors using cognate disease resistance proteins, a recognition that is highly specific and often elicits rapid and localized cell death (Xing et al. 2007). The hypersensitive response (abbreviated as HyR to distinguish from horizontal resistance, HR) is a deliberate sacrifice of cells around the site of infection, locally confining the pathogen and deprives it of water and nutrients to stop it from further advancing. HyR is, therefore, a type of programmed cell death (PCD) akin to apoptosis in mammalian cells (Heath 1998). The most common features of HyR are the autofluorescence of dead cells under UV exposure and subsequent browning of cells caused by oxidized phenolic accumulation. Although ion fluxes and generation of ROS commonly precede cell death, direct involvement of ROS may vary with the plant-pathogen combination (Park 2005). Oxidative burst also occur in many instances, but it is not necessarily a requirement for PCD (Groover et al. 1997). HyR is an effector specific reaction and therefore is more pathogen specific. The effector recognition follows signal transduction for the production of specific resistant (R) gene products or R proteins that induce HyR. On successful confinement of pathogens, plants set off effector-triggered immunity (ETI) that produces visible symptoms of HyR. ETI follows classical gene-for-gene theory and a strong ETI is responsible for an incompatible interaction or specific resistance (Göhre and Robatzek 2008).

Reactions similar to HyR, in which the cells around the penetration hyphae collapse, have been reported from rubber clones that are resistant to *Microcyclus ulei* infection. Deposition of autofluorescent compounds and callose, activation of ROS, scopoletin accumulation and cell death are found to occur leaving a limited necrotic patch surrounding the penetrating hyphae (Garcia et al. 1999; Lieberei 2007). Responses similar to HyR were also reported from rubber roots infected with root rot pathogen, *Phellinus noxius* (Nicole et al. 1992).

Naturally rust resistant coffee varieties too show HyR, (Lam et al. 2001; Morel and Dangl 1997) manifested by death of subsidiary and guard cells of stomata around the site of fungal penetration (Martins and Moraes 1996; Silva et al. 2002).

Systemic acquired resistance

The activation of ETI enables host tissues to combat a broad range of pathogens for an extended period, known as systemic acquired resistance (SAR) or 'whole-plant' resistance (Hunt and Ryals 1996; Neuenschwander et al. 1996; Ryals et al. 1996). The chemical activation of SAR requires accumulation of endogenous salicylic acid (SA) that induce a wide range of genes including PR genes (Durrant and Dong 2004; Zhang et al. 2010a) leading to production of chitinases, β -(1, 3)-glucanases, lysozyme, permatins and PR proteins (Ryals et al. 1996; Schneider et al. 1996).

There are many reports suggesting the presence of SAR in plantation crops, but conclusive evidences are still at large. If direct measurement of enzyme activities

(Heil 1999) is to be taken as SAR indicator, rubber tree latex has prominent chitinase activity (Van Parijs et al. 1991) and presence of β -(1,3)-glucanases and many PR proteins (Hoffmann-Sommergruber 2002). Recently, many artificial elicitors such as benzothiadiazoles and harpin protein are being introduced to mimic host-pathogen interaction leading to SAR (Gorlach et al. 1996; de Capdeville et al. 2001). Chemical elicitors such as salicylic acid (Mayers et al. 2005), jasmonic acid (Cohen et al. 1993), DL- β -aminobutyric acid (BABA) (Hong et al. 1999), oxalic acid (Mucharromah and Kuć 1991) and acibenzolar-S-methyl benzo-(1,2,3)-thiadiazole-7-carboxylic acid S-methyl ester (ASM) (Gullino et al. 2000) have been successfully used as SAR elicitors. Significant increase in PAL, peroxidase and β -1,3-glucanase activities on elicitor treated tea leaves challenged with pathogen and 25% decrease in disease intensity have been reported under field conditions. They are preferred because of relatively lesser risk they pose to non-target organisms and environment than toxic chemical fungicides.

Induced systemic resistance

Tree endophytes are silent colonizers of healthy internal plant tissues (Sieber 2007). Although some of the colonizers are potentially pathogenic, during symbiotic existence, disease is not generally incited, perhaps due to the endosymbiotic suppression of disease induction factors (Giordano et al. 2009; Botella et al. 2010). However, endosymbionts stimulate resistance reaction in host plants similar to SAR known as induced systemic resistance (ISR). ISR is therefore just another type of adaptation among crops plants wherein symbiotic relations between the host and colonizing species has been exploited, as against antagonistic relations as in SAR. Notwithstanding, ISR and SAR are believed to be in crosstalk in host plants. Observations during the establishment of successful colonization between the host (cocoa) and the colonizer (*Trichoderma*) (Bailey et al. 2006) indicate high induction of fungal genes such as glucosyl hydrolase family, serine protease and alcohol oxidase. This suggests of host-colonizer genetic crosstalk that results in endophyte-stimulated production of many secondary metabolites, including those involved in induced defense in host (Ryan et al. 2008; Gao et al. 2010).

Of different type of resistant mechanisms, ISR has been the least known in plantation crops. The first report of ISR in a woody species was made in citrus, against *Phoma trachetiphila* that causes mal secco disease (Solel et al. 1995). Among endophytic fungi, many species of *Trichoderma* are prominent colonizers in cocoa and in few other plantation crops (Holmes et al. 2004). Rubini et al. (2005) demonstrated that *Gliocladium catenulatum*, an endophytic fungus, could reduce the incidence of witches' broom disease in cocoa seedlings up to 70% accentuating their usefulness against fungal pathogens as biological control agents (Mejía et al. 2008). Comprehensive reviews on endophytic fungal diversity and use as biocontrol agents in cocoa and coffee are available (Mejía et al. 2008; Vega et al. 2009).

Use of two endophytic bacteria (*Burkholderia cepacia* and *Pseudomonas aeruginosa*) have been reported from oil palm, which could reduce the incidence of basal

stem rot disease caused by *Ganoderma boninense* to a tune of 76% (Sapak et al. 2008). Plant growth promoting rhizobacterial (PGPR) bioformulations of *Pseudomonas fluorescens* was successfully used in tea to induce ISR to counter blister blight pathogen under field conditions with treated plants developing high accumulation of PAL, peroxidases and polyphenol oxidases (Saravanakumar et al. 2007). Further, *in vitro* tea plantlets when treated with two native rhizosphere bacterial isolates of *Azospirillum brasilense* and *Trichoderma harzianum* on hardening process, did not develop root rot and wilt diseases commonly found to infect *in vitro* seedlings during hardening process. These inoculated seedlings were found to have higher activities of defense enzymes like PAL, peroxidase and β -1,3-glucanase (Thomas et al. 2010).

In rubber trees, induction of systemic tolerance was demonstrated through lesser incidence of *Corynespora cassicola* infection when endophytic bacteria isolated from different organs were inoculated artificially (Philip et al 2005). Rocha et al. (2011) have isolated and characterized endophytic fungi from cultivated *Hevea brasiliensis*, and found that these endophytic fungi exhibit marked inhibitory activity on *M. ulei* conidia germination *in vitro*. Moreover, arbuscular mycorrhizal fungi (AMF) were also found to improve plant growth and survival during greenhouse acclimatization of rubber seedlings (Rodríguez et al. 2009). AMF are naturally occurring group of soil fungi that exhibit symbiotic relationships with the roots of most vascular plant species (Vestberg et al. 2002). Further, AMF are suspected to induce systemic resistance, apart from improving plant growth by increasing nutrient uptake, especially phosphorus (Elsen et al. 2008).

RNA silencing

Recent evidences show that plants are capable of identifying and degrading pathogenic viral RNA by sophisticated mechanism of post-transcriptional gene silencing (PTGS) called RNA silencing, a process similar to RNA interference (RNAi) in animals. Plants contain small double-stranded RNA of 20 to 26 nucleotides in length, named short interfering RNA (siRNA) and endogenous small non-coding single stranded micro RNAs (miRNA) of an average 22 nucleotides. These classes of RNAs are related to several RNA biological processes such as the defense against viral invaders, developmental control, cell signaling, transposon silencing and heterochromatin formation (Vrettos and Tourmier 2007). During viral infection, siRNAs bind to a complementary viral RNA and induce its degradation, while miRNAs are capable of inhibiting messenger RNA (mRNA). On degradation, plants may retain the digested viral template so that in case future infections they will be able to initiate quick action (Carbonell et al. 2008).

Successful isolation of two siRNAs from coconut leaves infected with coconut cadang-cadang viroid (CCCVd) was reported (Vadamalai 2005). Computational prediction of several miRNA from oil palm expressed sequence tag (EST) sequences has also been reported (Nasaruddin et al. 2007).

3.3.2 Defense to Herbivory

Plantation species in general have well-organized adaptation systems against the most common herbivores, the insect pests. These crops have inbuilt fortifications to ward off most of the insect feeders, and a few very specific pests can survive on them. Some crops like rubber have no serious pest at all. Pest damage does not pose serious threat to these crops and damages seldom surpass economic threshold. However, few sucking pests in cardamom, cashew and tea, borers and spider mites in coffee and cocoa can sometimes become exceptionally serious. In overall, pest resistance is of marginal importance in commercial plantation crops.

Similar to that of pathogen defense, plant mechanisms for insect resistance can be either constitutive or inducible. Among the three mechanisms, antixenosis and antibiosis are prominent in plantation crops, while the requirement of tolerance is relatively low. Plantation crops are rich in alkaloids, volatile monoterpenes, polyterpene compounds, tannins, lignins, cyanogenic compounds, other phenolic compounds and allergens, through which defense against pests are arbitrated. These biomolecules, otherwise known as allelochemicals induce a variety of reactions in pests such as repulsion, toxicity, allergy and indigestion, jeopardizing their normal metabolism, reproduction and survival. For instance, leaf minor (*Leucoptera coffeella*) resistance in coffee species viz., *Coffea racemosa*, *C. setenophylla* and *C. kapakata* seems to be of antibiosis type wherein phytochemicals interfere with normal growth of the insects. While in *C. canephora*, the resistance is exhibited through antixenosis (Aviles et al. 1983). It has been reported that *C. arabica* leaves has larger concentrations of p-cymene, a monoterpene derivative, and lower levels of beta cymene that greatly enhanced oviposition preference to the leaf miner, which was not the case in *C. canephora* and *C. racemosa* leaves (Filho 2006). Maintaining higher levels of phenolics in the face of attack was found to be one of the strategies for the observed tolerance of certain tea varieties to insect attack especially to *Helopeltis* (Chakraborty and Chakraborty 2005). This feature is also observed in rubber tree making it a less preferred host by most of the insects.

Herbivore induced defense gene activation takes place throughout the plants within hours after suffering the injury. Systemins, a group of plant peptide signal molecules comprising of short 18 amino acid long peptides (Pearce et al. 1991) are known to play a major role in systemic wound signaling (Ryan and Pearce 2003). Similar to systemins, short hydroxyproline rich systemin glycopeptides (HypSys) processed from longer precursor molecules have also been discovered in plants actively involved in defense reaction. HypSys activates methyl jasmonate, amplifying defense response. Presence of HypSys (*CcHypSys* I, II and III) genes are reported in robusta coffee (Pearce et al. 2008).

