# Chapter 1
# Mechanisms and Adaptation of Plants to Environmental Stress: A Case of Woody Species

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## Contents

## 1  Introduction

Environmental stresses affect negatively plant growth, productivity, reproductive capacity, and survival. Their effects are predicted to become more pronounced in both duration and severity in the near future (Osakabe et al. 2012; Stella et al. 2013) partly, due to global climatic changes (Niinemets 2010).

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Among the total plant kingdom, woody plants and primarily forests greatly contribute to the world carbon biomass stock, biodiversity, and area protection (FAO 2011). Despite afforestation and natural expansion, the world's total forest area that corresponds to 31 % (3.8 billion ha) of the total land area exhibited an increasing reduction—according to the Global Forest Resources Assessment (FAO and JRC 2012) report—due to both anthropogenic and natural actions. The net annual forest loss increased significantly from 1990–2000 to 2000–2005 periods by 3.6 million ha (FAO and JRC 2012).

Environmental stress may result from abiotic factors including drought, salinity, extreme temperature, inadequate or excessive light conditions, ozone, pollution, and radioactivity. It can also be caused by biotic factors resulting from plant interaction with other organisms such as insects, fungi, bacteria, viruses, plant competition, and allelopathy. The occurrence of one abiotic stress may affect the plant functioning mechanisms through the induction of several interrelated changes at the morphological (Karakas et al. 2000; Vollenweider and Günthardt-Goerg 2005), anatomical (Bosabalidis and Kofidis 2002; Chartzoulakis et al. 2002a; Lesniewska et al. 2004; Fortescue and Turner 2005; Junghans et al. 2006; Chelli-Chaabouni et al. 2010; Ennajeh et al. 2010), physiological (Meena et al. 2003; Junghans et al. 2006; Rejsková et al. 2007), and biochemical levels (Kozlowski 1997; Chelli-Chaabouni et al. 2010; Krasensky and Jonak 2012). However, the effect of extra-optimal environmental factors on plant growth and development is not necessarily harmful. Speed at which the stressful factor installs as well as the intensity and duration of stress determines the beneficial or injuring effect of stress. Hence, the gradual physiological adjustments induced by the slow increase of stress may protect plants from inhibition of growth and/or injury resulting from suddenly imposed stress (Kozlowski and Pallardy 2002).

Woody plants are perennial plants (usually trees, shrubs, or lianas) that are predominately characterized by the production of secondary tissues in stems and roots. In these latter organs, wood is formed, year after year throughout ontogeny, in superposed layers from secondary xylem leading to the reinforcement of the tissue structures. As woody plants have long-lasting biological cycle, they would have to support stress for a long period of time. Therefore, they have evolved specific mechanisms to overcome detrimental injuries resulting from environmental stresses. The situation is more complicated when multiple stresses occur. The mechanisms adopted against one stress factor are not necessarily similar to those evolved to counteract multiple stresses. Plant response may differ when two or more stresses occur successively or simultaneously.

The specificity of woody plants such as longevity and size makes their use in experimental research studies much more complicated and hard but very informative and worthwhile. Most experimental studies on woody plants are performed on seedlings and young trees. However, plant behavior against environmental stresses may significantly differ throughout the successive developmental stages namely germination and both juvenile and adult stages (Ceulemans and Mousseau 1994; Stamp 2003; Boege and Marquis 2005).

As the effects of environmental stresses are well described in the previous sections, this chapter will make only a brief description on the way that various

environmental factors affect woody species. We will emphasize on the specific adaptation and resistance of woody plants to extra-optimal conditions and the current methods adopted to assess stress tolerance/resistance.

## 2 Plant Responses to Environmental Stresses

When subjected to environmental stresses including drought, salinity, frost, and herbivory attacks, woody plants need to reallocate energy in a way allowing stress adaptation (Skirycz and Inzé 2010) but also to maintain growth and productivity. These latter functions are closely related to water movements within the plant which are supported by vascular tissues (Osakabe et al. 2012). Plant controls gaseous exchanges and water loss mainly by the regulation of stomatal movements (Fini et al. 2013; Sapeta et al. 2013). To reach these vital objectives, plant responds by the activation of many metabolic processes controlling photosynthesis, ion homeostasis, and plant hormone signaling that may alter gene expression. These reactions are usually expressed at both phenotypic and genotypic levels.

### 2.1 Abiotic Stresses

Abiotic stresses may be defined as nonliving factors affecting growth and productivity of living organisms. They may be divided into two main categories: (1) physical stressful factors including drought, flooding, extreme temperature, and inadequate light quality or intensity; and (2) chemical stressful factors including salinity, ozone, elevated $CO_2$ level, and heavy metal pollution. Plants respond to abiotic stresses through morphological and anatomical symptoms concerning leaves, stems, and roots.

Drought, salinity, and cold are among the major abiotic stresses that cause serious problems to woody plants (Krasensky and Jonak 2012) including low water and nutrient availability, toxic concentrations of salt ions such as sodium (Na) and chlorides (Cl), and may lead to Ca deficiency (Marschner 1995). Apart from low water availability, an excess of water in the soil induces flooding stress for woody plants. The lack of oxygen resulting from root submersion induces physiological (Polacik and Maricle 2013) and metabolic changes that can be expressed through plant injury, changes of plant anatomy, inhibition of seed germination, decrease of vegetative and reproductive growths, early senescence, and even mortality (Kozlowski 1997; Glenz et al. 2008). Environmental pollution mainly results from widespread urbanization, industrialization, and agriculture intensification increased exponentially in a way making several pollutants reaching toxic levels for vegetation. Investigations on woody plant responses to phytotoxic levels of environmental pollutants have gained an interest since the early seventeenths. Due to the important extent of forests in space and duration ecosystems, particular interest on the impact of phytotoxic factors on forest trees increased. Short ultraviolet wavelength

radiations (UV-B) increased due to the depletion of stratospheric ozone ($O_3$) caused by gaseous pollutants, leading, to some extent, to an ecological imbalance and global climatic changes. A 3 years field study on *Pinus taeda* seedlings demonstrated the cumulative inhibitory effect of elevated UV-B on plant growth (Sullivan and Teramura 1992).

