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### Anatomical Changes of Cultivated Plants under Combined Stress: An Urgent Need for Investigation



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**G**LOBAL food production and its quality face a lot of challenges, which already decreased the availability of these foods. These challenges were mainly linked to global climate changes and their ramifications, which are expressed as environmental stresses like drought, flooding, low or high heat stress. The new pandemics like COVID-19 also represent a new challenge for the entire world. Although, there are increasing concerns about combined stress on cultivated plants, more studies are still needed to cover botanical issues including physiological, morphological, biochemical and histological traits. Further studies are required to focus on different combined or multiple stresses in particular the individual stress is rare in the nature. This is an invitation for publication reviews, comments, notes and original articles about the anatomical changes in stressful plants particularly under combined stress. The EBSS journal also welcomes the serious and promising studies, which will handle the environmental issues related to stress in the era of COVID-19.

**Keywords:** Salinity; Drought; Waterlogging; Physiological parameters, Morphological features

#### Introduction

Cultivated plants face generally during their growth environmental stresses including abiotic and biotic stress (El-Ramady et al. 2019). These stresses include drought, salinity (Akcin et al. 2017), waterlogging (Bansal and Srivastava 2017; Tian et al. 2021), high or low temperatures, high or low light, flooding, deficient or excess nutrients (Adejumo et al. 2020) and heavy metals (Abdalla et al. 2020; Stavridou et al. 2021; Seleiman et al. 2021). Several studies have been focused on the single or individual stress as a simple study

but recently increasing concerns on combined stress have reported like drought and heat stress (Duc et al. 2018; Parvathi et al. 2020; Li et al. 2021; Stavridou et al. 2021), salinity and heat stress (Bayoumi et al. 2021; Shalaby et al. 2021), salinity and nutrient stress (Chrysargyris et al. 2019; Pandey et al. 2019), drought and pathogen infection (Dixit et al. 2019; Gupta et al. 2020), drought and element stress (Naz et al. 2021), salinity and waterlogging stress (Duan et al. 2018; Duhan et al. 2018; Gill et al. 2019; Cheng et al. 2021), etc.

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Under environmental stress, many adverse impacts or changes in cultivated plants could happen on physiological, morphological, biochemical and molecular attributes as well as the anatomical features (Stavridou *et al.* 2021). The phytotomy or plant anatomy as an important discipline in plant biology started hundred years ago (may be the late 17<sup>th</sup> century) and still includes enormous reports in the literature based on the great efforts of several scientists like Theophrastus (Greek scientist), Gaspard Bauhin (Swiss physician and botanist) and Marcello Malpighi (Italian botanist). The first edition of the classic Plant Anatomy was published by Katherine Esau in 1953 and recently many distinguished books have been published such as Cutler *et al.* (2007), Beck (2010), Maitiet *et al.* (2012), Steeves and Sawhney (2017), Schweingruber and Börner (2018) and Fitzgerald (2020). The anatomical data could be applied for better understanding of the interrelationships of plants with the surrounding environment (Bákonyi *et al.* 2020). Therefore, the concepts of plant anatomy and its structure may provide us with a clearer picture of the interrelationship of cultivated plants under changing environments (Crang *et al.* 2018). The applied plant anatomy is considered a powerful tool that has been used to solve a lot of baffling problems particularly under stress in many recent studies (e.g., Ribeiro *et al.* 2019; Bákonyi *et al.* 2020; Bueno *et al.* 2020; dos Santos *et al.* 2020; Lobato *et al.* 2020; Moura *et al.* 2021).

Therefore, this review represents an attempt to highlight the potential changes of plant anatomy under different stressful conditions. This work is also a call for more and more studies on anatomy of different cultivated plants under combined stress as a promising tool in tolerating these cultivated plants to abiotic/biotic stress.

