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Salt stress and exclusion mechanism in woody plants

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Abstract

Many fruit tree species that are widely available in the world market continue to grow and bear fruit in the face of environmental stress. The negative impact of salt stress causes fruit trees to weaken and reduce their yield and quality. However, unlike annual plants, perennial fruit trees, which are exposed to many biotic and abiotic stresses under natural conditions, have developed many complex tolerance mechanisms to maintain their vital activities. Some fruit trees that can tolerate salt stress are able to exclude salt by maintaining their physiological and biochemical activities. In this review, we share the current knowledge on salt effects and tolerance in fruit trees and assess how salt is physiologically excluded from various parts of woody plants through the interaction of environmental factors.

Keywords: *Salinity, fruit stress, salt tolerance, abiotic stress*

Odunsu türlerde tuz stresi ve dışlama mekanizmaları

Öz

Dünya piyasasında yaygın olarak yer alan birçok meyve ağacı türü çevresel strese karşı mücadele içerisinde büyümeye ve meyve vermeye devam etmektedir. Tuz stresinin olumsuz etkisi, meyve ağaçlarının zayıflamasına, ürün ve kalitesinin azalmasına neden olmaktadır. Bununla birlikte, doğal koşullar altında birçok biyotik ve abiyotik strese maruz kalan çok yıllık meyve ağaçları, tek yıllık bitkilerden farklı olarak yaşamsal faaliyetlerini sürdürebilmek için karmaşık pek çok tolerans mekanizması geliştirmiştir. Tuz stresini tolere edebilen bazı meyve ağaçları, fizyolojik ve biyokimyasal faaliyetlerini

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sürdürerek tuzu dışlayabilmektedir. Bu derlemede, meyve ağaçlarında tuz etkileri ve toleransına ilişkin mevcut bilgiler paylaşılmakta ve çevresel faktörlerin etkileşimi yoluyla tuzun odunsu bitkilerin çeşitli kısımlarından fizyolojik olarak nasıl dışlandığı değerlendirilmektedir.

Anahtar kelimeler: *Tuzluluk, meyvelerde stres, tuz toleransı, abiyotik stres*

1. Introduction

Many perennial fruit species with important genetic diversity, rich in nutrients and suitable for every palate, are experiencing significant reductions in quality and yield due to many abiotic and biotic stress factors caused by climate change. The decline in soil and water quality makes it inevitable that the need for basic resources such as nutrients will become a competition. Salinity affects more than 1 billion hectares of land in more than 100 countries worldwide and these numbers are constantly increasing [1]. According to data obtained between 1986 and 2016, the total area affected by salt increased by more than 100 million hectares [2]. Stress factors can restrict all vital activities of plants, biotic and abiotic [3]. Salt stress, one of the most important abiotic stress factors, is one of the environmental conditions that plants cannot reproduce because they cannot survive if they cannot adapt through phenotypic plasticity [4]. Against these exogenous factors, plants can survive under difficult conditions despite the regression in development by showing short-term physiological or longer-term adaptation resulting from evolutionary mechanisms [5].

Plants in nature are divided into two groups: Halophytes (salt plants), which can develop in high salt accumulations by activating problem response mechanisms in terms of salt tolerance, and glycophytes, which are affected and damaged by high salt levels. Most glycophytic plants, defined as higher plants, such as the vegetables and fruits we consume, are in this scope and are sensitive to high salt concentrations [6]. However, responses to salinity vary among plant species and cultivars. In particular, it has been reported that the first phenotypic response of glycophyte plants to an increase in salinity in the root zone over weeks or months is a decrease in shoot growth [7], reporting that the most sensitive organ is the leaves. Depending on the tolerance level of the plant, salt stress inhibits growth and can cause chlorosis, necrotic spots, decrease in yield and quality, and even death. The toxic effect of salt first begins to appear on old leaves. This effect manifests itself as chlorosis, starting from the leaf tips and progressing to the leaf blade and stem, and then these parts become necrotic. The growth rate of plants grown in salty conditions is low, stunting occurs, the leaf surface becomes smaller and the color becomes darker [8, 9].