Moreover, rubber tree belongs to euphorbiaceae, a large plant family in which cyanogenesis is a common occurrence. Cyanogenesis is the ability to synthesize cyanogenic glycosides, which when enzymatically hydrolyzed by β -glucosidase (Poulton 1990; Francisco and Pinotti 2000) produces sugars and a cyanohydrin compound that spontaneously decomposes to HCN and a ketone or aldehyde.

This step is catalyzed by hydroxynitrile lyase enzyme. Both the enzymes, β -glucosidase and hydroxynitrile lyase are common in cyanogenic plants (Harborne 1993; Gruhnert et al. 1994). The cyanogenic glycosides are usually sequestered into vacuoles, while enzymes are present entirely in the mesophyll tissues (Poulton 1990). On injury, cell disruptions bring both glucoside precursor and the enzyme in contact resulting in the release of HCN (Gruhnert et al. 1994). Rubber leaves contain a broad substrate specific β -glucosidase, linamarase, and cyanogenic glucosides, linamarin and lotaustralin (Lieberei et al. 1985). Since the cyanogenesis is an obligate feature in rubber trees, all living tissues, including that in seeds are strongly cyanogenic and contain both accumulated cyanogenic precursor and respective β -glucosidase. In seeds, endosperm alone contains more than 90% of linamarin (Poulton 1990). Montoro et al. (2008) found that cyanogenesis provides very good defense against herbivores in rubber.

Furthermore, rubber tree is rich in compounds that are potential allergens to herbivores. Rubber latex contain chitinases (Type I and III), β -(1,3)-glucanases and lipid transfer proteins, which are both allergenic and pathogenesis related (Hoffmann-Sommergruber 2002), besides many other *Hev b* allergenic proteins. Thirteen types of allergenic proteins found in latex include rubber elongation factor, small rubber particle proteins, hevein, prohevein, acid transfer proteins, endochitinases and superoxide dismutase (Yeast 2004).

Mechanical defense against herbivory is also found in plantation species, especially in palms. Coconut and other palms protect nuts by providing multiple layers of thick and strong husk. The chemical makeup and abundance of external protectives like waxes keeps pests away from preferring these crops for colonizing (Kolattukudy 1987). Structural adaptations for pest resistance are observed in few crops. Coconut palms with small nuts are more susceptible to eriophyid mites, than palms with larger nuts. Studies by Mariau (1977) revealed that in smaller nuts perianth is less firmly attached to nut enabling mites to access interspace between nut and lower perianth lobes for colonization, whereas in larger nuts this gap is mostly impenetrable. Further, it was observed that on infestation, some palms with smaller nuts do resist the damage by increasing the perianth-nut gap that makes the mites uncomfortable to settle, while exposing them to predators (Aratchige et al. 2007).

3.3.3 Allelopathy

Allelopathy is a natural adaptation to defend plant-plant competition, which causes difficulties in replanting orchards and vineyards and causes poor establishment, stunted growth and even complete mortality in the subsequent plantings. Autotoxicity induced by caffeine has been reported in coffee plants (Waller et al. 1989) and by other alkaloids from coffee such as theobromine, theophylline, paraxanthine and scopolectin (Peneva 2007). Allelopathic effects have also been reported in Eucalyptus (Sasikumar et al 2001; Liu et al. 2008).

3.3.4 *Physiological Disorders*

Sustained physiological stress due to factors other than pathogens and pests brings out visible symptoms in plantation crops. Although the term physiological disorder is very broad and can include symptoms of abiotic stresses, in a narrow perspective it is used to denote disorders of unknown etiology. Physiological disorders due to known factors can be revert back to normal by stress alleviation, while unknown factors can bring more severe permanent disturbances. Tapping panel dryness (TPD) of rubber is one of the widely known physiological disorders among plantation crops. Hot and cold disease of coffee is a physiological disorder caused in higher elevations due excessive cooling followed by heating. Other disorders of unknown etiology in coconut are pencil point disease, bristle top, dry bud rot, finschafen disease, frond rot, leaf scorch decline and Malaysia wilt.

3.3.4.1 **Tapping Panel Dryness**

The TPD, also known as ‘brown bast’ is a serious condition that affects productivity in rubber plantations. TPD is generally manifested as sudden drying up of latex vessels in tree bark at lower side of the tapping panel, rapidly spreading to wider areas on the tree trunk. Bark necrosis occurs usually after a period of prolonged flow of diluted latex, but sudden drying up without this symptom is also seen. As necrosis advances affected bark turn dry, crack and peel off either from the entire trunk or on from one side. Degeneration of normal bark happens simultaneously with the production new bark underneath, which lacks uniform structure and texture. Woody malformations are commonly found interspersed in the new bark rendering it unsuitable for tapping. Apart from the bark degeneration, the affected tree otherwise remain healthy and grow normally.

Observations suggest that TPD is a disorder resulting from continuous wounding of latex tapping that may trigger a non-compensated oxidative stress (Faridah et al. 1996). The disorder may be associated with nutrient depletion (Fan and Yang 1994), metabolic destabilization leading to bursting of luteoids followed by internal latex coagulation, followed by oxidative stress (Chrestin 1989). Apparent differences in metabolic profile between affected and normal bark are observed (Krishnakumar et al. 2001) including putative changes in protein profiles (Sookmark et al. 2002). Genotype variations in onset of TPD are also observed implying the existence of natural adaptation to the unknown causal factors (Yan and Fan 1995; Chen et al. 2003).

Recent evidences indicate association of Myb TFs with TPD (Chen et al. 2003), along with many differentially expressed water-stress-related genes (Mongkolsuk and Schumann 2009). Further, Venkatachalam et al (2007) reported up-regulation genes like cysteine protease like mRNA (CP), PR-osmotin precursor gene (PRO), ethylene biosynthesis related gene (EB), annexin-like protein RJ4 (ALP), phosphatidic acid phosphatase-related gene (PAP) and ASR (abscisic acid, stress and ripening) like protein 2 (ASR-2) in TPD affected bark. However, putative MyB TF and translationally

controlled tumor protein (TCTP) were found down regulated. Besides, transcripts of genes *HbTOM20* (*Hevea brasiliensis* translocase of the outer mitochondrial membrane) and *HbTK* (*H. brasiliensis* thymidine kinase), a putative plant thymidine kinase were found significantly down regulated in TPD-affected trees when compared to healthy ones (Venkatachalam et al. 2009, 2010).

3.3.4.2 Stem Tapering

Narrowing of the stem or stem tapering is a common phenomenon in palms. In coconut plantations, it is commonly known as pencil point disease. Although there are no specific factors implicated to cause stem tapering in coconut, any condition that deprives water and nutrients to the growing meristem can cause this symptom. Therefore, associated factors can be drought, disease, pest, mineral deficiencies, inadequate drainage and competition from weeds or any combination thereof. Palms recover in full when the causal factors diminish, but symptoms already produced on trunks do not revert. Stem tapering is also common in palms that are transplanted or relocated. Since the tapered portion remains mechanically weak, wind damage is an associated risk with stem tapering (Ohler 1999).

3.3.5 Wounding

Wounds are common occurrence in biotic and abiotic stresses. Plant tissues are damaged in and around the site of wound, exposing underlying healthy tissues to pest and pathogen invasion. In a controlled experiment in cocoa using conidial suspension of *Verticillium dahliae*, it was demonstrated that stem puncture predisposes quicker pathogenic infection than soil application (Resende et al. 1995). Therefore, plants need to activate quick expression of defense during wounding. Wound healing is the primary response triggered, during which damaged cells die, turn necrotic due to the action of lytic enzymes and form a protective barrier. The superficial layers become lignified and suberized and cambial activity is accelerated. Wound healing is a stressful and energy expensive process, which falls outside the normal metabolism of plants. Moreover, the nature and duration of healing process depends on type and extent of wound (Thomas et al. 1995). Although natural wounding occurs in varying degrees throughout plants' lifespan, deliberate and continuous mechanical wounding causes perpetual stress in plantation crops like rubber and coconut. Wounding stress occurs in rubber while latex harvesting, whereas it occurs when palm wine is tapped from coconut palm. Agronomic practices such as plucking of tea buds and pruning of coffee can also develop wound related stress.

Wounding induces different types of signals in plants, targeted towards defense and healing process (de Bruxelles and Roberts 2001). Ethylene synthesis is found to occur in rubber in response to wound healing, wherein ACC oxidase (ACO) production is upregulated (Kuswanhadi et al. 2010). When Ethephon (2-Chloroethylphosphonic

acid), an ethylene releasing stimulant was applied, in a positive feedback mechanism, ethylene produced was found to enhance expression of genes in the ethylene biosynthesis itself. Further, among three ACO genes, *HbACO1*, *HbACO2* and *HbACO3*, basal levels of ethylene production appeared to be under the control of *HbACO1*, while *HbACO2* and *HbACO3* were responsible for the positive feedback mechanism and wounding response in leaves, but not in the latex. Whereas, a cysteine protease gene, *HbCP1* (*Hevea brasiliensis* cysteine protease) was induced in latex during wound healing, suggesting that *HbCP1* may be actively involved in protecting rubber plants against pathogen invasion and environmental stresses that involve ethylene signaling (Peng et al. 2008).

Studies using an isolated cDNA sequence of isoflavone reductase-like protein, namely *CaIRL*, from coffee (*C. arabica*) leaves showed that they encode for a novel type of phosphoinositide (PIP) family of NADPH-dependent reductases, which are known to be involved in biosynthesis of defense signaling molecules. Expression studies showed enhanced accumulation of these gene products in coffee leaves following mechanical wounding and fungal exposure (Brandalise et al. 2009).

Catechins are synthesized in tea, as an adaptive response to protect against tissue damage (Jaakola et al. 2002; Liu et al. 2006). During wounding, enhanced catechin production was found to occur mediated through the expressions of *Camellia sinensis* dihydroflavonol 4-reductase (*CsDFR*; Singh et al. 2009a), *Camellia sinensis* CoA ligase (*Cs4CL*; Singh et al. 2008; Rani et al. 2009), PAL enzymes (*CsPAL*) and cinnamate 4-hydroxylase (*CsC4H*) (Singh et al. 2009b). Harvesting of tea is done by plucking out of terminal bud with two internodes below it, which has meristematically most active cells. These cells have highest activity of N assimilation enzymes like cytosolic glutamine synthetase, *CsGS* (*Camellia sinensis* Glutamine synthetase; Rana et al. 2010), cell cycle proteins like histones, *CsH3* (Singh et al. 2009c) and ribosomal proteins like QM protein, *CsQM* (Singh et al. 2009d). Plucking process therefore, drains vital nutrients and compounds involved in growth and development and put tea plants into tremendous stress resulting in accumulation many stress related compounds.

Palm wine extraction from inflorescences of coconut and other palms also drains off vital nutrients, sugars and biochemical compounds. Palm tapping is a common practice in South and Southeast Asian and African countries. In coconut, although this practice adversely affects growth and production of palms, no systematic studies are available on stress effects of this traditional practice.

3.4 Management of Stresses

Stress management is a major imperative in production systems of plantation crops. In plantations, ultimate adaptability of a crop species may be associated with several interacting and interrelated factors, as well as their carryover effects. Therefore, unlike that of annuals, plantation species require counterbalancing mechanisms for more sustained stress management.

Sustainable adaptation to stress factors needs to be built-in the genotypes to tide over stress impact. External management can leverage the genetic adaptation potential so that the crops do not suffer beyond economic threshold. So stress management in plantation species needs primarily be genetic and then agronomic.