Heavy metal concentrations increased at promising toxic levels in the last few years (Sainger et al. 2011). Apart from the direct effect of heavy metals on woody plant growth and survival (Fernández et al. 2013), their effects on soil animals and microorganisms may indirectly decrease organic mineralization (nitrogen and phosphorous mineralization) and subsequently limit nutrient availability to plants (Tyler 1984).

Many morphological and anatomical changes occur in leaves, as they are an important site of photosynthesis and biochemical reactions including defensive mechanisms. Several stresses including drought, salinity, and high light intensity may cause leaf injury varying from chlorosis (Rochdi et al. 2005) to total leaf necrosis (Chelli-Chaabouni et al. 2010). Marginal leaf scorch was associated with sodium accumulation in salt-stressed peach (Karakas et al. 2000). Salt stress may affect cell elongation and expansion inducing a reduction of leaf area (Curtis and Läuchli 1987; Abbruzzese et al. 2009). It affects stomatal characteristics such as stomata density and guard cell length which reflects to stomatal conductance and hydraulic status of the plant (Abbruzzese et al. 2009).

Abiotic stresses could cause severe injuries to woody plant stems. Mechanical effects of strong winds may break twigs and provoke flower bud falls. Epidermis of newly formed shoots may be burned by high solar radiations that occur for a relatively long period of time. At an anatomical level, a reduction of xylem differentiation under salt stress leads to a decrease of vessel lamina due to low nutrient supply to the cambium and low potassium ion ($K^+$) content in the shoots of salt-sensitive poplar species (Escalante-Pérez et al. 2009).

Roots are affected by abiotic stresses in many ways. Drought and salinity induce a reduction of root system biomass through an increase in root length and width. Cotton seedlings growing in hydroponic salt solution produced less and thinner roots with increasing salinity. Root anatomical analysis showed shorter and more nearly iso-diametrical cortical cells than those of control plants (Kurth et al. 1986). Salt stress may lead to root lignifications in pistachio (Walker et al. 1987). Under soil anaerobiosis conditions (waterlogging or flooding), roots suffer from asphyxia before final death (Kozlowski and Pallardy 2002).

Fruits are also affected by many abiotic stresses either directly or indirectly under climatic conditions favoring pathogen proliferation and growth. Strong or sandy winds and hail falling may be harmful to the fruits especially at the maturation stages. In early stages of fruit development, non-optimal temperatures may affect fruit formation and growth. The ovule of banana tree (*Musa* species) affected by sustained tow temperature before anthesis showed many changes (size reduction, low growth, and more rounded shape) in comparison with unaffected ones (Fortescue and Turner 2005).

Plant growth and productivity may be affected by abiotic stresses such as drought (Picchioni et al. 1990; Ramoliya et al. 2004), salinity (Chelli-Chaabouni et al. 2010;

Akça and Samsunlu 2012), and flooding (Kozlowski and Pallardy 2002; Capon et al. 2009; Glenz et al. 2008). Growth is either inhibited or stimulated according to the nature, severity, and duration of stress. Environmental stresses that induce water and nutrient deficiency affect leaf regeneration and growth by the reduction of new formed leaves and the decrease of leaf area. Plant increases photosynthate allocation to the roots in expense of shoots.

In mature woody plants, the negative correlation between vegetative and reproductive growths (Kozlowski and Pallardy 2002) plays a major role under moderate stress conditions. The vegetative stage of development at which drought occurs is determinant in further growth response. A short period of water deficit may induce stimulation of reproductive growth through flower bud formation, break of flower bud dormancy, and flowering according to the time at which stress happens (Kozlowski and Pallardy 2002). Stimulation of reproductive growth may occur simultaneously with vegetative growth inhibition.

The disruption of stomatal conductance by stress affects directly gaseous exchanges that are mainly related to photosynthesis ($CO_2$) and photorespiration ($O_2$). Various stresses such as drought (Angelopoulos et al. 1996; Flexas and Medrano 2001; Faraloni et al. 2011; Fini et al. 2013), salinity (Walker et al. 1988; Chartzoulakis et al. 2002b; Tabatabaei 2006; Abbruzzese et al. 2009), flooding (Glenz et al. 2006; Polacik and Maricle 2013), and sub- (Costa e Silva et al. 2008) or supraoptimal temperatures (Kozlowski and Pallardy 2002) may affect photosynthesis. Plants control transpiration through early stomatal closure to diminish water loss and enhance water use efficiency. The leaf water status affects photosynthesis through the efficiency of the photosystem II (PSII) activity (Fini et al. 2013). For instance, the olive cultivars that maintained high relative water content (RWC) under water deficit conditions sustained a high chlorophyll fluorescence ratio $F_v/F_m$ and showed less injury to PSII performance (Faraloni et al. 2011). Sublethal high temperatures may inhibit photosynthesis and cause membrane injury and protein aggregation and denaturation (Kozlowski and Pallardy 2002). In leaves of poplar, drought induced changes in photosynthetic reactions through a decrease of rubisco content and the changes of light-related and membrane-related proteins (Durand et al. 2011). The progressive decline of carbon assimilation under stress may result from both stomatal and metabolic limitations (Angelopoulos et al. 1996; Flexas and Medrano 2001). Under severe water stress the decrease of non-stomatal component of photosynthesis in olive trees was thought to be due to light-dependent inactivation of the primary photochemistry related to PSII (Angelopoulos et al. 1996). Photosynthetic metabolisms including ribulose 1,5-biphosphate (RuBP) regeneration capacity, adenosine triphosphate (ATP) synthesis, and ribulose 1,5-biphosphate carboxylase/oxidase (Rubisco) activity could be disturbed (Flexas and Medrano 2001). At the onset of flooding in greenhouse experimental conditions, photosynthesis of *Tamarix ramosissima* decreased by non-stomatal limitations while oxygen stress increased (Polacik and Maricle 2013).