The interactions of woody plant species with salt stress are more complex [10, 11]. As long-lived species, they must cope with adverse conditions by developing different mechanisms depending on the stage of development [12], intensity and duration of environmental conditions [13, 14]. Some long-term studies for fruit trees have shown that salts accumulate in woody tissue for several years, followed by a rapid decline in tree growth when concentrations become toxic [15]. When salt storage capacity is exceeded, Na^+ moves towards the leaves, rapidly killing the tree [16]. However, to understand why some fruit species and cultivars are more tolerant to salinity than others, the underlying mechanism needs to be well understood [17]. Such mechanisms include changes in morphology, anatomy, water relations, photosynthesis, hormonal profile, toxic ion distribution and biochemical adaptation [18, 19]. The responses of plant species to salt stress vary according to the duration and degree of stress [mild, moderate, severe], the type of plant, the stage of plant development and the regions of the plant [20, 21]. Some fruit species are more tolerant at the seedling stage, while others exhibit higher tolerance during vegetative growth, flowering, or fruiting periods.

2. Adverse effect of salt stress

In the light of the studies, salinity stress, ion toxicity (Na^+ and Cl- accumulation), osmotic stress and nutritional disorders are the three factors that inhibit plant growth [22, 23]. When the salt concentration in the soil solution increases and the water potential decreases, the osmotic potential of root cells decreases and the division or elongation of plant cells suddenly slows down [24]. The increase in salt also inhibits the expansion of cell walls [25]. Under these stress conditions, plants usually try to conserve water and reduce transpiration by closing their stomata with the increase of abscisic acid. Thus, the plant tries to minimize water loss and prevent the uptake of high amounts of salt along with water from the soil. As a result, photosynthesis decreases and if these stress conditions continue, it causes plant growth to stop completely [26, 7]. If this situation continues for a long time, leaf photorespiration stops, causing severe defoliation and the sudden death of the plant [19]. Decrease in biomass accumulation, decrease in stem, and shoot length, decrease in plant wet and dry weights, decrease in leaf area and number, decrease in chlorophyll content, deterioration in yield, fruit taste and color [21]. When the plant is under salinity stress for a long time, ion toxicity and water deficiency in old leaves and carbohydrate deficiency and related symptoms in young leaves are recorded [27].

The detrimental effects of Na^+ cation and Cl- anion on the green parts were determined by radioactive markers. In terms of photosynthetic capacity, both ions can significantly inhibit photosynthesis and carbohydrate assimilation and therefore, if not corrected, can have negative consequences on the economic value of the crops. The sodium damage symptoms start much earlier than chlorine [28]. Typical symptoms of chlorine stress are mid-leaf burning and green tip blight. Tip blight and burn cause chlorosis. In advanced stages, necrotic tissue can cover 50% or more of the leaf, resulting in a large decrease in the photosynthetic activity of the plant [29]. The distribution of sodium in various plants is of great importance. Although the concentrations of Na^+ ion in leaves are very low, it is commonly more abundant in roots [30]. In addition to the decrease in growth rates, CO_2 fixation per unit area decreases with the decrease in leaf area. All this is accompanied by increased respiration. Since the plant, which consumes a lot of energy to survive, cannot replace what it spends by photosynthesizing less, development and growth are retarded. The decrease in net CO_2 fixation under salt stress is due to water deficit, closure of stomata, accumulation of salt in the chloroplast and loss of turgor in mesophyll cells or direct toxicity of salt ions [31, 29].

2. Exclusion tolerance in salt tolerance

2.1.Exclusion level at cellular level

Some woody glycophyte species have developed various mechanisms for adaptation to salt stress [32]. Salt tolerance in plants is divided into those that prevent salt entry into the plant and those that minimize salt accumulation in the cytoplasm. In the first mechanism in woody plants, plants avoid different physical, physiological, and metabolic obstacles due to the negative effects of salt stress. They do this by excluding salt from the cells and tissues of the plant and preventing the accumulation of Na^+ and Cl^- [33]. During this adjustment, it tries to prevent ion entry and maintain cell membrane integrity by increasing the accumulation of suberin in cell membranes. Secondly, intrinsic mechanisms ensure successful survival despite the effects of salt stress [34]. Once salt enters the plant cell, it tries to control the intracellular salt flow by controlling the activity of aquaporins. It tries to prevent ion toxicity caused by salt and to maintain osmotic balance by accumulating salt in vacuoles within the cell and distributing it intercellularly [35].