3.4.1 Crop Improvement

Crop improvement plays a vital role in enhancing stress adaptation potential of crops. Adaptive flexibility of genotypes not only can help in intensive and extensive cultivation but can aid in enduring unforeseen stresses also. For example, increasing the crop area under irrigation has several limitations such as unreliable rains and non-availability of perpetual irrigation, therefore, most feasible approach is to develop varieties that can sustain under limited moisture. These varieties have an added advantage to withstand unexpected moisture stress conditions in the field.

Being crops of perennial nature, focused attempt for breeding against stresses is seldom practiced in plantation crops because of limited genetic variability and long breeding cycle. Conventional breeding is highly cumbersome in plantation crops, because it involves many generations running for decades and expensive in terms of time, space and large volume of individuals handled. Except in case of palms, however, fixation of a superior individual identified at any stage of breeding is rather easy by vegetative propagation. Therefore, integrated breeding aimed at improvement of yield, quality and resistance, is the ideal approach in plantation crops. Notably, improved tolerance to abiotic stress must prove to be stable and inheritable unlike that against biotic stress wherein the tolerance breaks with the evolution of a new biotype. It is a challenge to plant breeders to generate crop plants that can stand, reproduce and set seeds in mild to moderate levels of abiotic stress, if not in extremes. The concern now is to consolidate these advancements in different crops and make further in-roads in raising the genetic level of stress tolerance. Notwithstanding, modern biotechnological tools promise of accelerated breeding to incorporate resistance through gene transformation, marker assisted introgression in many of the plantation crops.

3.4.1.1 Diversity and Genetics of Stress Resistance

In recently domesticated plantation crops like rubber, introduced genetic variation is relatively very limited when compared to wild progenitors. Furthermore, attempts to create of artificial variability by induced mutation and polyploidization has met only with limited success. Therefore, it is prudent to depend on natural diversity to target genetic adaptation to environmental constraints. There are several attempts to identify the genes and their control imparting resistance to various stress factors. While most of them are turned out to be polygenically controlled, there are few reports of monogenic and oligogenic inheritance as well.

The genus *Coffea* has about 90 species, with only two cultivated species, *C. arabica* (arabica) and *C. canephora* (robusta). *C. arabica* is a natural tetraploid, while *C. canephora* is a diploid (Chevalier 1948) with a lot of inter and intraspecific diversity among them. However, *C. arabica* has relatively low diversity when compared to *C. canephora* (Lashermes et al. 2000) and lack resistance to major diseases and pests. Low genetic diversity of *C. arabica* has been attributed to its allotetraploid origin, reproductive biology and evolution process (Etienne et al. 2002). *C. canephora* on the other hand, has wider adaptability to different agro-climatic conditions and show tolerance to leaf rust pathogen, *H. vastatrix*. Besides, *C. canephora* provides the main source of resistance to other disease and pest including CBD (*C. kahawae*), and root-knot nematode (*Meloidogyne* spp.). There are at least nine dominant genes (*SH1-SH9*) conferring resistance against leaf rust in coffee (Bettencourt and Rodrigues 1988). Of these genes *SH1*, *SH2*, *SH4* and *SH5* comes from *C. arabica*; *SH3* from *C. liberica*; and *SH6- SH9* from *Hibrido de Timor* (HDT, a spontaneous natural hybrid between *C. arabica* x *C. canephora*) derivatives (Rodrigues et al. 1975; Bettencourt and Rodrigues 1988). Moreover, *C. liberica* also provides resistance against leaf rust (Srinivasan and Narasimhaswamy 1975), while *C. racemosa* provides coffee leaf miner resistance (Filho et al. 1999). CBD resistance is complete in *C. canephora* and partial in *C. arabica*. Genetic studies on CBD resistance conclude that three major genes viz., *R*, *K* and *T* are responsible for resistance. Partial resistance observed in arabica and HDT derivatives were due to recessive nature of these genes at least at any one locus (van der Vossen and Walyaro 1980). Recent reports, however, suggests of oligogenic and quantitative resistance to CBD (Silva et al. 2006). Recently, a major dominant gene, *Ck-1* has been mapped for CBD resistance in *C. arabica* (Gichuru et al. 2008), which may perhaps be synonymous to the *T* locus. Inheritance studies on high-level resistance found in *C. canephora* against root-knot nematode, *Meloidogyne exigua* reveals that a simply inherited major gene, *Mex-1* (Noir et al. 2003), controls resistance.

The tea genus, *Camellia*, seems to be a genetically obscure one because of inconsistent and subtle genetic variation at species level and of genetic instability due to high out-breeding nature. The cultivated tea, *C. sinensis* and its progenitors have originated from Irrawaddy river basin in Myanmar extending between Southeast China and Assam in Northeast India (Eden 1976). Recorded diversity history shows that species count increased from 82 species in 1958 (Sealy 1958) to more than 325 species in 2000 (Mondal 2002). Presently, more than 600 varieties are under cultivation world over, of which some are unique in caffeine content and disease tolerance. Cultivated tea hybridizes well with wild relatives, creating a myriad of variants in tea genetic pool. One of the particularly interesting wild species is *C. irrawadiensis* whose morphological distribution overlaps with that of cultivated tea (Banerjee 1992) and a few desirable traits such as anthocyanin pigmentation and special quality characters of Darjeeling tea might have originated from these species (Wood and Barua 1958). It is widely accepted that three species i.e. *C. assamica*, *C. sinensis* and *C. irrawadiensis* have predominantly contributed to the cultivated gene pool of tea that includes progenies and the hybrids between them (Mondal et al. 2004). The information available on genetic resistance to various stresses in tea is rather limited.

Resistance to grey blight caused by *Pestalotiopsis longiseta* is high among *C. assamica* and two dominant genes, *Pl1* and *Pl2* are reported so far. The *Pl1* gene, imparts a higher level of resistance, and has an epistatic action with the *Pl2* gene, which has a moderate level of resistance (Takeda 2002, 2003). Besides, there are partial resistant sources to blister blight (Premkumar et al. 2008), anthracnose and cold damage (Takeda et al. 1987).

The genus *Hevea* to which rubber tree belongs has ten recognized species, of which *H. brasiliensis* alone is cultivated. Major world production of natural rubber takes place in its introduced home in the South and Southeast Asian countries because of a potentially devastating disease, SALB, in its native land. Therefore, rubber cultivation in Asia is virtually on a vulnerable threat from SALB because of two reasons, (a) the variability of the introduced genetic pool is very narrow and (b) no genetic resistance to SALB is available. Further, a little information is available with respect to genetics of resistance for other diseases of rubber. Various parameters indicative of possible resistance has been described in the case of SALB such as incubation time, latency, lesion size and number, sporulation, time taken for stromata to appear, and time from inoculation to leaf fall. Simmonds (1990) suggested that complete resistance to SALB was likely to be monogenic. However, no conclusive evidence on this claim is available so far. Possibility of combining durable resistance to SALB looks remote, as the pathogen can adapt so quickly to the host resistance, much faster than the development of a resistant combination (Rivano et al. 2010). Notwithstanding, it is reported that resistance to *Corynespora cassiicola* in rubber was articulated by two dominant genes *A* and *B*. Gene *A* is in epistatic interaction with *B* in which recessive form of *A* suppresses expression of *B* (Hadi et al. 2004). Le Guen et al. (2000) used isozyme marker based linkage mapping approach to map a qualitatively inherited dominant gene, *Phr* lying at 14.7 cM from the *adh* locus, conferring resistance to *Phyllachora huberi*, which causes black crust disease. Genotypic variations exist for tolerance to disease as well as environmental variations in rubber clones (Raj et al. 2005).

Among the palms, coconut is the only species in the genus *Cocos*. Although there are many genetic variants in cultivated coconuts, exact evolutionary relations between them are still obscure. Genetic studies on economic traits show quantitative inheritance, while there are only a few attempts to study genetics of disease resistance. Studies on complex diseases like lethal yellowing, root wilt etc. are particularly difficult because of the difficulty in effectively inducing diseases under controlled situations. However, there are many reports confirming genotype variability in resistance to most of the stress factors in coconut, with some varieties carrying exceptionally high level of resistance.

The genus *Eucalyptus* harbors high inter- and intraspecific genetic variability for resistance to stress factors. Variation in abiotic stress tolerance may extend from frost susceptibility to extreme frost tolerance as well as tolerance to drought. Besides, resistance to diseases enables adequate disease management by planting resistant clones, progenies or species. In *E. grandis*, a single dominant gene, *Ppr-1* (Junghans et al. 2003), governs resistance to rust pathogen, *Puccinia psidii*, while a general level of tolerance is exhibited to *Cylindrocladium* leaf blight.

3.4.1.2 Classical Approaches

Breeding for resistance to stress has not been a major breeding objective in plantation crops until the beginning of 20th century. However, stress resistance breeding has become a major objective in breeding most of these crops now, because of following reasons. Catastrophic events of crop destruction around the world due to various stress factors has led to better understanding of the biological events related to stress. Shrinking resources for cultivation and increasing demand for various plantation commodities had led to perpetuation of plantation crops to non-traditional regions. Further, better understanding of genetics of stress adaptation and modern tools in crop improvement has opened new avenues for crop improvement.

The utilization of vertical resistance (VR) in breeding for stress resistance especially for biotic stresses in annual and seasonal crops had been very successful, occasional disasters notwithstanding. However, in plantation crops that grow in nearly non-seasonal environments, effective use of VR is not an ideal option. This is because any attempt to use VR in these crops had resulted only in transient, non-durable resistance. The experiences shows that pyramiding of VR only helped in delaying in the development of new pathotypes a little. Further, introgression of VR genes from wild species would lead a breeder to a very low genetic purity level in respect of other characters, which would require several backcrosses and many decades of efforts for improvement.

Nevertheless, the use of horizontal resistance (HR) is promising as the only choice in plantation crops because HR is reasonably heritable in all these crops. Further, offspring produced between ideal parents are slightly more resistant than the parents are. Notwithstanding, directed selection for resistance is not only done individually, but done also at a particular location in overall, discarding unhealthy and susceptible genotypes, and selecting only resistant ones. This method of selection has been the most successful breeding strategy in plantation crops for stress resistance as it accumulates HR, albeit in congruence with yield and quality traits. For effective selection, however, pre-breeding is an essential necessity for developing best lineages and for accumulating favorable alleles in the breeding population.