The biochemical and enzymatic activities of woody plants may change under stressful conditions. They include antioxidant activities (Zhang et al. 2013), lipid peroxidation (Fernández et al. 2013), proline and glycine-bétaine-metabolizing system (Ahmad et al. 2010), and cellulose biosynthesis (Zhong and Läuchli 1988; Delmer

and Armor 1995). Low temperatures induce changes in the concentrations of hormones and metabolites such as sugar and protective proteins and cause alterations in gene expression (Zhu et al. 2007).

Stomatal closure due to many abiotic stresses (including drought, salinity, high light, extra-optimal temperatures, and pathogen attacks) leads to a reduction of assimilation rate and the production of reactive oxygen species (ROS) that are responsible of oxidative stress (Osakabe et al. 2012). ROS are highly destructive to lipids, nucleic acids, and proteins (Türkan and Demiral 2009) and have been shown as important second messengers for stress signal transduction pathways. ROS may affect the cellular activity of the plant through molecular, functional, and structural alterations such as protein, DNA, and lipid oxidative damages (Apel and Hirt 2004). Plant exposure to low temperature may cause mild oxidative stress that show many similarities with plant response to water deficits (Costa e Silva et al. 2008).

## 2.2   Biotic Stresses

Many reports describe the close relationship between plant biotic stresses resulting from pests and diseases and abiotic environmental conditions (Shoeneweiss 1981; Luther et al. 1997). The proliferation of insects, bacteria, fungus, and viruses in woody plants depends on climatic and soil conditions in natural habits but also on orchard management systems of cultivated trees and shrubs (Valdés-Gómez et al. 2011) such as a large amount of coarse woody debris in managed forests that may host an important source of pathogens influencing the stability of forest stands (Santini et al. 2008). Apart from their direct effects, the physico-chemical characteristics of the surrounding environment may have an indirect impact on the plant-parasite biological development and proliferation through their interactions with other insects, fungi, or bacteria. The inter- and intraspecific interactions (symbiotic, parasitic, and synergetic) between these organisms determine the level of stress severity.

The severity of pathogen attacks is also associated to host plant physiology and anatomy (Pérez-Contreras et al. 2008; Rieske and Dillaway 2008; Inbar 2011). The host shifting is a specific trait of phytophagous insects such as aphides and lepidoptera. For examples, aphids of *Pistacia* species assess plant chemical, anatomical, physiological, and structural traits before choosing the adequate host plant (Inbar 2011). Herbivore-induced extensive defoliation of oak forests was correlated with depressed C/N ratio and elevated foliar nitrogen (Rieske and Dillaway 2008). Two main hypotheses are suggested to explain herbivore host plant selection strategy. The "plant-stress hypothesis," mainly adopted by generalist herbivores, states that stressed plants are less able to synthesize defensive chemicals to resist insect attacks and are then more vulnerable (White 1969). The "plant-vigour hypothesis" states that herbivore is indifferent to the level of plant defense and prefers feeding on healthy and vigorous plants (Price 1991). This latter hypothesis is likely preferred by specialist herbivores. However, both main hypotheses may explain plant

selection by herbivores for depositing of eggs namely oviposition (Pérez-Contreras et al. 2008).

Biotic stresses affect plant growth through a reduction of photosynthesis (Christen et al. 2007; Bilgin et al. 2010). Bilgin et al. (2010) attempted to understand how do various biotic stresses (including arthropods, fungi, bacteria, and viruses) affect plant photosynthesis activity at a genetic level. They compared transcriptome data from microarray experiments after 22 different forms of biotic damage on eight plant species. Results revealed that regardless of the nature of biotic factor, transcript levels related to photosynthetic activity decreased. The photosynthetic gene down-regulation was accompanied by an up-regulation of genes coding for synthesis of jasmonic acid and those involved in the responses to salicylic acid and ethylene. Authors suggested that these reactions may be a part of defense mechanism.

In natural ecosystems, woody plants may compete with other woody or herbaceous species for resources in different ways such as the large and deep root invasion of the rhizosphere (Schenk 2006) for water and nutrient uptake, the increase of plant height to enhance light availability (Sterck and Bongers 2001), and the release of chemicals namely allelopathy that inhibit or stimulate growth and survival of the neighboring plant and microorganism species (Maclaren 1983). In some cases, different strategies may explain the inter- and intraspecific plant interactions (Inderjit and Mallik 2002). The plant's release of allelo-chemical products may have several effects on individual neighboring plants and, consequently, on organism ecosystem distribution. At the individual plant level, these products may affect the seed germination ability (Blanco 2007), plant growth (Lodhi 1976), physiology (e.g., respiration, photosynthesis, and hormonal and enzymatic processes), the cellular functioning system (e.g., membrane permeability, chloroplast activity, and chlorophyll concentration), the water and nutrient uptake, and transport.