#### *Changes in cultivated plants under stress*

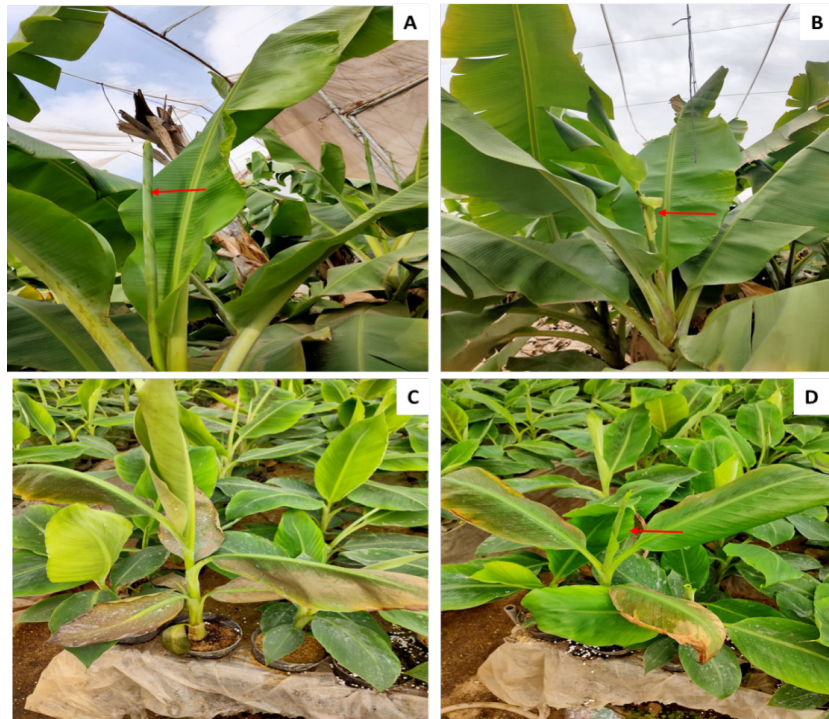
During the next decades, global food production and its quality may have serious challenges including global climate changes, which lead to several stresses particularly temperature rising, drought, flooding and rainfall reducing (Hosseini *et al.* 2021). These stresses already have been individually investigated several decades ago, but in the last decade more concerns have been paid towards the combined and multiple stresses on crop productivity like banana (Figs. 1-3). It is well documented that “*plants under combined stresses exhibit a prominent shift in molecular responses compared with plants exposed to the*

*same stresses independently*” (Gupta *et al.* 2020). The main mirror, which reflects any changes in stressful plants is the plant genes besides the morphological, physiological, biochemical and anatomical features. These genes could be identified the responses of stressful plants to individual and combined stressors at the gene expression level (Hosseini *et al.* 2021). we could list some published studies during the last five years on the combined stress on cultivated plants in Table 1.

Under stress, different changes might be impaired in morphological, physiological and biochemical traits and processes in stressful plants. These processes may include all biological processes in stressful plants such as leaf photosynthesis (Fan *et al.* 2020), metabolism of pollens (Nischal and Sharma 2020), and nearly all processes. The biochemical traits may include the antioxidant defense system and enzymes, whereas the physiological parameters may include all physiological processes like photosynthesis and the morphological features involve all features linked to the shape of plant organs like leaves, stems, and roots (Seleiman *et al.* 2021). The anatomical features are still needed to be investigated in stressful plants.

#### *Call for anatomical studies*

Under stress, plants should transport carbohydrates *via* phloem into tissues for the plant defense and its survival. The general response of stressed plants represents in control of water loss from stomata to guarantee the plant integrity and its water supply (Sala *et al.* 2010). This stomatal control of loss water may be linked to the leaf anatomy and its resilience or due to the efficiency of plant hydraulic system (Sevanto 2019). Under water stress, the plants could close the stomata earlier when they have a higher xylem vulnerability to embolism (i.e., less robust root system) compared to plants that have low xylem vulnerability (McCulloh *et al.* 2012). Recently, during drought many questions have gained attention about the importance of plant C-reserves and their redistribution to improve the prediction of plant survival under stress (Sala *et al.* 2010; Savage *et al.* 2016). It has been reported that the transport *via* phloem beside xylem may also be directly influenced by stress (e.g., drought) and the hydraulic connection may allow phloem using the xylem as a water source, but under water deficit (i.e., increasing the water tension) could limit the capacity of phloem transport



**Fig. 1.** stress on banana plant, (A) healthy plant with normal shoot tip (red arrow); (B) Cold stress with calcium deficiency (red arrow); (C) heat and drought stress on banana seedling and (D) Restoration plant from heat stress (red arrow)



**Fig. 2.** Stress on banana plant, (A) Normal banana farm; (B) Banana farm suffering the drought stress; (C) Plant at the first stage of drought stress and (D) Plant suffering hard of drought stress



**Fig. 3. Stress on banana plant due to the large difference between day (29 °C) and night (8 °C) temperature; (A) normal shoot tip growth; (B) abnormal shoot tip growth**