In coffee, one of the main breeding objectives worldwide is to transfer disease resistance from diploid species such as *C. canephora* or *C. liberica* into cultivars of *C. arabica* without affecting coffee quality (Etienne et al. 2002). Several stages are involved in the improvement of *C. arabica*, of which the first stage is selection and testing of superior individuals. These superior individuals are seed propagated, and two cycles of selfing is done before testing the characters in each line for stability. Thereafter, superior lines are intercrossed, in double or multiple crossings, and selection is done from progenies for improved individuals with respect to resistance and allied traits. Backcrossing may produce varieties that are more superior. The best selections emerging out of the selection process are cloned for further multiplication and released for commercial cultivation. Robinson (1976) employed a crash-breeding program in Ethiopian coffee, by screening and selection for CBD resistance among naturally occurring variation in planter's crop. The seeds collected from the selections were grown and progeny tested for durability of resistance along with

yield and quality. This intense screening resulted in superior populations with balanced domestication in seven years. Clonal selection is the most important procedure followed in rubber breeding. Because of longer selection cycle and possibility of occurrence of multiple stresses, stress endurance is used as a selection parameter in rubber along with yield traits. Clones can be evolved at any stage of breeding. Selective hybridization of promising clones is further done either among themselves or with wild germplasm lines. The progenies are directly selected from seedling nurseries and cloned for further evaluation. Natural open pollinated half-sib populations are also screened for desirable characters including resistance. Susceptible and poor performing clones are normally discarded while selection. Polycross gardens comprising of pre-potent clones are also utilized and the selection is generally exercised in the polyclonal seedling orchards, even at maturity stage. In India, increased resistance to biotic and abiotic stresses has now been re-emphasized in rubber breeding and selection (Venkatachalam et al. 2006), in particular, for low temperature tolerance and resistance to *Corynespora* leaf fall disease. In the case of SALB, no durable resistance has been reported so far in rubber, although source of putative total resistance, characterized by absence of spores on leaves, are found in some wild clones of *H. brasiliensis* and in other species such as *H. benthamiana*, *H. guianensis*, *H. pauciflora* and *H. spruceana* (Simmonds 1990). Introduction of unexploited genetic variability from wild to augment narrowing genetic base of the cultivated gene pool was carried out by the International Rubber Research and Development Board (IRRDB) in 1981. An expedition, carried out in the Amazon basin spread across three districts of Acre, Rondonia and Mato Grosso of Brazil, collected 194 high yielding trees which were not affected by *Phytophthora* and SALB along with a total of 63768 seeds, 1413 meters of budwood and 1160 seedlings (Ong et al. 1983). These collections show continuous variation for SALB resistance in French Guyana (Clement-Damage et al. 1998) and for *Phytophthora* resistance in India (Mercy et al. 1995).

In tea breeding, mostly conventional approaches are being practiced (Chen et al. 2007), with yield and quality as the prime targets. Nevertheless, breeding for resistance against stress factors has received only little emphasis, because it has not been largely successful. Natural selection plays an important role in adaptation of tea clones to a set of stress factors by eliminating susceptible clones during early stages of multiplication. Since only tolerant clones survive, a well-buffered population survives under every geographical niche where tea is cultivated. Even if any related species is identified with a great degree of resistance to a particular stress, such species are not included in breeding programs because, most of the wild cross produce very inferior quality tea that is not acceptable (Bezbaruah 1987) and difficult to improve upon. Therefore, a compromise on quality with respect to resistance can be more economically devastating than the stress factor itself. Since available genetic base of cultivated tea is narrow, particularly with respect to quality, scope for further improvement for resistance within the available base remain limited (Willson 1999). Notwithstanding, breeding attempts for stress resistance have not been without any success. In Japan, distant hybridization of cultivated and 26 wild species, resulted in isolation of an interspecific hybrid, Chatsubaki (*C. sinensis* × *C. japonica*), with

high resistance to tea anthracnose, grey blight and low temperature besides having low caffeine content (Takeda et al. 1987). Chatsubaki is now used in regular tea breeding programs. In India, a high yielding standard tea variety has been developed by interspecific hybridizations involving *C. irrawadiensis*, *C. assamica* and *C. sinensis* (Bezbaruah 1987). Recently, it has been reported from China that one excellent new clone with high cup quality, resistant to disease, suitable for fine green tea and very early sprouting in the spring has been selected from the Cobalt-60 γ -ray irradiated offspring of Longjing 43 cuttings (Yang et al. 2003). This clone is undergoing adaptability tests and may become the first clone bred using induced mutagenesis in plantation crops (Chen et al. 2007).

As a crop of economic importance, at one time, coconut was considered neglected in terms of breeding and genetics (Harries and de Poerck 1971; Williams et al. 1975). Owing to various practical constraints in palm breeding, therefore, genetic improvement in coconut had made a slow progress. However, declining nut production and shrinking cultivation in the major production environments has restored the efforts for breeding for resistance in coconut recently. Further, widespread incidences of lethal yellowing in the Caribbean and Africa, cadang-cadang in the Philippines, root wilt disease and recent outbreak of eriophyid mites (*Aceria guerreronis*) in India have raised serious concerns, because most of these threats are beyond control by conventional plant protection measures. Although a long-term process, development of resistant/tolerant genotypes is the only practical solution to combat these stress factors.

In coconut, screening of exotic germplasm had resulted in identification of Malaysian dwarfs (yellow, red and green) tolerant to lethal yellowing in Jamaica in 1950s. These were recommended for planting on a large scale in Jamaica and Florida, only to be withdrawn sooner due to their susceptibility to many other climatic constraints. Nevertheless, this has led to the development of a resistant hybrid, Maypan, obtained from the cross Malaysian yellow dwarf (MYD) \times Panama tall (Harries and Romney 1974). Maypan could revive the Jamaican coconut industry largely, until it was massively destroyed by fresh outbreak of the disease (Broschat et al. 2002). Recent reports suggest genetic contamination among parents as the reason for loss of resistance (Lebrun et al. 2008), but other reasons like development of virulence in pathogen and/or vector and very narrow window of genetic variation among the cultivars cannot be ruled out (Baudouin et al. 2008).

In root wilt screening program in India, disease escapes are selected from 'hot spot' areas belonging to tall (T) as well as dwarf (D) types and serologically tested for the presence of phytoplasma. Disease free plants are then intermated in combinations of T \times T, T \times D, D \times T and D \times D. Seedlings raised from these crosses were understory planted in 'hot spots' to subject them for vigorous natural selection. Disease escapes were further tested serologically to ensure absence of root wilt pathogen. Some D \times T hybrids involving disease-free Chowghat green dwarf (CGD) palms and west coast tall (WCT) palms planted in 1991 remained disease free a long period (Nair et al. 2006). This program has now resulted in the development and release of two selections Kalparaksha (Nair et al. 2009) and Kalpasree and one hybrid Kalpa Sankara with field resistance/ tolerance to root (wilt) disease and yield potential.

3.4.1.3 In Vitro Approaches

In plantation crops, several tissue culture techniques such as somatic embryogenesis, meristem and axillary bud culture, induction of adventitious buds, androgenesis and protoplast culture are used for plant regeneration and micropropagation. One of the extreme advantages of a cell culture system is the facility for artificial screening of germplasm and mutant lines to identify stress tolerant genotypes, mutants and somaclonal variants those can augment accelerated breeding programs. Stress factors that are introduced in the culture media include increased salinity, pathogenic toxins, low nutrient content, heavy metal and induced water deficit. Regeneration of genetically engineered plants (transgenics) is yet another possibility under *in vitro* systems. Besides, micropropagation helps in developing disease free planting materials in plantation spices like cardamom (Babu et al. 1998).

In vitro selection

Most widely explored stress factor using *in vitro* systems in crop plants is salt tolerance. Cell culture systems offer several unique advantages in studying cellular level mechanisms and functions of salt tolerance and provide alternative methods for screening, selecting, and characterizing salt tolerance at the cellular level. Sodium chloride (NaCl) is the most frequently used salt for salt tolerance screening, although use of other salts and dilutions of seawater have been reported. Spontaneous variability generally appears in cell culture, sufficient to allow effective selection; use of mutagens such as ethyl methanesulfonate (EMS) and methyl methanesulfonate (MMS) helps to increase mutation frequencies. Selected salt tolerant cell lines are further evaluated to see if the tolerance remains stable after the cells had been moved to salt-free culture systems. There are several reports detailing mechanisms of salt tolerance as well as successful isolation of tolerant cell lines in many plantation species. In *Eucalyptus microtheca*, nodal segments cultured *in vitro*, showed varying degree of ion accumulation, with decreasing K^+/Na^+ ratio with increase in salinity, implying a simple way of *in vitro* screening than the cumbersome *in vivo* screening (Morabito et al. 1994). Pollen germination *in vitro* in the presence of elevated salt concentrations has been implicated as a reliable index of pollen tolerance to salinity in olive, a Mediterranean tree crop similar to tropical plantation crops. Further, a close correlation between pollen (gametophyte) tolerance and whole plant (sporophyte) responses to salinity was also found in olive (Soleimani et al. 2010).

Induction of artificial water deficit by incorporating polyethylene glycol (PEG-6000), mannitol and NaCl into *in vitro* culture of excised coconut embryos revealed that embryos from putative drought tolerant lines were able to withstand NaCl, but not PEG and mannitol (Karunaratne et al. 1991). The survival of embryos in high NaCl concentrations is perhaps indicative of the halophytic nature of coconut and it is assumed that same mechanism plays a role in drought tolerance as well.

Selection for disease resistance under *in vitro* systems is reported in coffee, oil palm, cardamom and date palm. Partially purified culture filtrate (PPCFs) containing

C. kahawae phytotoxins was used in varying concentrations for screening hypocotyl explants obtained from CBD resistant (HDT) and susceptible arabica (N39) genotypes, showed that calli from HDT showed rapid growth and no necrosis, while N39 calli had varying degree of necrosis and growth suppression. Selections from the surviving calli of N39 on regeneration had shown increased CBD resistance (Nyange et al. 1995). Dorcas et al. (2010) isolated basal rot resistant somaclones using PPCF of *Fusarium oxysporum* from a series of *in vitro* screenings in cardamom. They used somaclones derived from plants that withstood an initial pathogenicity test in the screen house. These somaclones were then cultured through a series on PPCF concentrations, selecting only those survived, until the selected lines survived undiluted PPCF. In date palm, pathotoxins such as fusaric, succinic, 3-phenyl lactic acids and their derivatives, marasmins and peptidic toxins as selective agents in cell culture are being used for isolating resistant lines against *Fusarium oxysporum* f. sp. *albedinis* that caused fusariosis wilt or bayoud (El Hadrami et al. 2005; El Modafar 2010).

Shoot cultures of *Eucalyptus camaldulensis* clones with different levels of salt tolerance were exposed to NaCl and ABA *in vitro* showed that proline accumulation increased significantly in all the clones. However, when the cultures were exposed to NaCl alone, resistant clones had significant high proline accumulation whereas in susceptible clones proline content remained unchanged (Woodward and Bennett 2005). Substantial accumulation of proline, polyamines (PA) and ABA occurs in plants during adaptation to various environmental stresses such as salinity, drought and high and low temperatures. Proline is a known osmoprotectant during drought stress in plants, and can serve as a nitrogen and carbon source during stress recovery process (Galiba 1994), and its accumulation is positively correlated to the salinity level or to the intensity of water stress (Heuer 1999). Elevation of endogenous ABA in response to cold treatment is hypothesized to induce synthesis of proteins that are responsible for the increase of frost hardiness (Chen et al. 1983). ABA dramatically increases freezing tolerance of the cells cultured *in vitro*, and enables cultured plant cells to survive freezing temperatures without previous cold treatment (Galiba et al. 1995).

Genetic Transformation

One of the remarkable achievements in plant cell culture is the opportunity to transfer genes across organisms through plant transformation employing somatic embryogenesis. Transgenic technology has now been tried in almost all cultivated species and is one of the remarkable technologies in the area of biotic stress management. The most successful event of genetic transformation in plants is transferring of *cry* (crystalline protein) genes from the soil bacterium, *Bacillus thuringiensis* (Bt) for imparting insect resistance. Although herbicide tolerance has also been achieved through transgenic technology, nevertheless, it is of little importance in plantation crops, except in the case of cardamom. Herbicide tolerance is incorporated in coffee and eucalyptus, primarily as selective agents during transgene development or as model transgenesis system rather than for agronomic use.

