Chapter 3

Histological Responses of Horticultural Plants to Abiotic Stress Conditions

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Abstract

Plants are exposed to various environmental stress conditions throughout their life cycles. These stress factors cause significant changes in the morphological, physiological, biochemical, and histological characteristics of plants. Abiotic stresses include environmental factors such as drought, salinity, and flooding. Histological adaptations developed in horticultural plants to these stress conditions are an important part of plant survival strategies. Drought stress causes water loss and plasmolysis in cells, leading to thickening of the cell wall, denser cuticle, and tightening of the leaf mesophyll tissue. Under salinity stress, plants often thicken their epidermal cell walls to prevent water loss from leaves. During flooding, aerenchyma tissue develops in roots due to hypoxic conditions. This tissue facilitates oxygen transport within the plant, reducing the negative effects of anaerobic respiration in root tissues. Consequently, the histological responses of horticultural plants to abiotic stresses are key indicators of plant resilience. These responses vary depending on genetic makeup and species characteristics. Understanding the cellular and tissue changes that occur under stress conditions significantly contributes to the development of highly stress-tolerant varieties and the sustainable production of horticultural crops.

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1. INTRODUCTION

Plants are exposed to numerous stress factors throughout the growing season. These stress factors are generally divided into two categories: abiotic and biotic. Biotic factors consist of living factors such as bacteria and fungi, while abiotic factors arise from nonliving factors such as drought, salinity, and low temperatures. These stress factors cause various symptoms and damage to plants, leading to yield and quality losses.

Plants respond differently to stress factors. These responses can be morphological, physiological, biochemical, or histological. Responses to stress are crucial for establishing and/or triggering plant defense mechanisms. Changes at the anatomical level are crucial in plant responses to stress. Anatomical structures, particularly vascular bundles, cortical cells, spongy and palisade parenchyma, and stomata, play important roles in defense mechanisms. Histology, also known as microscopic anatomy, is the science of tissue. Specific parts of histology are stained with special stains to examine anatomical structures. This section will examine the anatomical structures that can be examined histologically and how these structures respond differently to stress conditions in horticultural plants.

2. ABIOTIC STRESSES IN HORTICULTURAL PLANTS

Plants are directly affected by environmental conditions throughout their life cycle. Changes in environmental factors such as soil, water, temperature, light, and atmospheric conditions largely determine plant growth, development, and productivity (Mondal et al., 2016). Adverse changes in these environmental factors are called abiotic stresses. The term “abiotic” refers to non-living environmental factors. These stresses lead to both yield loss and quality decline, particularly in economically important crops such as horticultural crops.

Abiotic stresses are generally classified as drought (water stress), salinity, temperature extremes (extreme heat and cold), light stress, heavy metal toxicity, radiation, air pollution, and nutrient deficiencies. Each stress factor causes specific changes in the plant’s physiological, biochemical, and histological structure. These changes determine the plant’s survival strategies and its ability to adapt to environmental conditions.

Drought stress occurs when the balance between water uptake and water loss in plants is disrupted. This typically occurs due to a decrease in soil water potential or an increase in atmospheric vapor pressure deficit (Bodner et al., 2015; Çopur Doğrusöz ve Gülümser, 2024). Drought stress in horticultural crops causes serious problems, especially during summer months, under conditions of high temperature and low humidity. Under drought stress, plant stomata close, transpiration decreases, and photosynthetic activity declines. As cells lose water, turgor pressure decreases, leading to growth retardation. Histologically, epidermal cell shrinkage, reduced spaces between mesophyll cells, thickened cuticle layers, and increased xylem lignification are observed (Manokari et al., 2021). Furthermore, the accumulation of osmotic regulating compounds such as proline, sugar alcohols, and betaine helps maintain intracellular water balance (Singh et al., 2015; Aykoç et al., 2025). Morpho-anatomical adaptations such as reduced leaf surface area, reduced stomata, and thickened cell walls are evident in drought-tolerant species. These structural changes minimize water loss, thus ensuring plant survival.