2.2.Exclusion mechanism from root zone

Regarding salt exclusion by fruit trees, they have several mechanisms to cope with salt in the soil. First, the roots of many fruit trees have the ability to exclude salt by selectively absorbing water and nutrients while minimizing salt uptake [36]. Studies at the cellular level in the root zone have shown that salt accumulates in sinks in the root [13]. The results indicated that different cultivars has an exclusion mechanism in the root xylem parenchyma cells that restricts the uptake and transport of Na^+ or Cl^- [37]. Na^+ accumulation in the root region increased with salt application, and salt accumulation was observed in root voxels. It was reported that the accumulation of suberin in the endodermis and exodermis layers, which are apoplastic barriers in the root cell, increased with salt stress (Figure 1). It was reported that seedlings obtained from hybridisation studies prevented ion entry in the root cell more. Thanks to hybrid rootstocks, it was stated that there was less salt accumulation in the root voxel of the hybrid rootstock [38]. It has been reported that species with superior rootstock quality are able to exclude salt through different apoplastic adjustments from roots to shoots, which play a role in reducing toxic ion fluxes [39, 40].

Regulating salt uptake through root systems is a common strategy. Fruit trees have the ability to control the movement of salt into their roots by actively selecting and excluding ions that are harmful or not essential for their growth [41]. These cultivars have genetic traits that allow them to accumulate lower levels of sodium in their tissues, withstand salt-induced osmotic stress and maintain favorable water balance [42].

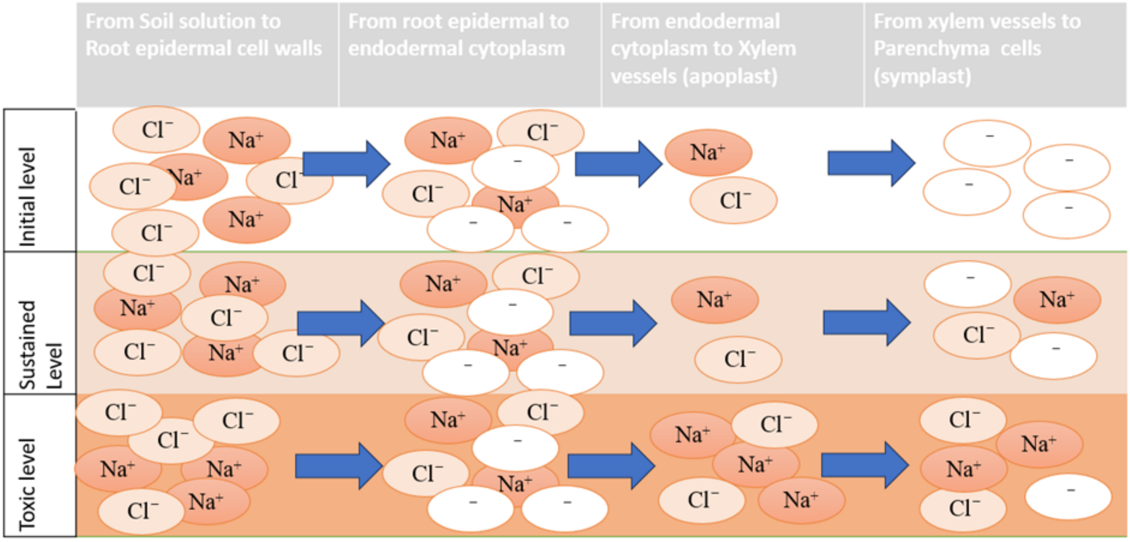

Figure 1. Possible changes in membrane potentials under exposure to high salinity in the root or stem [11]