Agrobacterium tumefaciens mediated genetic transformation is widely used in plantation crops. Although *A. rhizogenes* and biolistic methods have been tried, the popularity of *A. tumefaciens* system is attributed to its simplicity and ease of generating transgenic derivatives. Coffee was among the early perennials in which successful transformation events for stress tolerance were reported. Transgenic coffee plants containing the *cryIA(c)* gene were produced using both *A. rhizogenes* (Leroy et al. 1997) and *A. tumefaciens* (Leroy et al. 2000) mediated transformation systems. The *cryIA(c)* gene encodes for an insecticidal crystal protein that is toxic to certain insects including the coffee minor, *Perileucoptera coffeella* (Filho et al. 1998). Transformed plants showed high degree of field tolerance to leaf miner in French Guyana (Perthuis et al. 2005). Other than coffee, successful regeneration of transgenic plants with augmented stress tolerance was reported rubber, oil palm, eucalyptus, cocoa and tea (Table 3.3). Successful incorporation of cowpea trypsin inhibitor (*cpTI*) gene (Abdullah et al. 2003; Ismail et al. 2010) and *Bt* gene (Lee et al. 2006) is reported recently towards achieving insect resistance in oil palm. Transgenic plants obtained are undergoing screening.

Whilst, most of the transformation attempts are targeted against pests, chitinases and antibody linked small chain variable fragment (scFv) genes are used for generating disease resistant transgenes. The scFv genes coding for antibodies specific to pathogenic toxins were recently demonstrated to be efficient against toxin producing pathogens like *Corynespora cassiicola* in rubber (Sunderasan et al. 2009). This provides opportunities to incorporate such genes in tissue transformation systems to incorporate resistance against pathogens. In oil palm, white rot pathogen, *Ganoderma boninense* establishes by destroying lignin fraction of woody tissues and exposing white cellulose, which fungus utilizes by causing rot. Resistance against *G. boninense* is being attempted through transfer of chitinase and ribosome inactivating protein (RIP) genes (Hashim et al. 2002). Lignin content has been genetically modified in plantation crops like eucalyptus, opening the possibility of attempting such systems in oil palm (Price et al. 2007; Paterson et al. 2009).

Transgenesis towards abiotic stress tolerance were reported in rubber against oxidative stress in which superoxide dismutase (*HbSOD*) gene (Jayashree et al. 2003) and Mn-superoxide dismutase (*Mn-SOD*) gene (Sobha et al. 2003) were successfully incorporated. Transgenic development to tackle abiotic stresses has also been attempted for freezing tolerance in eucalyptus (Zhang et al. 2010b) and for salinity tolerance in tea (IHBT 2006). In eucalyptus, cold hardiness is incorporated through a protein TF called C-repeat binding factor (CBF), such as *Eucalyptus gunnii* derived *EguCBF1a* and *EguCBF1b* (El Kayal et al. 2006). CBF are known to regulate expression of a number of genes conferring frost hardiness. Driven by cold inducible dehydrin promoters, CBF transgene expression occurred only during cold stress thereby improving freeze tolerance significantly without negatively influencing other agronomically important traits (Zhang et al. 2010a).

Therefore, outlook on transgenic development now focuses on genes that are expressed only 'in need' to tackle stress situations. For instance, if a constitutive promoter such as CaMV35S was used in eucalyptus transformation, CBF mediated negative impacts such as reduced growth, reduced leaf area and increased thickness

associated with a decrease in cell size, higher oil gland density and a wax deposition on the cuticle could have encountered in the transgenic plants (Navarro et al. 2011). Constitutive gene expression of a stress related transgene at non-target sites and at time of no stress can therefore be unavoidable. Further, this will effect in channeling of metabolic energy and accumulation of unnecessary proteins besides other adverse side effects. For that reason, a stress-inducible promoter would be ideal when the transgenic plants are targeted to deal with abiotic stresses (Zhang et al. 2000). Following the successful use of stress inducible promoters in eucalyptus, leaf specific promoters are being tested in coffee against leaf miners and leaf rust (Brandalise et al. 2009).

Haploid Recovery

Haploids and doubled haploids (DH) have been identified as a tool in crop breeding, because they aid in understanding genetic mechanisms of trait expression, including stress resistance. Notwithstanding, they provide opportunity to develop homozygous lines, those are useful as parental lines for hybrid development as well as in inducing mutations and transformations. DH lines are also used in linkage map development using various marker systems, and in mapping putative quantitative trait loci (QTL) linked to various agronomic traits. Harnessing of gametoclonal variants can be an additional benefit from cultured gametes.

In plantation crops, attempts to recover haploids from anther and ovule culture have been reported in coffee (Lashermes et al. 1994; Carneiro 1999), rubber (Cheng 1983), tea (Srivastava and Chaturvedi 2008), coconut (Perera et al. 2009) and date palm (Chaibi et al. 2002), although the success of plant regeneration in woody species was not encouraging (Peixe et al. 2004). Recently, isolation of spontaneous haploids and DH lines has been reported in oil palm, by high throughput screens of naturally occurring population (Dunwell et al. 2010). Although haploids and DH lines have not been greatly employed in developing stress resistant lines in plantation crops, they can still be useful auxiliary tools in studying genetics and development of new breeding lines in the future.

3.4.1.4 Molecular Breeding

Genetics of stress resistance in crop plants is relatively simple and is under regulatory control of fewer genes. However, adaptive genetic regulation for complex factors such as drought, which influences plant metabolism both in temporal and spatial dimensions, necessarily needs to be multigenic. Additionally, mutagenic stress factors such as UV radiation are capable of inducing adaptive mutations to the same stress that caused them. Since crop adaptation to various stress factors is as old as the crop itself, evolutionary lineages among resistance genes are a common feature, occurring across either species or genus. A great deal of biotechnological research is underway at identifying, mapping, isolating and transferring resistance genes in cultivated species, because of the power and versatility of molecular marker technology.

Table 3.3 Summary of transformation studies for stress tolerance in plantation species

| Crop | Species | Stress | Fungal pathogens | Target gene | Promoter | Transformation | Tissue system | Reference |
|-------------------------|-------------------------|---------------------------|------------------|--------------------|---------------------------|----------------|--------------------|------------------------------|
| Cocoa | <i>T. cacao</i> | Fungal pathogens | | TcChi1 | CaMV 35S (E12- Ω) | A. tumefaciens | Cotyledon explants | Maximova et al. (2003, 2006) |
| Coffee | <i>T. cacao</i> | Pod borer | | CryI/Ba, CryIIa | CaMV 35S | A. tumefaciens | Somatic embryos | Chaidamsari (2005) |
| | <i>C. arabica</i> | Herbicide – Chlorsulfuron | | Csr1-1 | CaMV 35S | A. tumefaciens | Leaf explants | Leroy et al. (2000) |
| | <i>C. arabica</i> | Leaf miner | | CryIAC | CaMV 35S | A. tumefaciens | Leaf explants | Leroy et al. (2000) |
| | <i>C. arabica</i> | Berry borer | | α -AII | PHA-L | Biolistic | Embryogenic calli | Barbosa et al. (2010) |
| | <i>C. canephora</i> | Leaf miner | | CryIAC | CaMV 35S | A. rhizogens | Leaf explants | Leroy et al. (1997) |
| | <i>C. canephora</i> | Herbicide – Chlorsulfuron | | Csr1-1 | CaMV 35S | A. rhizogens | Leaf explants | Leroy et al. (1997) |
| | <i>C. canephora</i> | Herbicide – Chlorsulfuron | | Csr1-1 | CaMV 35S | A. tumefaciens | Leaf explants | Leroy et al. (2000) |
| | <i>C. canephora</i> | Leaf miner | | CryIAC | CaMV 35S | A. tumefaciens | Leaf explants | Leroy et al. (2000) |
| | <i>C. canephora</i> | Herbicide – Glufosinate | | bar | CaMV 35S | Biolistic | Leaf explants | Ribas et al. (2006) |
| | <i>C. canephora</i> | Herbicide – Glufosinate | | bar | CaMV 35S | A. tumefaciens | Leaf explants | Ribas et al. (2006) |
| Eucalypt | <i>E. grandis</i> | Herbicide – Glyphosate | | ? | ? | A. tumefaciens | ? | Llewellyn (1999) |
| | <i>E. camaldulensis</i> | Leaf beetle | | Cry3A | CaMV 35S | A. tumefaciens | Cotyledon explants | Harcourt et al. (2000) |
| <i>E. camaldulensis</i> | | Herbicide – Glufosinate | | bar | CaMV 35S | A. tumefaciens | Cotyledon explants | Harcourt et al. (2000) |
| | <i>Eucalyptus</i> sp. | Freezing | | EguCBF1a, EguCBF1b | CaMV 35S | A. tumefaciens | Leaf explants | Navarro et al. (2011) |
| Oil palm | <i>Eucalyptus</i> sp. | Freezing | | CBF | Dehydrin | A. tumefaciens | Somatic explants | Zhang et al. (2010a) |
| | <i>E. guineensis</i> | Basal stem rot | | Chitinase | ? | ? | ? | Hashim et al. (2002) |
| | <i>E. guineensis</i> | Basal stem rot | | RIP | ? | ? | ? | Hashim et al. (2002) |
| | <i>E. guineensis</i> | Bagworm | | CpTI | ? | Biolistic | Immature embryos | Abdullah et al. (2003) |
| | <i>E. guineensis</i> | Insect | | CryIAb | Rubisco promoter | Biolistic | Immature embryos | Lee et al. (2006) |
| <i>E. guineensis</i> | | Herbicide – Glufosinate | | bar | Ubiquitin | A. tumefaciens | Embryogenic calli | Masli et al. (2009) |
| | <i>E. guineensis</i> | Insect | | CpTI | ACT1-5' | Biolistic | Embryogenic calli | Ismail et al. (2010) |

| | | | | | | | |
|-------------|------------------------|----------------|------------------|--------------|----------------|-----------------|-------------------------|
| Rubber tree | <i>H. brasiliensis</i> | Pathotoxins | scFv | CaMV 35S | A. tumefaciens | Somatic embryos | Yeang et al. (2002) |
| | <i>H. brasiliensis</i> | Oxidative | SOD (HbSOD) | CaMV 35S | A. tumefaciens | Anther derived | Jayashree et al. (2003) |
| | <i>H. brasiliensis</i> | Oxidative | SOD (Mn-SOD) | FMV 34S | A. tumefaciens | Anther derived | Sobha et al. (2003) |
| | <i>H. brasiliensis</i> | TPD | IPT | ipt promoter | A. tumefaciens | Somatic embryos | Kala et al. (2003) |
| | <i>H. brasiliensis</i> | TPD | SOD antisense | CaMV 35S | A. tumefaciens | Somatic embryos | Rekha et al. (2006) |
| | <i>H. brasiliensis</i> | Oxidative | SOD (CuZnSOD) | CaMV 35S | A. tumefaciens | Somatic embryos | Leclercq et al. (2007) |
| Tea | <i>C. sinensis</i> | Blister blight | Chitinase | ? | Biolistic | Somatic embryos | IHBT (2006) |
| | <i>C. sinensis</i> | Abiotic | Osmotin | ? | Biolistic | Somatic embryos | IHBT (2006) |
| | <i>C. sinensis</i> | Insect | CryIAc | ? | ? | ? | Mondal (2008) |