Salinity is an abiotic stress factor that occurs particularly when irrigation water or soil contains high levels of NaCl (Güleç Şen et al., 2023). Salt stress creates both osmotic pressure and ion toxicity (Arif et al., 2020). High salt concentrations impede plant water uptake and disrupt ion balance. In horticultural crops, histological responses to salt stress include increased suberinization and lignification in roots, vacuole growth, and epidermal thickening. Deeper burial of stomata in leaves, thickening of the cuticle, and accumulation of phenolic compounds are important defensive responses to salt stress. Additionally, plants store Na^+ and Cl^- ions in vacuoles to keep them out of the cytoplasm. This reduces the harmful effects of ion toxicity. Some salt-tolerant plants (halophytes) have developed salt glands or salt vesicles to excrete excess salt. These anatomical structures allow the plant to maintain growth under stress conditions by maintaining ion balance.

While the optimum temperature for plant growth and development varies by species, exposure to temperatures above or below these limits creates stress (Aras and Özyalın, 2023). Excessive heat results in protein denaturation, membrane disruption, and disruption of chloroplast function (Wang et al., 2018). Low temperature, on the other hand, causes intracellular water freezing, membrane ruptures, and metabolic slowdown. Histologically, high-temperature conditions distort chloroplast shape, increase vacuolation in the cytoplasm, and anthocyanin accumulation in the epidermis (Ďúranová et al., 2023). Under cold stress, protoplasm condenses, ice crystals accumulate in intercellular spaces, and cell wall lignification increases. Furthermore, meristematic activity in the root apex decreases, and growth stalls.

Horticultural plants protect their cellular structures against such stresses by synthesizing heat shock proteins (HSPs) and antifreeze proteins. These proteins play critical roles in maintaining membrane integrity and preventing protein denaturation.

Plants require light for photosynthesis, but excessive or insufficient light conditions are also stress factors. Under insufficient light, leaf surface area expands, chlorophyll content decreases, and photosynthetic efficiency decreases. Excessive light, in turn, leads to the accumulation of reactive oxygen species (ROS) and photooxidative damage. Histologically, under shade conditions, the palisade parenchyma thins, the number of chloroplasts decreases, and mesophyll cells enlarge. Under excessive light conditions, the epidermis thickens, the cuticle expands, and anthocyanin and flavonoid pigments increase. These pigments mitigate the harmful effects of UV radiation and protect the plant from oxidative stress.

Heavy metals (Cd, Pb, Ni, Zn, Cu) accumulated in the soil due to industrial activities, mining, and chemicals used in agriculture are toxic to plants (Alengebawy et al., 2021). Heavy metals disrupt the ionic balance in the cell membrane, inhibit enzyme activity, and reduce chlorophyll synthesis. Histologically, symptoms such as parenchymal degeneration, plasmolysis, and mitochondrial and chloroplast deformation are observed in the root cortex. Lignin and cutin accumulation increases in the xylem and phloem walls; this is a defense mechanism developed to limit the transport of metal ions. Furthermore, pectin and phenolic compounds accumulate in the cell wall, which bind metal ions and reduce their intracellular toxicity. In tolerant species, heavy metals are stored in complex form in vacuoles, thus protecting the cytoplasm.

Deficiencies of macronutrients (N, P, K, Ca, Mg, S) and micronutrients (Fe, Mn, Zn, Cu, B, Mo), which are essential for healthy plant development, are also important abiotic stress factors. Deficiencies in each element cause specific physiological and histological changes. For example, nitrogen deficiency results in small and pale leaves and a decrease in chloroplast numbers. Phosphorus deficiency results in poor root system development, while potassium deficiency results in necrosis of leaf margins and stomatal dysfunction. Calcium deficiency results in weakened cell walls, and necrotic areas form in meristematic tissues. Many of these changes manifest microscopically as cell wall thinning, vacuole shrinkage, and parenchymal tissue deterioration.