Fungi and bacteria, including decomposers and organic matter decomposers, mycorrhizae contribute to the breakdown of organic matter in the soil. This process improves soil structure, aeration and drainage, creating an improved root environment for fruit trees [43]. The contribution of arbuscular mycorrhizae (AM) and inoculation of fungal strains in the root zone is important for salt exclusion [44]. Arbuscular mycorrhizae support the growth and health of fruit trees by forming symbiotic relationships with their roots, forming a network of fibers (hyphae) that extend beyond the reach of the tree's roots. These hyphae have access to nutrients in the soil that the tree cannot access, such as phosphorus and micronutrients. This increased nutrient uptake helps to improve the overall health and growth of fruit trees [45]. Mycorrhizal hyphae can also increase water absorption by increasing root surface area and exploring a larger soil volume [46]. Some mycorrhizal fungi and bacteria produce growth-promoting phytohormones such as auxins and cytokinins. These hormones can stimulate root growth and branching, leading to healthier and more robust root systems. Through this symbiotic relationship, mycorrhizae increase the potential for salt accumulation in root vacuoles, thereby excluding salt and preventing its transport from the roots to the upper parts of the plant. The overall effect of these symbiotic relationships is enhanced plant growth, which can translate into increased fruit production, better fruit quality and potentially higher yields. It can increase the ability to tolerate various environmental stresses such as salinity. It is important to note that not all fruit tree species have the same mycorrhizal associations and the benefits provided by these symbiotic associations may vary depending on factors such as soil type, tree species and environmental conditions [47].

2.3.Exclusion mechanism from grafting point at the stem

Rootstock compatibility in fruit trees refers to the successful fusion and growth of pen and rootstock, ensuring that they can grow together harmoniously. Some grafted on rootstock combinations may have better compatibility, resulting in healthier and more productive fruit trees [48]. It has been stated in studies that woody tissue acts as a sink and the suberin structure accumulates the salt in the parts that act as this sink and does not allow the salt to pass to the xylem and phloem socket located in the inner part of the woody tissues [49]. It was stated that Na$^+$ and Cl$^-$ concentrations can be significantly reduced as the movement of water due to transpiration from the xylem to the parenchyma cells and from there to the cell membranes [50]. It was concluded that this exclusion contributes to the protection of leaves against Na^+ and Cl^-toxicity [51]. It was stated that the use of salt-tolerant grafted rootstocks is important in reducing the amount of Na^+ and Cl^-in plants. It has been reported that Cl^-in the leaves circulates through the phloem and takes Na^+ with it and travels back to the grafting point, where it excludes sodium and chlorine ions [11].

It has also been stated that strong rootstock-penciller scion matching greatly affects this system [52]. Researchers have indicated that in perennial plants, parenchyma cells can store ions at greater rates than root and leaf tissues, but at the same time, they can ensure survival, potentially limiting their Na storage capacity over time [53]. In 10-year-old grafted trees, Na^+ and Cl^-concentrations increased as one moves from the cambium to the xylem, and significant decreases in Na and Cl^-in the graft union were observed over the years for both PGI and UCB1 rootstocks. In addition, the growth ring formed annually in the stem was used to determine sodium exclusion in the studies. A significant decrease in the amount of Na^+ and Cl^-ions was observed as the age ring approached the outside [11].

2.4.Exclusion mechanism from leaves

Foliar sodium exclusion is a process by which plants limit the uptake and accumulation of excess sodium (Na+) through their leaves. High levels of sodium in plant tissues can be detrimental to plant health and growth, especially in environments with saline soils. Foliar sodium exclusion mechanisms help plants to maintain a favourable balance of essential nutrients and ions while preventing sodium toxicity [54]. Some salt-tolerant fruit tree species may accumulate salt in older leaves, resulting in leaf thickening, defoliation or the growth of new leaves that are not affected by salt. This process, known as salt secretion or salt excretion, helps to prevent salt accumulation in the tree's system [55, 56, 57]. The cuticle is a waxy layer on the surface of leaves that acts as a physical barrier, limiting the entry of ions, including water and sodium, into the leaf tissue. The outer layer of epidermal cells also acts as a barrier to prevent excessive sodium uptake. Some plant species, especially those adapted to saline environments, have specialized structures in their leaves called salt glands or salt trichomes. These glands actively secrete excess sodium and other salts to the leaf surface and prevent their entry into the plant [58, 56]. Plant cells undergo a salt acclimation phase with ion channels and transporters that selectively allow some ions to enter while excluding others [59]. It can actively transport essential ions such as potassium (K^+) into cells, except sodium. Leaves can compartmentalise sodium ions in specific vacuoles within cells. This prevents sodium from interfering with vital cellular processes and reduces the risk of sodium toxicity in the cytoplasm [60].