## 3  Multiple Stresses: Occurrence and Interaction

The occurrence of only one stress at the same time in the field or in the natural conditions is seldom rare. Often, two or more stresses are simultaneously or successively associated. For example, drought stress is closely related to high temperature and luminosity in hot climate arid and semiarid areas. Plants respond to multiple stresses by the activation of one specific mechanism (Rizhsky et al. 2004) through the activation of numerous biochemical and molecular reactions (Osakabe et al. 2012; Perdiguero et al. 2013). The multiple stress combination may lead to a modification in the plant stress susceptibility. The occurrence of one environmental stress may indispose or predispose plant to a second stress. At the genetic level, the over-expression of genes to adapt to a given stress may incur tradeoffs for acclimation to other stresses (Lynch and St Clair 2004). For example, the increase of plant transpiration resulting from pollutants such as sulfur dioxide ($SO_2$) may expose plant to drought stress (Shoeneweiss 1981). Inversely, stomatal closure in response to many abiotic stresses including drought, flooding, and low atmospheric

humidity may lead to higher tolerance to air pollutants (Kozlowski and Pallardy 2002). Similarly, elevated atmospheric $CO_2$ due to global climatic changes may alleviate oxidative stress (drought and salinity) and enhance plant tolerance through the availability of more energy that can be allocated to defensive mechanisms (Kyoro et al. 2012).

In the particular case of biotic and abiotic stresses association, the occurrence of an abiotic stress can enhance or reduce plant resistance to a pest or pathogen and vice versa (Atkinson and Urwin 2012). Abiotic stresses such as water deficit, salinity, freezing, or heavy metal pollution may weaken plants and make them more vulnerable to the attack of some pests and diseases (Shoeneweiss 1981). For forest stands, this vulnerability may be extended to ecosystem level as reported by Luther et al. (1997) in the case of insect defoliation of balsam fir stands. Under abiotic stress, the normal carbon allocation patterns may be deviated in a way making higher carbohydrate allocation to the root and leaves in favor of carbohydrates left for carbon reserve and defense compound biosynthesis (Luther et al. 1997). At a molecular level, the metabolic signaling pathways of such stress combinations can act antagonistically (Anderson et al. 2004). In light of this, studying plant stress tolerance by imposing each stress individually may not reflect the exact plant response in the field (Mittler and Blumwald 2010).

## 4   Plant Response to Stress Throughout Ontogeny

Several structural (Loney et al. 2006), physiological, and biochemical (Loney et al. 2006; Juvany et al. 2013) changes occur during plant development. As woody plants develop, they show usually an increase in carbon/nutrient balance and carbon storage capacity (Niinemets 2010) as well as greater accessibility to water, nutrients, and sunlight but also a decrease in growth rate, root/shoot ratio, photosynthesis, stomatal conductance, and metabolic activities (Boege 2005). The tree responses to stress vary throughout the ontogeny (Niinemets 2010) in relation with age-related changes of physiological and biochemical processes controlling carbon assimilation and storage, growth rate, and defensive mechanisms. Compared to seedlings and saplings, many reports described greater resistance of large non-senescent trees to abiotic (Kozlowski 1997; Cavender-Bares and Bazzaz 2000; Rozas et al. 2009) and biotic stresses (Basey et al. 1988; Luther et al. 1997). However, regarding plant resistance to herbivore stresses, both positive (Loney et al. 2006) and negative (Schappert and Shore 2000) relationships between ontogeny and resistance were reported for several woody species (Boege and Marquis 2005). During plant development, Boege and Marquis (2005) proposed a pattern of changes in plant defense and tolerance during ontogeny based on the assumption that plant resources may act as a constraining trait of tolerance and resistance of vegetative tissues. Armas and Pugnaire (2009) findings support this statement as the interaction of the two dominant shrub species *Pistacia lentiscus* and *Juniperus phoenicea* did not benefit any species at seedling stage but when plants became progressively mature, *Pistacia* species

gained competitive growth and survival advantage. It should be emphasized that ontogeny has an effect not only on the ability of plant to respond to a given stress but also on the growth recovery after the disappearance of stress (Boege 2005).

At a seedling stage, plants may produce defensive compounds to resist herbivory attacks (Schappert and Shore 2000), but as the plants gain in maturity, the biochemical protective strategy decreases progressively while many protective structural changes (greater leaf thickness, higher lignin and fiber content) occur (Loney et al. 2006). The decrease of plant defensive biochemical synthesis with age was suggested as the result of natural selection based on the reallocation of energy according to the cost/benefit ratio. Plants maximize the production of protective chemicals at developmental stages of great risk of herbivore attack or low tolerance (Schappert and Shore 2000; Stamp 2003).

## 5    Influence of Biomes on Stress Occurrence and Severity

The severity and timing of stresses vary throughout the growing season according to the nature of a given ecosystem as illustrated by Niinemets (2010). For example, in cool temperate ecosystems, the plant tolerance to frost stress is lower during the early winter period corresponding to the plant dormancy; plants are more susceptible in middle and late winter when temperature becomes progressively warmer (Ögren 1996). In the Mediterranean environments, long-lasting supraoptimal temperatures and light are among the major factors of stress (Angelopoulos et al. 1996). In these areas, plants are exposed to drought and photo-inhibition (Guàrdia et al. 2012) but the severity of stress differs from coastal to high altitudes (Flexas et al. 2001; Yang and Miao 2010). Under progressive drought stress *P. kangdingensis*, originating from higher altitude, displayed superior height growth and leaf development as well as greater increments in soluble proteins, soluble sugars, free proline, and antioxidant enzyme synthesis than *P. cathayana* that grows in lower altitude (Yang and Miao 2010). However, even in Mediterranean areas, woody plants may be subjected to episodic low temperature events (below 0 °C) that limit expansion of species such as *Eucalyptus globulus* (Costa e Silva et al. 2008).

Differing from Mediterranean and cool temperate forest ecosystems, the temperate bogs are subjected to chronic nutrient deficiency and waterlogging (Niinemets 2010).