CaMV cauliflower mosaic virus, *FMV* Figwort Mosaic Virus, *PHA-L* phytohemagglutinin promoter, *SOD* superoxide dismutase, *bar* bialaphos resistance, *cry* crystal protein, *TcChil* *Theobroma cacao* Cass I chitinase, *Csr* Chlorsulfuron resistant, *CBF* C-repeat binding factor, *CpTI* cowpea trypsin inhibitor, *ACT1* actin promoter, *scFv* small chain variable fragment, α -*AI1* α -amylase inhibitor1, *IPT* isopentenyl transferase, *RIP* ribosome inactivating protein, ? no data available

Quantitative Trait Loci and Marker Assisted Selection

Inheritance pattern of molecular marker alleles between two contrasting individuals, which is visualized as differentiable banding patterns in their progenies, is the basis of molecular mapping in plants. Since many markers are found in close physical proximity to each other on a chromosome, generating a linkage map using marker segregation is rather easy. Further, by analyzing segregation pattern of markers with that of agronomic traits, putative associations between them can be estimated. Therefore, co-segregating markers with a trait should be linked to the genes responsible for the trait expression. Hence, marker can be linked to a qualitative gene (a major gene) as in the case of disease resistance or to a polygene (a quantitative trait locus, QTL) as in the case of quantitative traits. Presently, most widely used markers are microsatellites (simple sequence repeats, SSRs), candidate gene markers and more recently single nucleotide polymorphisms (SNPs). Many recent reviews detailing marker based linkage map development, QTL mapping and marker assisted selection (MAS) in plantation crops are available - Ceasheew (Cavalcanti and Wilkinson 2007; Paiva et al. 2009), cocoa (Figueira and Alemanno 2005; Bhattacharjee and Kumar 2007; Guiltinan et al. 2008), coconut (Hoher et al. 2005; Batugal et al. 2009), coffee (Lashermes and Anthony 2007; Lashermes et al. 2008), eucalyptus (Myburg et al. 2007; Grattapaglia 2008), oil palm (Rival and Parveez 2005; Price et al. 2007; Mayes et al. 2008; Sambanthamurthi et al. 2009; Billotte et al. 2010), rubber tree (Priyadarshan 2007; Priyadarshan et al. 2009) and tea (Tanaka and Taniguchi 2007; Kamunya et al. 2010).

In plantation crops, many QTLs are mapped for tolerance to various stresses (Table 3.4). Early successful QTL mapping for a stress tolerant trait was reported from interspecific hybrids of *Eucalyptus gunnii* and *E. globulus* for frost tolerance (Vaillancourt et al. 1995). They identified one random amplified polymorphic DNA (RAPD) marker linked to the trait that explained 18.5% of the phenotypic variation among interspecific F2 progenies. Subsequently, Byrne et al. (1997) identified two QTLs for frost tolerance that explained 7.7 to 10.8% of the phenotypic variation from a controlled bred family of *E. nitens*, using restriction fragment length polymorphism (RFLP) markers. QTLs related cuticular wax content has been mapped in coconut using interval mapping, on a fairly robust linkage map developed from a population between East African Tall (EAT) and Rennell Island Tall palms (Riedel et al. 2009). Since waxes are implicated in plant defense against abiotic stresses, this study offers a large number of markers useful for coconut breeding as well as having potential for oil palm and other related palm species.

In rubber tree, Lespinasse et al. (2000b) identified eight QTLs associated with SALB resistance from a F1 population, for which a dense linkage map was constructed earlier (Lespinasse et al. 2000a), by controlled inoculation of different strains of *M. ulei*. They mapped a large effect QTL on linkage group g13, which was subsequently remapped by Le Guen et al. (2003) as a major QTL (*M13-1bn*) for SALB resistance. This QTL explained 36 to 89% of the phenotypic variance for field resistance under natural conditions rather than under controlled inoculation.

Many QTLs were mapped in cocoa for resistance to black pod disease, followed by witches' broom and frosty pod diseases. Lanaud et al. (2009) carried out a meta-analysis of disease resistance QTLs by analyzing sixteen QTL experiments, and projected 76 QTLs detected on a progressively established consensus map. Several hot spots, with QTLs for resistance to different diseases, were observed. They identified thirteen consensus QTLs for *Phytophthora* resistance, six for witches' broom and five for frosty pod resistance, suggesting that these QTLs would be unambiguous choice for MAS programs (Goffinet and Gerber 2000). Although few QTL mapping studies have been reported in coconut, most of them were targeted to agronomic traits. A bulked segregant analysis (BSA) was carried out within three native coconut populations of lethal yellowing susceptible West African Tall (WAT), and two resistant populations of Malayan Yellow Dwarf (MYD) and Atlantic Tall (AT) palms to differentiate tolerant and susceptible palms using RAPD markers (Cardeña et al. 2003). Recently, Shalini et al. (2007) examined a native palm population differing in eriophyid mite tolerance, using simple sequence repeat (SSR) and RAPD markers, and reported marker-trait association for mite resistance. In date palm, presence of mitochondrial plasmids, designated as R and S were reported to be reliable molecular markers for resistance to vascular wilt (Bayoud disease) caused by the fungus *Fusarium oxysporum* f. sp. *albedinis* (Quenzar et al. 2001). However, recent report suggests that these molecular markers have failed to distinguish resistance and susceptible date palms (El Modafar 2010).

Discovering More Stress-Related Genes

Genes responsible for stress resistance can be identified by searching for genes that regulate key proteins and biochemical pathways responsible for proactive mechanisms. A more recent approach is to look for TFs that are part of signaling network, because they constitute the initially activated genes in response to stress. Publically available annotated crop specific gene databases are now developed in plantation crops (Table 3.5). Interestingly, observations from most of the crop plants show similarities in gene expression in response to stresses of similar kinds. Although plant response to stresses remains a complex multigenic event, number of genes isolated, cloned and characterized so far is scanty. Therefore, there is an urgent need to enrich the databases with novel stress responsive genes. With advances in functional genomics and microarray technology, having a complete gene expression profile of stress response is not remote (Zhang et al. 2000).

There are many unknown genes conferring biotic resistance in crop plants. These resistance (R) genes are found to have conserved sequence motifs shared between a variety of plants resistant to diverse pathogens (Richter and Ronald 2000). Using degenerate primers based on the conserved motifs, nine distinct classes of R gene like sequences have been identified in coffee (Noir et al. 2001). These sequences or resistant gene analogues (RGAs), represent substantial variability, and share closely related sequences (Etienne et al. 2002).

Table 3.4 Stress resistance associated quantitative trait loci and genomic regions mapped in plantation crops

| Crop | Stress | Population | QTLs | Marker | References |
|---------|------------------|---------------------------------------|------|-----------------|---------------------------------|
| Cashew | Black mould | CP 1001/CP 96 | 1 | AFLP, SSR | Cavalcanti and Wilkinson (2007) |
| | Black pod | UPA402/UJ676 | 2 | AFLP | Lanaud et al. (2000) |
| Cocoa | Black pod | Catongo/Pound 12 | 6 | RFLP | Crouzillat et al. (2000) |
| | Black pod | IMC57/Catongo | 3 | - | Motilal et al. (2000) |
| | Black pod | Na34/IMC60/IFC2, Na34/IMC60/IFC5 | 5 | AFLP | Flament et al. (2001) |
| | Black pod | Scavina/HI/IFC1 | 13 | AFLP | Risternucci et al. (2003) |
| | Black pod | DR1/Catongo, ICM78/Catongo | 1 | AFLP | Clement et al. (2003) |
| | Black pod | UPA402/UJ676 | 4 | SSR, RGA | Lanaud et al. (2004) |
| | Black pod | Pound 7/UJ273 | 3 | SSR, RGA | Brown et al. (2007) |
| | Witches' broom | Scavina6/ICS1 | 1 | AFLP | Queiroz et al. (2003) |
| | Witches' broom | Scavina6/ICS1 | 2 | SSR, RGA | Brown et al. (2005) |
| | Witches' broom | Scavina6/ICS1 | 1 | RAPD, AFLP, SSR | Faleiro et al. (2006) |
| Coconut | Frosty pod | Pound7/UJ273 | 5 | SSR, RGA | Brown et al. (2007) |
| | Lethal yellowing | WAT, MYD, AT | 5(?) | RAPD | Cardena et al. (2003) |
| | Mite | Local population | 5 | RAPD, SSR | Shalimi et al. (2007) |
| | Abiotic stress | East African Tall/Rennell Island Tall | 46 | AFLP, SSR | Riedel et al. (2009) |
| | Berry disease | Matari/S.288 | 21 | AFLP | Prakash et al. (2004) |
| Coffee | Berry disease | Matari/S.288, Matari/S.288/2* Matari | 10 | AFLP, SSR | Mahé et al. (2008) |
| | Berry disease | Caturra/DI200 | 7 | AFLP, SSR | Herrera et al. (2009) |
| | Berry disease | Hibrido de Timor/Catuai Amarelo | 3 | AFLP | de Brito et al. (2010) |
| | Berry disease | Caturra/DI200 | 5 | RGA | Romero et al. (2010) |

| | | | | | | |
|------------|-----------------|---------------------------------------------------------|--------------------------------|----------------------|--------------------------------|---------------------------|
| Eucalyptus | Frost | E. gunni/E. globulus | 1 | RAPD | Vaillancourt et al. (1995) | |
| | Frost | E. nitens | 2 | RFLP | Byrne et al. (1997) | |
| | Frost | E. globulus | 3(?) | RAPD | Fernández et al. (2006) | |
| | Leaf spot (MLD) | E. globulus | 2 | SSR | Freeman et al. (2008a) | |
| | Herbivory | E. nitens | 45 | RFLP, SSR, EST | Henery et al. (2007) | |
| | Herbivory | E. globulus | 3 | SSR | Freeman et al. (2008b) | |
| | Herbivory | E. globulus | 11 | AFLP, SSR | O'Reilly-Wapstra et al. (2010) | |
| | Puccinia rust | E. grandis | 1 | RAPD | Junghans et al. (2003) | |
| | Puccinia rust | E. grandis/E. tereticornis, E. grandis/E. camaldulensis | 2 | SSR | Mamani et al. (2010) | |
| | Rubber tree | SALB | H. brasiliensis/H. benthamiana | 9 | RFLP, AFLP, SSR, ISO | Lespinasse et al. (2000b) |
| | | SALB | H. brasiliensis/H. benthamiana | 6 | RFLP, AFLP, SSR, ISO | Le Guen et al. (2003) |
| SALB | | H. brasiliensis/H. benthamiana | 8 | RFLP, AFLP, SSR, ISO | Le Guen et al. (2007) | |
| Tea | Drought | TRFCA SFSI50/AHP S15/10 | 13 | AFLP, RAPD | Kamunya et al. (2010) | |
| | Nematode | TRFCA SFSI50/TRFK 303/577 | 1 | RAPD | Kamunya et al. (2010) | |