Some plants can replace sodium with other cations such as calcium (Ca_2^+) or potassium (K^+) through ion exchange processes. This helps to maintain a favorable ion balance in plant tissues [54]. Stomata are small openings in the leaf surface that regulate gas exchange and water loss. Plants can adjust the opening and closing of stomata to control sodium entry into the leaf. Under high sodium conditions, stomatal closure can help reduce sodium uptake [61, 62]. Some fruit species have developed physiological adaptations that allow them to tolerate high sodium levels [63]. These adaptations include minimising water requirements by increasing leaf moisture content, the presence of antioxidant enzymes such as CAT, SOD and APX in the cell membranes or young leaves, preomotic changes, regulation of genes to adapt to salt tolerance, and salt exclusion [64, 65, 66]. In cases where salinity has a toxic effect, it has blunted the immunity of old leaves through the signaling of abscisic acid, one of the growth inhibitory hormones, but it has been reported that some genes that are the signaling component of salicylic acid, which is specified as an exclusion phytohormone, are active in young leaves [67, 68].

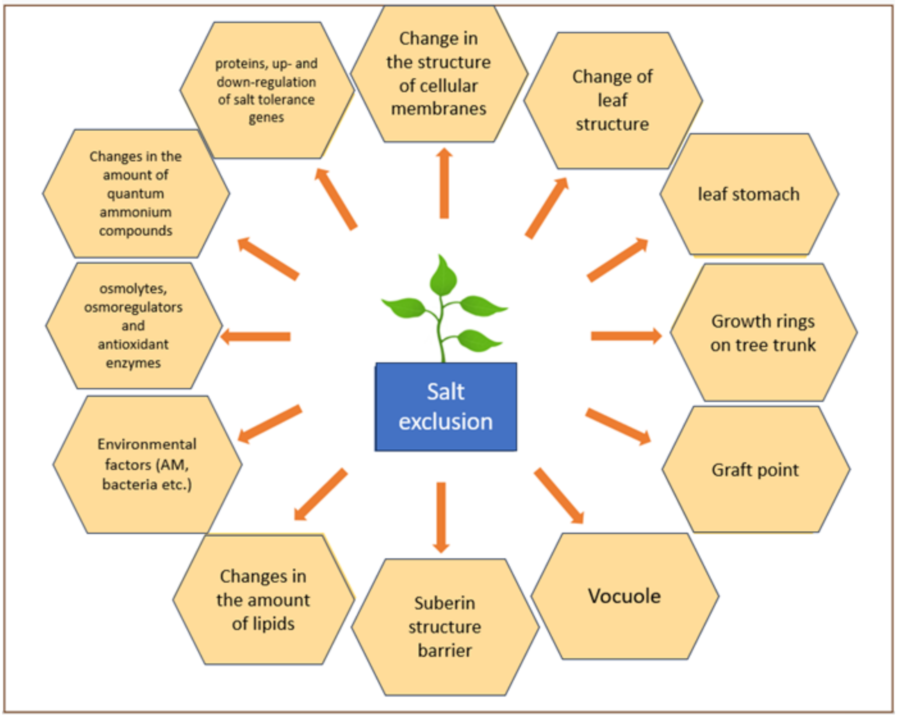

Figure 2. Salt exclusion on woody plants

3. Conclusion

The uptake and accumulation of salt ions by plants were found at different rates in various organs of woody species (Figure 2). Growth, physiological and biochemical mechanisms of salt tolerance and exclusion differed among species and cultivars. The efficiency of these mechanisms may vary among plant species and depends on factors such as genetic traits, environmental conditions, soil properties and the severity of sodium stress. In addition, while foliar sodium uptake can help plants cope with sodium stress to some extent, the best strategy to manage high sodium levels in soil requires selecting appropriate plant species, improving soil drainage and salinity management, and providing appropriate irrigation practices to prevent excessive sodium accumulation. It has been reported that rootstock alone does not play a role in salt tolerance, and that a combination of strong rootstock and penciller scion that can adapt to salt and rootstock-penciller scion compatibility may be more successful. At the same time, there are also studies in which hybridization studies yielded positive results.

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