Climate is an important factor that influences and modulates ecosystem composition and scope. Increasing temperatures may lead some species to move to higher altitudes that are suitable for their growth and development. Increasing plant competition for water and nutrients in arid and semiarid biomes may lead to a dominance of the most adapted species at the expense of species showing lower stress tolerance (Armas and Pugnaire 2009; Eilts and Huxman 2013). Moreover, plant response and susceptibility to various biotic stresses may be affected by the biome (Slippers and Wingfield 2007) as well as by the predicted global climatic changes (Veteli et al. 2002; Allen et al. 2010). Table 1.1 indicates abiotic factors of stress encountered in various temperate climatic conditions.

**Table 1.1** Major stress factors encountered in temperate climates

| Climate nature | Stress factors | References |
|---|---|---|
| Cold and cool temperate climates | Waterlogging and flooding | Kozlowski and Pallardy (2002) and Niinemets (2010) |
| | Nutrient deficiency | Niinemets (2010) |
| | Elevated $CO_2$ | Tjoelker et al. (1998) |
| Arid and semiarid regions and Mediterranean climates | Drought | Chartzoulakis et al. (2002a) and Guàrdia et al. (2012) |
| | Salinity | Chartzoulakis et al. (2002b) and Lynch and St Clair (2004) |
| | Episodic low temperatures (<0 °C) | Costa e Silva et al. (2008) |
| Tropical and subtropical regions | Soil acidity | Lynch and St Clair (2004) |
| | Mineral toxicity and deficiency | Lynch and St Clair (2004) |
| | Light deficiency | Sterck and Bongers (2001) |

# 6 Adaptation and Mechanisms of Stress Tolerance/Resistance

The previous three sections have provided insights into specific responses of woody trees to one or multiple stresses according to many intrinsic or extrinsic factors (multi-stress interactions, response throughout ontogeny, biome influence). Plants may activate different mechanisms at various structural and functional levels to overcome possible injury that may be induced by one stressful condition. These mechanisms act simultaneously or successively in relation with the nature of stress, its duration, and severity. As stated by Glenz et al. (2006) for flooding tolerance, specific biotic factors (developed adaptation and capacity of acclimation) related to the woody species influence the final response of plant to a given stress. As one mechanism may be involved by species under various kinds of environmental stresses (for instance, osmotic adjustment is implicated in both drought and salt stress), we will present the main adaptive strategies adopted by plants at structural (morphology and anatomy) as well as functional (growth, physiology, ionic relations, biochemical and enzymatic activities, and genetics) levels.

## 6.1 Structural Adaptation

The major feature that determines the plant stress tolerance is concerned with leaf as it is the principal site of gaseous exchange, photosynthesis, and metabolic activities. In many species exposed to various biotic and abiotic forms of stress such as drought, salinity, wounding, and pathogen attacks, an increase in leaf cuticle thickness (Bacelar et al. 2004; Bosabalidis and Kofidis 2002) and epidermis (Kulkarni et al. 2010), a reduction of size and density of epidermal cells (Chartzoulakis et al. 2002a) and xylem (Bosabalidis and Kofidis 2002; Kulkarni et al. 2010), and a

greater cell wall lignification (Niinemets et al. 1999; Osakabe et al. 2011) have been considered as stress-tolerant traits. Drought-stressed olive plants reduced the size of stomata and epidermal and mesophyll cells, increased cell and stomatal density, and reduced the number of nonglandular hairs (Bosabalidis and Kofidis 2002).

These anatomical and morphological modifications reflect a better control of water loss through cuticular transpiration in water deficit conditions. For instance, several olive species tend to diminish leaf area, develop thicker epidermal leaves, and increase trichome density when subjected to drought stress (Ennajeh et al. 2010). The increased leaf fracture toughness seems to be useful in the protection from herbivore damage (Choong et al. 1992) as it improves leaf mechanical properties through the thickening of smaller vein walls forming a venous network (Lucas et al. 1991).

The plant-protective roles of cuticular waxes are widely reported from many species (Shepherd and Griffiths 2006). Cuticular-wax layers are predominately composed from long-chain hydrocarbon compounds, including alkanes, primary alcohols, aldehydes, secondary alcohols, ketones, esters, and other derived compounds (Shepherd and Griffiths 2006). Waxy species are reported to modify reflectance in a way that changes light absorption and consequently photosynthetic activity (Cameron 1970; Holmes and Keiller 2002). The plant reflectance ability plays a major protective role against high radiations in drought conditions and UV-B harmful radiations due to the stratospheric ozone layer damage. Reflectivity is highly influenced by the surface topography of leaves, primary hairs, and cuticular waxes (Shepherd and Griffiths 2006).

The resistance of xylem to cavitation events is an important parameter that determines stress resistance (Tyree and Ewers 1991). The drought-stressed bald cypress plants used their biomass in a way that strengthens the xylem and reduces its vulnerability to cavitation (Stiller 2009). Similarly, woody plants respond to salinity by the reduction of vessel lumina and the increase of wall strength to counteract the reduction of xylem hydraulic conductivity resulting from salt stress. For example, the decrease of the vessel lumina of the salt-resistant poplar species *Populus euphratica* under salt stress conditions was lower than that of the salt-sensitive *Populus × canescens* species (Junghans et al. 2006).

In anoxic conditions such as submersion of the root system, plants develop hypertrophied lenticels that present a pathway for the diffusion of oxygen ($O_2$) through living bark cells and the release of toxic compounds related to anaerobiosis (Glenz et al. 2006). The presence of lenticels as a morphological adaption to flooding is reported for many Central European trees and shrubs including *Acer campestre*, *Alnus glutinosa*, *Fraxinus excelsior*, *Populus nigra*, and *Salix alba* (Siebel et al. 1998; Hook 1984). In addition of lenticels, aerenchyma tissues are thought to be a morphological adaptation of woody plants to anaerobiosis as they constitute an extensive intercellular air space allowing the diffusion of oxygen from the aerial part of the plant to the roots (Glenz et al. 2006; Wang and Cao 2012).