AFLP amplified fragment length polymorphism, *RAPD* random amplified polymorphic DNA, *RFLP* Restriction fragment length polymorphism, *SSR* simple sequence repeats; *IRAP* inter-retrotransposon amplified polymorphism, *RGA* resistant gene analogues, *EST* expressed sequence tags, *ISO* isozymes, *SCAR* sequence characterized amplified regions, *DArT* diversity array technology, *SALB* South American leaf blight, *MLD* *Mycosphaerella* leaf disease, *WAT* West African Tall, *MYD* Malaysian Yellow Dwarf, *AT* Atlantic Tall, *BSA* bulked segregant analysis, *IM* interval mapping, *SMA* single marker analysis, *SMRA* step-wise multiple regression analysis, ? data in conclusive

Table 3.5 Online databases on genomic resources of plantation crops

| Crop | DataBase name | Maintained by | Web address |
|-------------|---------------|------------------------------|-----------------------------------------------------------------------------------------------------------|
| Cardamom | NCBI | NCBI | http://www.ncbi.nlm.nih.gov |
| Cashew | NCBI | NCBI | http://www.ncbi.nlm.nih.gov |
| Cocoa | TropGENE DB | CIRAD | http://tropgenedb.cirad.fr/en/cocoa.html |
| | CocoaGenDB | CIRAD | http://cocoaendb.cirad.fr/ |
| Coconut | TropGENE DB | CIRAD | http://tropgenedb.cirad.fr/en/coconut.html |
| Coffee | TropGENE DB | CIRAD | http://tropgenedb.cirad.fr/en/coffee.html |
| | CoffeeDNA | University of Trieste, Italy | http://www.coffeedna.net/ |
| | MoccaDB | IRD | http://moccadb.mpl.ird.fr/ |
| Date plum | NCBI | NCBI | http://www.ncbi.nlm.nih.gov |
| Eucalyptus | TreeGenes | UCDAVIS | http://dendrome.ucdavis.edu/treegenes/ |
| Oil palm | TropGENE DB | CIRAD | http://tropgenedb.cirad.fr/en/oilpalm.html |
| | PalmGenes | MPOB | http://palmoilis.mpob.gov.my/palmgenes.html |
| Rubber tree | TropGENE DB | CIRAD | http://tropgenedb.cirad.fr/en/rubbertree.html |
| Tea | NCBI | NCBI | http://www.ncbi.nlm.nih.gov |

MPOB Malaysian Palm Oil Board, Selangor; *IRD* Institut de Recherche pour le Développement, Marseille; *UCDAVIS* University of California, Davis; *CIRAD* Centre de Coopération Internationale en Recherche Agronomique pour le Développement, Paris, *NCBI* National Center for Biotechnology Information, Maryland

3.4.2 Crop Management

Crop improvement is no panacea for stress management. For effective mitigation, improved cultivars need to be agronomically facilitated to cope up with the stress situation. For instance, tree survival can be increased by deep plowing or subsoiling before planting to improve aeration, and by soil fumigation, which destroys nematodes and fungi. Rational irrigation scheduling is a way of management of drought stress in irrigated plantation crops.

3.4.2.1 Plant Protection

Various methods are practiced to protect plants directly from drought, high temperature, sunlight exposure and wounding. In rubber, mulching prevents damage to the collar region in the nursery from sun scorch and prevents moisture lose from plant base. Placing shade baskets and plaited coconut leaves, or simply covering with hey or thatch grass around the stem is practiced generally to protect young plants in initial years of planting. When plants reach a height of more than one meter, lime washing of stem is done to protect the plants from sun scorch. If sun scorch, fire or lightning damage occurs, affected areas are carefully scrapped, cleaned and wound dressing compounds such as petroleum jelly or bitumen is

applied along with fungicides (Kothandaraman and Idicula 2000). Similar management systems prevail in crops like coffee, cocoa, tea (Whitmore 2000).

Detailed and recent comprehensive coverage of chemical and cultural methods of plant protection against diseases and pest is available for all plantation crops (Shanmugavelu et al. 2010; Nair 2010). A recent review on diseases of tropical perennial crops (Ploetz 2007) discusses on strategies and techniques in management of various diseases under diverse environments. Besides, individual crop compilations are also available dealing at length on many of these agronomic practices; cardamom (Ravindran and Madhusoodanan 2002), cashew (Ohler 1979), cocoa (Wood and Lass 2001), coconut (Thampan 1993), coffee (Wrigley 1988), date palm (ECSSR 2003), eucalyptus (Coppen 2002), oil palm (Hartley 1988), rubber (Webster and Baulkwill 1989) and tea (Eden 1976).

3.4.2.2 Biocontrol

Control of plant pathogens and pests using biological organisms has been accepted as a most natural and environment friendly alternative to the chemical treatments. Entomopathogenic agents such as bacteria and viruses as well as entomophagous agents and parasitoids have been used for the control of insect pests while hyperparasites and mycophagous agents have been employed in targeting pathogens in crop plants as supplementary modes to tackle biotic stresses (Shah and Pell 2003; Pell et al. 2010; Lundgren 2009). Details of many of the endophytic entomopathogens have been described in a recent review (Ownley et al. 2010). To a very limited extent, phytophagous agents are used in control of weeds.

Entomopathogens

Most widely tested entomopathogenic agents against lepidopteran and coleopteran pests are *Bacillus thuringiensis*, nuclear polyhedrosis virus (NPV) and fungi such as *Metarhizium anisopliae* and *Beauveria bassiana*. *M. anisopliae* is one of the first biocontrol agents to be used against insects (Sorokin 1883). Also popularly known as 'green fungi', use of *M. anisopliae* for controlling the larvae of coconut black beetle, *Oryctes rhinoceros* has been a popular practice in all coconut growing regions (Nirula et al. 1955; Fernando et al. 1994). Subsequently, *B. bassiana* was found effective against coconut weevil, *Pantorhytes plutus* (Prior et al. 1988) and the cocoa mirid bug, *Helopeltis theobromae* (Tong-Kwee et al. 1989). In Indonesia, both *M. anisopliae* var. *anisopliae* and *B. bassiana* were reported as promising natural enemies of *Brontispa longissima*, the coconut hispid beetle (Hosang et al. 2004). Many entomopathogenic fungi are now described (Vega 2007). A comprehensive review on entomopathogenic fungi for coffee berry borer has been provided by Vega et al. (2008). Bacterial isolates of *Pseudomonas alcaligenes* was found to cause septicemia in black beetle grubs (Gopal et al. 2002). In coconut, use of

entomopathogenic viral agents, such as *Oryctes* specific non-occluded virus resulted in large-scale suppression of black beetles (Bedford 1980; Mohan and Pillai 1993). In oil palm, control of a defoliating pest, *Latoia viridissima* (Lepidoptera: Limacodidae) was reported by spraying a picornavirus suspension (Fedière et al. 1990). Nakai (2009) has reported use of granuloviruses in control of two important tea pests, *Adoxophyes honmai* and *Homona magnanima* (Tortricidae: Lepidoptera).

Entomophagy

Predators and parasitoids of insect pests have been known for a long. In Indonesia, a pupal parasitoid, *Tetrastichus brontispae* (Hymenoptera: Eulophidae) of the coconut hispid beetle, *Brontispa longissima* was reported as one of the promising natural enemies in coconut (Hosang et al. 2004). Among the predatory mites on coconut eriophyid mite, *Aceria guerreronis*, the most frequently found species was *Neoseiulus baraki* (Acari: Phytoseiidae) (Fernando et al. 2003; de Moraes et al. 2004) in Sri Lanka. *N. baraki* has a flat and elongated idiosoma (de Moraes et al. 2004), that help these mites to creep into narrow spaces (Aratchige et al. 2007). Stylops or strepsipterans (Insecta: Strepsiptera) are endoparasites on other insects such as bees, wasps, leafhoppers, silverfish, and cockroaches (Whiting 2009). Many strepsipteran parasites have been reported in plantation pests. For example, *Halictophagus palmae* is a strepsipteran parasite on the plant hopper, *Proutista moesta*, a vector of many pathogens of coconut, oil palm and betel nut. Females of *Stichotrema dallatorreanum* parasites on the long-horned grasshoppers, *Segestes decoratus* and *Segestidea novaeguineae* (Orthoptera: Tettigoniidae), two severe pests of oil palm in Papua New Guinea. Similarly, *S. dallatorreanum* is used as a biocontrol agent against two grasshopper species that cause severe defoliation of oil palm, *Segestidea defoliaria defoliaria* in West New Britain and *S. gracilis gracilis* in New Ireland Provinces (Kathirithamby and Caudwell 2003). For biocontrol of coffee berry borer, three hymenopteran parasitoids, *Prorops nasuta*, *Cephalonomia stephanoderis* and *Phymastichus coffea* were introduced in many coffee producing countries (Espinoza et al. 2009). Recently, a species of predatory thrips, *Karnyothrips flavipes* (Thysanoptera: Phlaeothripidae) is reported from Kenya that were found feeding on coffee berry borer eggs and larvae (Jaramillo et al. 2010). Parasitoids against two common pests in tea plantations, *Adoxophyes honmai* and *Homona magnanima* has been reported from Japan (Nakai 2009). In eucalyptus, successful use of a parasitoid in minimizing the target pest population below economic threshold, resulting in total withdrawal of chemical use, was reported from California. The blue gum psyllid, *Ctenarytaina eucalypti*, a pest of *Eucalyptus pulverulenta* was successfully suppressed by the introduction of a parasitoid wasp, *Psyllaephagus pilosus* from Australia in 1992. By 1994, recommendation for chemical control of blue gum psyllid could be withdrawn owing to the establishment of parasitoid population throughout California (Dahlsten et al. 1998). Similarly, another wasp *P. bliteus* has been released to control spotted gum psyllid, *Eucalyptolyma maideni* (Dahlsten et al. 2003).

Hyperparasitism and mycophagy

Most widely used anti-pathogenic agents are *Trichoderma*, *Bacillus* and *Pseudomonas*. These have been established as useful biocontrol agents against *Ganoderma boninense* (Susanto et al. 2005), *Ceratocystis paradoxa* (Eziashi et al. 2006) in oil palm and coconut (Srinivasulu et al. 2008). Among *Trichoderma* species, *T. viride* (Bastos 1996) and *T. stromaticum* (Samuels et al. 2000) are identified as efficient epiphytic mycoparasites in controlling the witches' broom disease in cocoa. Antagonistic suppression on *Schizopyllum commune*, a soil borne pathogen in oil palm, using bacterial isolates of *Burkholderia cepacia* and *Serratia* sp. (Dikin et al. 2003) have been identified, suggesting the usefulness of these bacteria as biocontrol agents. In rubber, biological control of SALB pathogen using a hyperparasitic fungus, *Dicyma pulvinata* that colonizes ascostromata of *M. ulei* is reported (Mello et al. 2005, 2006; Melo et al. 2008). Kim et al. (2009) demonstrated antagonism of a phylloplane bacterial isolate of *Bacillus subtilis* against tea anthracnose pathogen, *Colletotrichum theae-sinensis*. Control of soil borne pathogens like *Pythium*, *Rhizoctonia* and *Phytophthora* using mycophagous soil fauna comprising of a nematode (*Aphelenchus avenae*), mite and a collembolan insect was reported recently (Taylor 2010). Further, microorganisms implicated in ISR including AMF are widely used as biocontrol agents.