With increasing industrialization, air pollution has become a serious source of abiotic stress on plants. Ozone (O_3), sulfur dioxide (SO_2), and nitrogen oxides (NO_x), in particular, cause oxidative damage to leaf tissues. These gases oxidize lipids in the cell membrane, disrupting membrane permeability. Histologically, degeneration of epidermal cells, destruction of chloroplasts, widening of vacuoles in the mesophyll tissue, and necrotic lesions are observed in leaves. Radiation stress (e.g., UV-B) can also cause DNA damage and cell death. In response, plants attempt to mitigate the harmful effects of radiation by producing phenolic compounds and anthocyanin pigments.

Horticultural plants develop similar defense strategies against different types of stress. These can be summarized as follows:

Osmotic regulation: Intracellular water balance is maintained through the accumulation of compounds such as proline, sugar, and polyamines.

Antioxidative defense: Reactive oxygen species are neutralized by the enzymes superoxide dismutase (SOD), catalase (CAT), and peroxidase (POD).

Cell wall strengthening: Tissue durability is increased through the accumulation of lignin, suberin, and cutin.

Stomatal and cuticle changes: Stomatal density decreases and the cuticle thickens to reduce water loss.

Pigment accumulation: Anthocyanins, carotenoids, and phenolic compounds protect against stress-induced oxidative damage.

These structural and biochemical adaptations are key factors determining the resilience of horticultural plants to environmental stresses.

3. ANATOMICAL STRUCTURES OF HORTICULTURAL PLANTS

Horticultural plants are classified as higher plants and include the categories of fruit, vegetable, vine, and ornamental plants. The tissues of these plants contain specialized anatomical structures. Horticultural plants have two vascular bundles: xylem and phloem. These vascular bundles are responsible for the transport of many substances, such as mineral nutrients, proteins, hormones, and sugars. Xylem is a dead tissue that cannot regenerate and consists of a phenolic compound called lignin (Meinzer et al., 2001; Liu et al., 2015). Xylem is primarily responsible for the unidirectional (bottom-up) transport of water and nutrients (Aras et al., 2021). The phloem vascular bundle, on the other hand, facilitates both bottom-up and top-down transport and is particularly capable of transporting phytochemicals such as sugars and hormones (Lee et al., 2020).

In horticultural plants, every organ and/or living cell consists of cortex cells. These cortex cells possess the ability to divide in the initial developmental stage of the tissue in which they are located. In the subsequent stages, this division phase is completed and they acquire the ability to grow (Gonzalez et al., 2012). Cortex cells have been reported to contain many substances, such as water, nutrients, and proteins (Singh et al., 2013).

When leaves are examined in general, the outermost layer consists of the cuticle and epidermal cells (Jetter et al., 2020). This cuticle layer is coated with wax. The middle part of the leaf contains palisade and spongy parenchyma (Gonçalves et al., 2008). The palisade parenchyma contains color pigments such as chlorophyll, which are involved in photosynthesis, and is capable of photosynthesis. The spongy parenchyma, on the other hand, has air spaces and plays a major role in gas storage. Stomata are located on the underside of the leaves of horticultural plants, and gas exchange and transpiration occur in this section (Bai et al., 2013).

4. HISTOLOGICAL RESPONSES TO ABIOTIC STRESSES

Horticultural plants exhibit different histological responses to abiotic stressors (Aras and Özyalın, 2024). When examining histological responses, each stress factor must be evaluated separately. Because plants live in fixed locations, they cannot develop behavioral responses such as escape or hiding in response to changes in environmental conditions. Therefore, abiotic stress factors—such as drought, salinity, temperature extremes, heavy metal toxicity, light deficiency or excess, radiation, and air pollution—produce direct physiological and morphological effects on plants. Many of these effects manifest as histological changes observable at the tissue level. In horticultural plants, these histological responses are important adaptation mechanisms that increase resistance to stress conditions or limit damage.

Drought stress is one of the most common abiotic stresses. In plants exposed to water deficit, epidermal cells shrink, the cuticle thickens, and stomatal density may decrease. In some species, stomata are buried deeper to minimize water loss. The intercellular spaces between mesophyll cells decrease, increasing water-holding capacity in tissues. Increased lignification and narrowing of vessel diameters are observed in xylem elements, reducing the risk of cavitation in water transport. At the same time, cell wall thickening increases mechanical strength.