The variation of cell wall elasticity under stressful conditions was supported as a trait of stress tolerance of some woody species. However, both positive (Chartzoulakis et al. 2002a) and negative (Patakas and Noitsakis 1997) roles of tissue elasticity were suggested as a mechanism of adaptation to stress. As examples of the two

**Table 1.2** Morphological and anatomical traits of stress tolerance that have been cited in woody plants

| Trait | Stress | Species | References |
|---|---|---|---|
| Increase of leaf cuticle thickness | Drought | *Olea europaea* | Bacelar et al. (2004) and Bosabalidis and Kofidis (2002) |
| Increase of leaf epidermis | | *Ziziphus mauritiana* (Lamk.) | Kulkarni et al. (2010) |
| Increase of thick palissade mesophyll layers | Salinity | *Olea europaea* | Bacelar et al. (2004) |
| Reduction of size and density of epidermal cells | Wounding | *Olea europaea* | Chartzoulakis et al. (2002a) |
| Reduction of size and density of xylem | | *Olea europaea* | Bosabalidis and Kofidis (2002) and Kulkarni et al. (2010) |
| Cell wall lignification | Pathogen attacks | *Ziziphus mauritiana* (Lamk.) Several species | Niinemets et al. (1999) Osakabe et al. (2011) |
| Great leaf anatomical plasticity | Drought | *Quercus* species (*Q. velutina*, *Q. coccinea*, and *Q. rubra*) | Ashton and Berlyn (1994) |
| Increased leaf fracture toughness | Herbivore damage | 42 tropical tree species | Choong et al. (1992) |
| Presence of hair and cuticular waxes | High light intensity | *Eucalyptus* species | Cameron (1970) |
| | | 45 species including *Citrus*, *Eucalyptus*, *Quercus*, *Prunus* | Holmes and Keiller (2002) |
| | | Woody and non-woody species | Shepherd and Griffiths (2006) |
| Chloroplast movements | Light limiting conditions | *Tradescantia albiflora* | Park et al. (1996) |
| | | *Cissus*, *Eustrephus*, *Alocasia*, *Eucalyptus* | Williams et al. (2003) and Way and Pearcy (2012) |
| Lenticels, aerenchyma tissues, and adventitious roots | Flooding | Central European trees and shrub species | Glenz et al. (2006) |
| | | *Taxodium distichum* and *Sapium sebiferum* | Wang and Cao (2012) |
| | | Woody species (general review) | Kozlowski and Pallardy (2002) |
| Resistance to xylem cavitation | | Trees and woody plants | Tyree and Ewers (1991) |

cases, the reduction of cell wall elasticity was suggested as an efficient mechanism adopted by grapevine to overcome water deficit (Patakas and Noitsakis 1997) and high UV radiation (Lesniewska et al. 2004). Inversely, the increase in tissue elasticity and a decrease of osmotic potential were thought to be likely the two predominant mechanisms of adaptation in avocado (Chartzoulakis et al. 2002a). Table 1.2 shows number of morphological and anatomical traits that have been associated to stress tolerance in woody plants.

## 6.2  Physical Movements

Plants respond to various abiotic (e.g., drought, salinity, UV radiation, high temperature, and heavy metals) and biotic (e.g., herbivores, bacteria, virus, and fungi) stresses by leaf rolling (Bosabalidis and Kofidis 2002; Kadioglu et al. 2012). This physical movement combined with stomata closure plays a key role in the reduction of water loss and the maintenance of cell turgor in plants subjected to osmotic stress conditions. However, stomata closure leads to a reduction of gaseous exchanges through the leaves and a diminution of plant photosynthetic activity due to a reduction of $CO_2$ entry. In these conditions, plants optimize carbon uptake by different ways such as the modification of crown architecture and leaf angle positioning to adjust within crown irradiance (Egea et al. 2012) and heterogenic stomatal aperture (Guàrdia et al. 2012). At a cellular level, chloroplast movements operate to adjust photon flux density (Park et al. 1996; Way and Pearcy 2012). At low light conditions, chloroplasts move to increase light absorption. The rapidity of chloroplast rearrangements to periclinally or anticlinally position against leaf surface is a viable mechanism for leaves to reduce excess photon flux density interception (Williams et al. 2003; Way and Pearcy 2012). Within chloroplasts, the size and stacking of thylakoid grana may change within 10 min of high light exposure (Rozak et al. 2002).

## 6.3  Growth and Physiology

One of the adaptive responses to stress is the plant growth regulation by modulation of both cell division and expansion (Skirycz and Inzé 2010). Woody plants subjected to nutrient deficiency allocate higher amounts of photosynthate to roots (Kozlowski and Pallardy 2002). Tolerant plants use different ways to reactivate root system functioning and compensate from root alteration and mortalities. Under water deficit conditions, *Fagus* species stimulated fine root growth to compensate from root biomass losses during dry mid-summer (Leuschner et al. 2001). Similarly, plants adapt to flooding conditions by the regeneration and growth of adventitious roots to compensate from the alteration of asphyxiated initial roots. Root initiation takes place on the originated root system and/or submerged portion of the stems (Kozlowski and Pallardy 2002). Flood tolerance in woody plants is positively correlated with the ability of adventitious root regeneration, the conversion of toxins produced in the soil to less toxic compounds by rhizosphere oxidation, and the increase of root-synthesized gibberellins and cytokinins (Kozlowski and Pallardy 2002).

Many reports describe a general close association between morphological and anatomical traits and the efficiency of physiological activity in stressed plants (Ashton and Berlyn 1994; Bacelar et al. 2004; Kulkarni et al. 2010). Ashton and Berlyn (1994) found close correlations between anatomical measures of plasticity and physiological measures of plasticity in *Quercus* species. Stomatal density plasticity was correlated with both net photosynthesis and stomatal conductance plasticity.