Phytophagy and smothering

Although the use of phytophagous insects is seldom practiced in plantations, there had been attempts in the past to introduce some defoliating agents on noxious weeds. A project initiated by the CABI Bioscience (then Commonwealth Institute of Biological Control) in 1966, identified about 200 natural enemies of *Chromolaena odorata* (= *Eupatorium odoratum*), a common noxious weed in plantations. An arctiid moth, *Pareuchaetes pseudoinsulata* was one of the first natural feeders on *C. odorata* to be introduced in Asia and Africa; subsequently followed by other natural enemies (Muniappan and Bamba 2000). Attempts to identify and release of fungal pathogens as biocontrol agents to control another noxious weed in plantations, *Lantana camera* is detailed by Thomas and Ellison (2000).

Smothering of weed flora, by the use of fast growing beneficial plants as cover crops is a common practice in rubber, oil palm and cocoa plantations. In addition to weed suppression, these leguminous plants enrich soil by nitrogen fixation, add large quantities of biomass, conserve moisture and support many beneficial microflora. Most commonly used cover crops in rubber and oil palm plantations are *Peuraria phaseoloides* and *Mucuna bracteata*, while *Indigofera spicata* is grown widely in cocoa plantations. Other leguminous species used are creeping peanut (*Arachis pintoi*), *Calopogonium mucunoides*, *Centrosema pubescens*, *Macroptilium atropurpureum* and *Stylosanthes guianensis*. They are also grown in cashew and coconut plantations for their beneficial effects.

3.4.2.3 Agronomic Management

Agronomic management of plantation crops facilitates them to grow in most adequate environments, with optimal water and nutrient support, besides helping them to tide over stress situation greatly. Keeping up of soil health by addition of organic manures and mulches can help in the build-up of beneficial microflora, which helps in release of nutrients and suppress soil borne pathogens in the rhizosphere. In plantations and nurseries, providing windbreaks was often useful in preventing wind damage.

Cropping Systems

Selecting of cropping patterns based on the agro-ecological suitability is a very important proactive management strategy against stresses. In coffee, large scale planting of mixtures of coffee genotypes has been done as an effort to reduce anticipated infection by *Hemileia vastatrix* in Colombia (Ruiz et al. 1990). Region wise cropping recommendations are issued from time to time in all major rubber growing countries, which include proportional mixing of clones of different origin. In India, polyclonal (open pollinated seedlings collected from designated pre-potent clones grown together) gardens and use of polyclonal rootstocks are also recommended in extensive rubber culture to non-traditional regions.

Intercropping of more than one plantation crop is also practiced in India, China and Sri Lanka; such as rubber intercropped with banana, pineapple, medicinal plants, spices, vegetables, fodder crops, coffee, cocoa and tea (Punnoose et al. 2000). Three tier systems of rubber - coffee - pineapple are reported from China (Zheng and He 1991). In Ghana, a carefully designed intercropping system with coconut and cocoa was found mutually beneficial, with both crops showing better flowering, higher yield and without serious disease problems (Osei-Bonsu et al. 2002).

3.4.2.4 Soil and Plant Diagnosis

Soil and plant diagnosis are done to assess the nutrient deficiency and sufficiency, to evaluate crop quality and to assess stress effects. Although, the plant itself is the final proof of soil health in plantation species, plant analysis helps to predict the immediate crop nutrient requirements. A rationalization of fertilization may be beneficial in accordance with productivity-linked factors such as cultivation, growth and production. Plant nutrient analysis may be augmented with tests on soil pH, available nutrient status, elemental constitution and physical properties. Plant samples for analysis are collected according to the sampling methods described for each plantation crop (Table 3.6).

Foliar nutrient diagnosis must always be accompanied by soil analysis. Soil analyses require careful soil sampling with good judgment. It is better to collect soil samples annually (if required periodically) based on age, duration and rooting

Table 3.6 Plant tissue sampling techniques in plantation crops

| Crop | Growth stage/season | Plant part to sample | N ^a | Reference |
|------------|----------------------------------------|-------------------------------------------------------------------------------------------|----------------|--------------------------|
| Cardamom | Just before flowering | Fifth pair of leaves from panicle initiation tillers | 25 | Sadanandan et al. (2000) |
| Cocoa | 5–10 week old leaves | Third or fourth leaf of the last maturing flush | 30 | Pushparajah (1994) |
| Coconut | At the start of dry season | Leaf # 14 | 30 | Pushparajah (1994) |
| Coffee | Just before flowering | Third or fourth pairs of leaves from tips of fruit-bearing branches at mid-height of tree | 30 | Pushparajah (1994) |
| Oil palm | Before dry season | Leaf # 17 | 30 | Pushparajah (1994) |
| Rubber | 100 days after leaf formation | Basal leaves of top whorl of shoots of branches in shade of canopy | 30 | Pushparajah (1994) |
| Tea | Before the first harvest of the season | Third mature leaf from tip of the young shoot | 30–40 | Eden (1976) |
| Cashew | Just before flowering | Last fully matured leaf of the current season flush | 30 | Bhaskar et al. (1995) |
| Date palm | Late summer or early fall | 2–3ranks in the 'spiral of 13' from the top of the tree, 4–6 central leaflets | 10 | Krueger (2007) |
| Eucalyptus | First growing season | First fully expanded leaf | 20 | Shedley et al. (1995) |

^aN Number of plants to sample

pattern of the crops. Before sampling a field, its agricultural history, soil types etc. may be recorded. In plantation crops, a composite sample can represent up to 5 hectares in a field with apparent uniformity, else the field may be divided as per the judgment for taking composite samples.

Mitigation of Nutrient Toxicity

Although nutrient deficiency can be managed easily by supplementing the deficient nutrient, amelioration of nutrient toxicity is a formidable task. In plantation crops, excess quanta of essential nutrients are not known to create any problem, but that of supplementary elements can be problematic. Toxicity due to micronutrients, except Mo, can be corrected to a certain extent the addition of organic matter. This will help in bringing the soil pH to a level above 5.5 or to the optimum of 6.5. Application of green manures and growing cover crops can be sustainable practices that greatly reduce adverse effects of excess elements. Further, excess levels of Zn can be reduced by artificial inoculation of AMF into soil. However, excess B and Mo may require leaching with clean water, a difficult proposition to practice in plantation crops.

3.4.2.5 Remote Sensing

Technological advancements in space science and computation have extended applications in agriculture. One of the core applications is to assess plant stress caused by various biotic and abiotic stresses through analysis of spectroradiometry. Variations in spectral reflectance from crop canopy in response to stress can be easily detected and interpreted than by the field-based investigations. For this, aerial photography using multispectral imaging, thermal imaging or air-borne radar are used. Remote sensing has an added advantage of looking at a vast area, while comparing data between healthy and stressed crops all at the same time. Moreover, it can help in rapid and repetitive assessment of the extent of spread of drought, disease, pest, migration of locusts. In plant disease management, this new technique is called phytopathometry. Although application of remote sensing has varying success in agriculture, many potential and encouraging results are reported especially in the field of plant disease management (James and Barret 1989)

One of the pioneering demonstrations of the use of remote sensing technology in agriculture was reported in a plantation crop. In 1970, scientists from Indian Space Research Organization could identify root wilt affected coconut palms using aerial infrared photography (Dakshinamurti et al. 1971; Pisharoty 1972). They suggested that early detection of disease incidence could help in reducing crop loss by timely control measures. Remote sensed mapping and monitoring of disease incidence and damage assessment are reported in rubber. Successful plantation scale mapping of incidence and spread of leaf fall diseases caused by *Corynespora cassiicola* (Manju et al. 2001) and *Colletotrichum gloeosporioides* using satellite data during critical periods showed spread of the diseases throughout the South Canara region in India

with varying severity. Remote sensed data showed more than 90% agreement with the ground truth data. There was a significant reduction of near infrared, but an increase in red and short wave infrared reflectance in diseased plantations when compared to healthy, which helped in accurate measurements (Ranganath et al. 2004).

Remote sensing techniques have now been perfected in detecting physiological disturbances, caused by pests and parasites, by recording changes in foliar reflectance not perceivable by naked eye or near infrared photography. Using this technique, Nandris et al. (1985) could establish relationship between spectral reflectance and root disease in rubber. Spectral libraries for various leaf diseases and other stress factors are being developed for remote sensing applications in plantation crops. Further, using a ground-based handheld field spectroradiometer, spectral libraries of individual trees affected by diseases are also being developed in rubber (Jusoff et al. 2010).

3.4.2.6 Simulation and Modelling

In the modern era, computational advancements are being translated into practical predictions of abiotic and biotic stresses in plantation crops. These decision making systems, incorporate complex models evolved from multivariate relations of various parameters that define the stress reaction in plants. Simulation and modeling help in making predictions on the ensuing stress well in advance so that corrective measures can be initiated even before the onset of actual stress. Models incorporate various methodologies such as time series analysis, multivariate linear stepwise regressions, exponential computations and neural networks. Models are made in multidimensional patterns, either temporal, spatial or both. For instance, temporal development of adult population can be used to determine insecticide application timing, while spatial changes in the soil characteristics can be used to assess the dynamics of soil borne pathogens and pests such as root weevils and cockchafer beetles. In tea, drought sensitivity for individual clones could be predicted from a curvilinear yield reduction model related to advancing water deficit. This could help in determining appropriate time of drought sensitivity in each clone (Burgess and Carr 1996). Phenological models are used for accurate prediction of water requirement during dry periods as being done in rubber tree plantations (Guardiola-Claramonte et al. 2010). Nowadays, remotely sensed data on crop health, soil characteristics and weather parameters are being incorporated into modeling systems for improving precision of the forecasts.

3.5 Conclusions

Birth of the third millennium of the contemporary era, had witnessed dramatic advancements in scientific knowledge on stress biology of plants: genetics and breeding, physiology and biochemistry, molecular biology, genetic engineering,

bioinformatics, computational biology, nano-biotechnology, agrometeorology, agronomy, remote sensing and crop modeling. While plant physiology has provided new tools to understand complex network of stress related responses, a plethora of organic compounds have been identified in various biochemical pathways in stress related reactions. Advances in molecular genetics and breeding has led to the development of marker linkage frameworks of chromosomes, which enable tagging of genes on the crop genome, aiding selection and introgression of beneficial alleles based on marker segregation (Cattivelli et al. 2008). Automated methods for discovery of molecular markers and new technologies for high-throughput, low-cost molecular marker genotyping in plants have been developed. Genotyping methods include multiplexing of SSRs using Multiplex-Ready® marker technology (MRT); DArT genotyping; SNP genotyping using the Invader® assay, single base extension (SBE), oligonucleotide ligation assay (OLA) SNPlex™ system and Illumina GoldenGate™ and Infinium® methods. These techniques can be used in genetic linkage analysis, QTL mapping, diversity analysis, association mapping and marker-assisted selection (Appleby et al. 2008). Further, advances in molecular biology help in analyses of proteomes and transcriptomes of stress related gene expression by identifying the up and down regulated gene products; cloning of beneficial genes and development of transgenics. Bioinformatics has amassed voluminous genomic databases, which enable searching, comparing and recognizing genes across genomes and tools to manipulate genome information into marker sequences, gene constructs and single nucleotide polymorphisms. Still, use of these technologies need to be perfected in plantation crops to reap the benefits they promise. Development of most competent genotypes to tackle unknown threats of the future is the major challenge in plantation crops. Integration of scientific information accrued so far would leverage judicious use of technologies for the production of most competent genotypes that are environment friendly and conducive to agronomic management.

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