Under salinity stress, plasmolysis and protoplast shrinkage are frequently observed at the cellular level. Ion imbalances occur as cell membrane permeability is impaired. Plants attempt to maintain cytoplasmic ion balance by storing salt ions in vacuoles. Histologically, vacuole enlargement in parenchymal cells, salt crystal accumulation in epidermal cells, and increased suberinization in the root cortex are evident. The suberin layer limits water and ion transport, preventing excessive salt intrusion.

Extreme heat stress alters the fluidity of cell membranes and leads to protein denaturation. Histologically, chloroplasts are deformed, the granules are disorganized, and increased vacuolation is observed in the cytoplasm. High temperatures can also cause anthocyanin accumulation in the epidermis; these pigments protect cells from oxidative damage during light and heat stress. During cold stress, the accumulation of ice crystals in the intercellular spaces mechanically damages the plasma membrane. In response, plants mount defensive responses such as cell wall lignification and protoplasm condensation.

Heavy metal toxicity (e.g., cadmium, lead, nickel) directly affects cell structure in horticultural crops. Lignin and cutin accumulation increases in the cell walls of xylem and phloem tissues, limiting the transport of metal ions. Histological symptoms such as cortical parenchymal degeneration, mitochondrial and chloroplast deformations, and nuclear condensation are observed in root cells. Additionally, structural defenses such as phenolic compound accumulation and sclerenchymal tissue thickening are also activated.

Under light insufficiency (shade stress), the palisade parenchyma in leaf tissue thins, spongy parenchyma cells enlarge, and the number of chloroplasts decreases. Conversely, under excessive light, epidermal thickening, wax accumulation in the cuticle, and an increase in antioxidative pigments are observed. These changes are photoprotective adaptations designed to reduce the damaging effects of light.

As a result, horticultural plants have evolved a wide variety of histological responses to abiotic stress conditions. These responses include structural adaptations such as cell wall thickening, lignification, cuticle proliferation, stomatal modification, vacuolization, suberinization, and pigment accumulation. The purpose of these changes is to maintain cell integrity, maintain water and ion balance, protect vascular tissues, and sustain metabolic activities. These histological defense strategies are among the fundamental factors determining horticultural plant tolerance to environmental stresses.

5. HISTOLOGICAL RESPONSES TO LIME STRESS

Lime stress is one of the most significant stress factors encountered both in our country and world. This stress is caused by high levels of lime in the soil and/or irrigation water where horticultural crops are grown. Lime stress causes an increase in soil pH, negatively affecting plant growth. High pH reduces the availability of iron (Fe), thus restricting plant growth. The histological effects of lime stress on horticultural crops have not been extensively studied; the effects of Fe deficiency have been studied more extensively. It has been reported that the growth of cortical cells in leaves of peach saplings grown under iron deficiency is inhibited (Aras et al., 2022). Cortical cells are rich in nutrients and can also serve as reserves for these nutrients. It has also been determined that xylem vascular bundles fail to develop due to Fe deficiency. Because xylem is responsible for the transport of water and nutrients, its failure to develop can also lead to problems with nutrient transport. Another study examined the leaf stomata of peach saplings under Fe deficiency (Aras et al., 2021). Fe deficiency led to a decrease in stomatal conductance and area. Stomata are important as openings responsible for both gas exchange and transpiration and also play a major role in the plant's uptake of certain nutrients, such as Fe (Rios et al., 2016).

A study examining the quality of cucumber seedlings in calcareous soil reported that calcareous soil negatively affects the seedling's cortical cells and xylem, reducing seedling quality (Çoban and Aras, 2023). The study determined that lime stress limits xylem development and inhibits cortical cell growth. Fernández et al. (2008) determined that epidermal cells enlarge and stomatal guard cells remain small in size in pear and peach trees under Fe deficiency. They also reported that Fe deficiency negatively affects the anatomical structures that serve as leaf barriers, reducing leaf water potential.