The most drought-tolerant and higher light demanding *Q. velutina* species exhibited greater anatomical plasticity and higher net photosynthesis than *Q. coccinea* and *Q. rubra* species. *Quercus ilex* L. adapted to severe drought conditions by patchy stomatal closure leading to heterogenic photosynthesis (Guàrdia et al. 2012). Drought-tolerant *Jatropha curcas* accessions maintained high leaf RWC through water-saving strategy involving strict stomatal regulation and growth reduction (Sapeta et al. 2013).

## 6.4    Cell Homeostasis and Osmotic Adjustment

Drought and salt stress lead to the increase of osmotic pressure in the cytosol due to water deficiency (drought) or the uptake of large amounts of salts (salt stress). Salt-tolerant species develop different strategies either to exclude salt from the cells or to tolerate it within the cells (Kozlowski 1997; Parida and Das 2005). To maintain cell homeostasis and cell turgor and protect metabolic activities, osmotic adjustment mechanism is adopted by tolerant species through two ways: (1) sequestration of excess of salt ions in the vacuole and (2) biosynthesis of organic osmoprotectant compounds (Munns 2002). Osmoprotectants are named compatible solutes as they do not interfere with plant metabolism even if they accumulate to high concentrations. Main biochemical compounds implicated in osmoregulation are proline (Ahmad et al. 2010), glycine-bétaine, and soluble sugars (Kozlowski 1997; Clifford et al. 2002). The nature of biosynthesized osmoprotectants seems to be species-related (Pallardy 2007). The presence of mucilage and polysaccharides in leaves of drought-tolerant *Ziziphus* species is reported to act in osmotic adjustment by the remobilization of solutes allowing better efficiency in water uptake and translocation to the roots and stems before plant defoliation (Clifford et al. 2002). However, in the special case of salt stress, there is uncertainty with regard to the role of proline in salt tolerance. In fact, both positive (Hokmabadi et al. 2005) and negative (Ashraf 1989) associations of proline accumulation with tolerance to salt stress were reported. Similarly, instances of enhanced (Gucci and Tattini 1997) as well as unchanged and reduced soluble sugar contents were reported (Rejskovà et al. 2007).

## 6.5    Ionic Interactions

Stresses such as drought and salt stress may lead to an ionic imbalance. The disturbance of potassium ($K^+$) nutrition is a common feature under sodium chloride (NaCl) stress conditions and is often associated with potassium deficiency resulting from potassium–sodium interaction (Cramer et al. 1987; Slama 2004; Parida and Das 2005). Thus, the maintenance of normal cellular functions strongly depends on the $K^+$ nutrient status and $K^+$–$Na^+$ interaction through a selective uptake and transport of $K^+$ in depend of $Na^+$ into the shoots (Cramer et al. 1987). A high $K^+/Na^+$ ratio

in the leaves is considered as a salt-tolerant trait in many species (Chartzoulakis et al. 2002b; Meena et al. 2003) as it influences photosynthetic activity and nitrogen assimilation (Tabatabaei 2006). The accumulation of sodium ions in the roots is an adaptive strategy used by several woody species to avoid their toxicity in the shoots (Walker et al. 1987; Picchioni et al. 1990; Gucci and Tattini 1997). On the other hand, salt stress may induce an increase (Ramoliya et al. 2004; De Pascale et al. 2007) or a decrease (Gratten and Grieve 1999; Unno et al. 2002) of calcium ion ($Ca^{2+}$) content depending on the specific plant physiology as well as the nature and duration of stress. Calcium plays a key role in maintaining the plasma membrane integrity, thus limiting the toxic effect of $Na^+$ (Rengel 1992; Gucci and Tattini 1997), and acts as a secondary messenger in the regulation of the signal transduction pathways for the response to abiotic stresses (Rengel 1992; Maathuis and Amtmann 1999). It is also reported to control the $Na^+$ influx via a nonselective ion channel and to influence $K^+/Na^+$ selectivity. It was suggested that calcium plays a role in salt toxicity alleviation (Cramer et al. 1987; Rengel 1992; Gucci and Tattini 1997; Melgar et al. 2006; Sotiropoulos 2007). Accordingly, the ability of plants to control the root to shoot transport and a relative high $Ca^{2+}$ tissue content can serve as a criterion for stress tolerance. The measurements of $K^+/Na^+$ and $Ca^{2+}/Na^+$ ratios in the assessment of salt tolerance were suggested in non-woody (Dasgan et al. 2002; Maathuis and Amtmann 1999) and woody plant species (Heimler et al. 1995).

Many conifer species resist very low temperatures (down to −60 °C) through a freeze drying mechanism that allows the progressive expulsion of water from the tissues during cooling (Sakai 1979).

## 6.6 Hormonal and Enzymatic Activities

Environmental stresses can induce an imbalance in hormone physiology of woody species. Plant hormones play a key role in the regulation of the vascular tissue growth and secondary development in woody plants (Osakabe et al. 2012). Auxins are involved in cell division and expansion, apical dominance, root development, and vascular tissue development (Osakabe et al. 2012). They have a role in the regulation of secondary development (Nilsson et al. 2008). In response to developmental and environmental stimuli, trees have developed mechanisms to modulate auxin transport in the vascular meristem (Osakabe et al. 2012). Furthermore, the salt-resistant species may use auxin-conjugates in the stem as a source of auxin to overcome the auxin physiology imbalance due to salt stress. It is the case of the salt-resistant poplar species (*Populus euphratica*) who displayed an increase in IAA-amido-conjugates in the xylem in response to salt stress while the salt-sensitive *Populus × canescens* did not show any variation in this compound (Junghans et al. 2006).