6. HISTOLOGICAL RESPONSES TO FLOOD STRESS

Flooding is a significant environmental factor that limits plant growth and development. This stress negatively affects plant survival, biomass, and plant height (Loreti et al., 2016). Flooding stress causes oxygen depletion (hypoxia and anoxia) and root suffocation (asphyxia) in plant roots (Jackson and Colmer, 2005). This phenomenon is generally called asphyxia. Complete submersion of plants due to flooding can lead to oxygen deficiency in aboveground organs (Voesenek et al., 2006). When oxygen becomes limiting for respiration, plants experience hypoxia, while complete oxygen deprivation (anoxia) can lead to plant death. Horticultural plants are generally among the species susceptible to flooding stress (Blanke and Cooke, 2004).

Horticultural plants exhibit diverse histological responses to flooding stress. Horticultural plants can increase and/or structurally enhance aerenchyma, which are gas spaces, to facilitate gas storage (Takahashi et al., 2014). Plants can normally tolerate asphyxia stress through histological responses. Aerenchyma formation is an important indicator of a plant's tolerance to asphyxia (Liang et al., 2008). Aerenchyma is a tissue responsible for gas storage in plants (Evans, 2004) and can develop well in roots, leaves, and main leaf veins (Takahashi et al., 2014). Aerenchyma formation in tissues is crucial and can occur in leaves and roots (Takahashi et al., 2014). In addition, the apoplastic spaces between cells also play a role in gas storage, and for this purpose, the apoplastic spaces increase by increasing the size of the cortex cells (Nishiuchi et al., 2012).

In a study examining the histological responses of strawberry plants exposed to flood stress, it was reported that after 2 days of flooding, aerenchyma formation in the roots did not occur, but the area of the sponge parenchyma in the leaf mesophyll increased, creating more space for gas storage (Kaya et al., 2025). Pimentel et al. (2014) reported that the histological responses of rootstocks commonly used in stone fruit species to flood stress increased the size of lenticels, adventitious roots, and arenchyma tissue. In another study, it was reported that a cavity formed in the main vein of a peach leaf under flooding, increasing gas storage space (Xu et al., 2022).

7. HISTOLOGICAL RESPONSES TO SALT STRESS

Salt stress results from increased salinity in soil and/or irrigation water due to factors such as coastal farming and high doses of fertilization. While horticultural crops are generally known to be sensitive to salt stress, salinity exceeding 2.0 EC (electrical conductivity) can be quite damaging.

Plants have developed various adaptation mechanisms to the abiotic stress factors they encounter in their habitats. Among these stresses, salinity (salt stress) is one of the most significant environmental problems, particularly in agricultural areas, where soil salinity increases. High salt concentrations create both osmotic stress and ion toxicity in plants. Salt stress leads to a series of structural changes at the cellular and tissue levels; these changes are clearly observable in the plant's histological structure.

Salinity stress primarily affects root tissues. Increased Na^+ and Cl^- ions cause plasmolysis in root cells, resulting in water loss resulting in the separation of the cell membrane from the cell wall. This reduces cell turgor and limits root growth. In plants tolerant to salt stress, the root epidermis thickens, the spaces between cortical cells decrease, and suberinization increases in the endodermis. Suberin accumulation limits the permeation of ions into the xylem, preventing the transport of toxic ions. Furthermore, lignin and cutin accumulation is observed in the exodermis, which reduces water and ion exchange between the root and the external environment, creating a protective barrier.

Vacuole organization in roots also changes under salt stress. Plants store harmful ions in vacuoles to direct them away from the cytoplasm. This manifests histologically as vacuole enlargement and cytoplasmic volume reduction. Plasmodesmata, which provide intercellular communication, can partially close under salt stress, limiting ion transport.

Significant histological changes also occur in leaf tissues. In leaves exposed to salt stress, epidermal cells thicken and the cuticle layer expands, a process designed to reduce water loss. Furthermore, stomata are either reduced in number or buried deeper, minimizing water loss through transpiration. Within the mesophyll tissue, air spaces between cells are reduced, and cells become more tightly packed. This is an adaptation to increase the cells' water retention capacity under osmotic stress.