It should be emphasized that the plant tolerance to stress may be accomplished through variable mechanisms within a same species. Working on the drought tolerance of five field-grown olive cultivars, Bacelar et al. (2004) reported different

morphological and structural adaptations of three drought-tolerant cultivars. While Manzanilla and Negrinha cultivars tended to increase lamina thickness through building parenchyma tissues and increasing cuticle and epidermis thickness, *Cobrançosa* cultivar enhances protection against water loss through the increase of mesophyll tissues density and thick cuticle and trichome layers. Similarly, the wild almond species *Amygdalus webbii* Spach responded to water deficit by a great reduction of leaf area and low decrease of stomatal frequency whereas the common *Amygdalus communis* L. adopted the inverse behavior (Camposeo et al. 2011).

In woody plants, the assimilated carbon is stored in the secondary cell wall as cellulose and lignin; the disruption of cellulose synthase genes was suggested to affect osmotic stress response (Osakabe et al. 2012). In forest and fruit trees, carbon pool status is involved in environmental stress tolerance.

### *6.7 Biochemical Release*

Plants may produce defensive biochemical compounds to resist herbivore attacks. When tissues are altered, many plants react through the release of a respiratory poison. This phenomenon is called cyanogenesis; a plant biosynthesis of cyanogenic glycosides and cyanolipids which on hydrolysis liberate hydrogen cyanide (Poulton 1990; Miller et al. 2006).

### *6.8 Adaptation at the Genetic Level*

Plants respond to variable stresses by the modification of gene expression. Salt-tolerant woody species respond to high salinity by the regulation of the genes involved in ionic and osmotic homeostasis (Osakabe et al. 2012). Under different levels of drought stress, various genes of loblolly pine (*Pinus taeda*) are differently expressed. These genes include those encoding heat shock proteins (HSPs), late embryogenesis abundant proteins (LEAs), and enzymes in the aromatic acid and flavonoid biosynthetic pathways (Watkinson et al. 2003).

## 7 Assessment of Stress Tolerance/Resistance in Woody Plants

The long life biological cycle of woody plants and the large tree sizes are the two predominant traits that make environmental stress assessment on woody plant species more complicated and difficult than that of herbaceous species. Most studies in this topic have been performed in controlled growth chamber conditions, in

greenhouses, or in vitro. In vitro techniques have been reported to be valuable methods for screening of stress-tolerant lines (Fuller et al. 2006), studying defense mechanisms (Santos et al. 2001), and obtaining tolerant plants through genetic engineering tools. Different plant materials were used varying from whole plant (Shibli and Al-Juboory 2002; Mills et al. 2001; Zhang et al. 2004; Chelli-Chaabouni et al. 2010) to cell suspension cultures. Positive concordances of in vitro plant stress tolerance assessments with those experimented on whole plant in the field were described for several non-woody (Fuller et al. 2006) and woody plants (Vijayan et al. 2003; Faraloni et al. 2011) but relative discordances were also reported (Santos et al. 2001). However, data from in vitro woody plant assessment of stress tolerance should be taken with great caution due to the changes of stress responses as plant develops. When in vitro assessment was made, an additional evaluation in the field is highly recommended before final appreciations.

When woody plant assessments were realized in the field, seedlings and young trees or shrubs were often preferred to adult plant material to reduce the cost of experimentations related to the required spaces and the nature of measurement tools. Consequently, data obtained in these conditions may not be strongly enough correlated with what may happen for woody plants growing in the field or natural conditions due to great differences in spatio-temporal experimental conditions (Cornelissen et al. 2003). In fact, the occurrence of simultaneous or successive stresses as well as the plant interactions with other organisms in the surrounding environment may induce modifications in plant responses at the morphological, anatomical, physiological, biochemical, and molecular levels. Moreover, explanations about the whole plant behavior at both juvenile and reproductive stages are rarely to be realistic due to the variability of plant responses to stress throughout plant ontogeny. In the special case of trees, the within-canopy heterogeneity of organ responses according to sunlight penetration (Way and Pearcy 2012) may influence the whole plant response to stress (Küppers et al. 1996).

Given the above-mentioned specificities of woody plants, the plant response to stress has been generally assessed through multiparameter monitoring (such as growth, survival rate, water and mineral status, photosynthesis, chlorophyll and pigment concentrations, secondary metabolic compounds biosynthesis) using several experimental tools (e.g., growth measurement instruments, mineral analysis methods, sap flow sensors, molecular biology techniques).

## 8  Conclusion and Future Prospects

In this chapter, we presented an overview of the specific responses of woody plants to various abiotic and biotic stresses. These responses are tightly linked to the plant ontogeny, the nature, the duration and the severity of stress, and the characteristics of the surrounding environment. Woody plant adaptation to stress requires the reallocation of energy in a way allowing the activation of the mechanisms of adaptation and maintaining growth and productivity. They respond to extra-optimal conditions through structural, physiological, biochemical, and genetic modifications that are

traduced to one specific mechanism. Stressful conditions may be the results of multiple stress factor effects occurring successively or simultaneously. The occurrence of one stress may lead to more or less adaptation to another stress. Moreover, adaptation to stress may differ according to the plant interactions with the neighboring organisms. It may also be different from the trunk base to the top of canopy in the special case of forest stands and trees.

The above specificities of woody plant responses to environmental stress need to be considered in the assessment of plant stress tolerance/resistance. Furthermore, the impact of the predicted climatic changes on plant susceptibility to stress should also be taken into account to prevent wide damages that may occur to plantation and native forest stands. Well understanding the possible mechanisms evolved to cope with stressful conditions is a key issue for the appropriate management of genetic resources. The use of efficient tools for plant stress investigation and assessment such as new biotechnological methods including proteomics and genetic engineering appears to be promising.

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