Salt stress also produces significant changes in vascular tissues (xylem and phloem). Xylem elements narrow in diameter, and secondary wall thickening and lignification in vascular tissues increase. These structural changes reduce the risk of cavitation during water transport and stabilize the plant's hydraulic conduction system. However, under extreme salinity, xylem elements collapse and phloem transport slows.

Another histologically significant response is cell wall thickening. Wall thickening, particularly in parenchyma and collenchyma cells, increases mechanical resistance to changes in intracellular osmotic pressure. Microscopically, accumulation of phenolic compounds and flavonoids can also be observed. These compounds strengthen the cell wall and protect against oxidative stress.

Some halophyte plants have developed histological adaptations specific to salt stress. For example, excess salt is excreted in specialized epidermal structures called salt glands or salt vesicles. The presence of these structures maintains physiological balance by preventing ion accumulation in the plant's internal tissues. Furthermore, water-storing cells (hydrenchyma) can develop in leaves, which contribute to maintaining osmotic balance.

Salt stress limits the development of horticultural plants. This limitation stems primarily from the negative effects of salinity on cells and xylem vascular bundles. Cortex cell growth and xylem development have been reported to be inhibited in strawberry plants grown under salt stress (Aras, 2025). Histological responses in cucumber plants exposed to salt stress revealed increased palisade and spongy parenchyma thickness, and leaf structural integrity was impaired (Yuan et al., 2015). When tomato plant responses to salt stress were examined, it was reported that the size of the palisade and spongy parenchyma increased and stomatal aperture decreased to prevent water loss (Albaladejo et al., 2017). In pepper plant responses under salt stress, there were delays in cortex cell growth and xylem development (Coban, 2023). Problems in the development of xylem vascular bundles under salt stress have also been reported in tomato plants (Hoffmann et al., 2021). When grapevine leaf histological responses were examined, the epidermis and spongy parenchyma thicknesses and main vein width increased as a result of salt stress (El-Banna et al., 2022).

8. HISTOLOGICAL RESPONSES TO DROUGHT STRESS

Drought stress is one of the most common environmental stress factors, significantly reducing fruit yield and quality. Horticultural crops generally contain species that are susceptible to drought (Klamkowski and Treder, 2008; Razavi et al., 2008; Jiménez et al., 2013).

Drought stress is a significant factor limiting plant growth. When plants lose or cannot find water, it creates numerous problems in both vegetative development and physiology. This is reflected in the plant's fruit yield and quality. Some plants can develop resistance to drought stress through various defense mechanisms. Examples of these mechanisms include stomatal control, increased root development to access water, and the accumulation of various osmoprotectants (Singh et al., 2015; Pirasteh-Anosheh et al., 2016). Histological responses also play important roles in these defense mechanisms. Under drought stress, the number of sponge parenchymal cells increased and stomatal density decreased in almond (Rajabpoor et al., 2014). In a study examining the histological responses of different citrus rootstocks to drought, significant increases in epidermal cell thickness, vascular bundle length, and xylem thickness were found in drought-tolerant rootstocks (Shafqat et al., 2021). In a study on cucumber, the length and width of palisade cells decreased under drought (Liu et al., 2018). The thickness of the sponge parenchyma also decreased.

One of the first responses to drought stress is changes in stomatal density, size, and aperture (Anjum et al., 2011). Plants regulate stomatal movements to conserve available water, triggering their defenses against drought. Decreased stomatal size and density and/or narrowing of stomatal apertures under drought have been reported in many plants, including tomato (Liang et al., 2020), melon (Kusvuran, 2012), and apple (Aras and Keles, 2019).

9. HISTOLOGICAL RESPONSES TO EXTREME TEMPERATURE STRESS

Horticultural plants can be exposed to both low and high temperatures throughout the growing season. Histological responses within plants are crucial in triggering defenses (Miranda et al., 2025).

A study examining peach tree responses to low temperatures reported that increased xylem vascular bundle thickness plays a significant role in cold adaptation (Niu et al., 2023). A study examining cucumber histological responses determined that abscisic acid levels increase under low temperatures, closing stomatal apertures and thus providing defense (Ikkonen et al., 2012). This decreases root hydraulic conductivity, reducing water flow to shoots and preventing freezing.

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