**TABLE 1. List of some published studies on combined stress on some cultivated plants**

Cultivated plant	Combined stress	Main findings	Reference
Cucumber ( <i>Cucumis sativus</i> L.)	Salinity and heat stress	Grafting improved the productivity of cucumber and its fruit yield quality under studied stresses	Bayoumi et al. (2021)
Lentil ( <i>Lens culinaris</i> L.)	Drought and heat stresses	Regulation the response to these stresses are linked to multiple genes, which related to the antioxidant activity	Hosseini et al. (2021)
Sunflower ( <i>Helianthus annuus</i> L.)	Uranium and Cd stress	Applying PGRs was promoted plant growth and photosynthesis and alleviated toxicity of U and Cd stress	Chen et al. (2021)
Yellowhorn ( <i>Xanthoceras sorbifolium</i> L.)	Drought and heat stress	This plant mitigated combined drought and heat stress through modulation of ROS homeostasis and stomatal closure	Li et al. (2021)
Maize ( <i>Zea mays</i> L.)	Drought and chromium stress	Applied salicylic acid and the polyamine spermidine may boost the maize tolerance to studeied stresses	Naz et al. (2021)
Cucumber ( <i>Cucumis sativus</i> L.)	Salinity and heat stress	Applied nano-Se, silicon and H <sub>2</sub> O <sub>2</sub> can boost the plant tolerance to studied stresses by controlling stomatal opening and regulating the osmotic balance	Shalaby et al. (2021)
Tobacco ( <i>Nicotiana tabacum</i> L.)	Heat and drought stress	The gene of Pvgstu3–3 plays a leading role in protecting against combined studied stresses	Stavridou et al. (2021)
<i>Arabidopsis thaliana</i>	Drought and bacterial infection	The amelioration of combined stress was regulated by gene of ath-miR164c through the proline biosynthesis pathway	Gupta et al. (2020)
<i>Arabidopsis thaliana</i>	Drought and bacterial infection	At GBF3 gene can confer the tolerance to combined drought and <i>Pseudomonas syringae</i> stress as bacterial infection	Dixit et al. (2019)
Spearmint ( <i>Mentha spicata</i> L.)	Salinity and copper stress	Under salinity (150 mM NaCl) and excessive Cu stress (60 μM Cu) decreased nutrient content in leaves Zn, N and K and in roots K, Ca, P and Mg	Chrysargyris et al. (2019)
Barley ( <i>Hordeum vulgare</i> L.)	Water logging and salinity stress	Identification the quantitative trait loci for ROS tolerance in barley as an important tool in future breeding programs	Gill et al. (2019)
Tomato ( <i>Solanum lycopersicum</i> L.)	Drought and heat stress	The inoculation of arbuscular mycorrhizal particularly with <i>Septoglomus constrictum</i> can support tomato tolerance to these stresses	Duc et al. (2018)

Abbreviation, PGRs: Plant growth regulators, ROS: reactive oxygen species,

(Sevanto 2014; Dannoura et al. 2018; Sevanto et al. 2018). Similarly, under pathogens damage or insects the phloem might be limit and re-direct the transport of carbohydrates. The capacity transport through phloem may be also connected to the control stomata of photosynthesis by its impact on concentration of leaf sucrose (carbohydrate) based on the importance of phloem transport in plant survival under stress (Sevanto, 2019).

Plants may undergo many biochemical and anatomical adaptations under stress conditions to survive depending on the kind of stress (e.g., drought, salinity, waterlogging, heat stress, etc.). Under water deficit stress for example, the most important anatomical parameters, which suppress the growth of cultivated plants may include root cortex thickness, root diameter, chlorophyll contents, leaf phloem area and leaf midrib thickness, leaf vascular bundle area, stem diameter, stem vascular bundle area and stem phloem area (Ghafoor et al. 2019). Regarding paddy rice, rice roots could not grow under water deficit stress, but this stress strongly impeded the growth of roots and lateral root proliferation. It could be noticed also that, with increasing water deficit stress, an increase in the lignification, suberization and thickening of the endodermis of rice roots may result stronger radial barriers for water flow in rice especially near the root apex (Ouyang et al. 2020).

Concerning waterlogging stress, the individual or combined stress of waterlogging and salinity was confirmed to be more deleterious compared to alone previous stress (e.g., Duhan et al. 2016, 2017a, b, c; 2018; Duhan and Sheokand 2020). These previous studies confirmed that, under saline-hypoxic (salinity-waterlogging) conditions, pigeon pea plants could form aerenchyma in roots to be tolerant against this deleterious condition. For barley plants, tolerant genotype to waterlogging had a much larger number of adventitious roots compared to the sensitive ones, as well as more leaf intercellular spaces and better integrated chloroplast membrane structures in tolerant ones, which could increase the content of ethylene, decrease content of ABA and less accumulation of ROS (Luan et al. 2018).

Soil salinization over the last few decades has reduced more than 50% of the global production of main crops, whereas, half of the arable lands will be affected by 2050 (Shao et al. 2019). Based

on the salinity stress is considered one of the most common and important abiotic stress worldwide, a survey on the anatomical behavior of some cultivated plants under salinity stress was listed in Table 2. Recently, more studies have published including the anatomy of different cultivated plants under stress such as heat stress on *Rhododendron* (Shen et al. 2017), flooding on poplar (Peng et al. 2017), waterlogging on pigeonpea (Bansal and Srivastava 2017) or on wheat (Shen et al. 2020), drought stress on *Eucalyptus* (Otto et al. 2017) or sorghum (Guha et al. 2018) or poplar (Lu et al. 2019), *Schinus molle* under lead stress (Ribeiro et al. 2019), water deficit on pigeonpea or gum tree (Lobato et al. 2020; Bueno et al. 2020), zinc (Zn) stress on soybean (dos Santos et al. 2020), copper stress on barley (Minkina et al. 2020) and lead stress on some plants (Adejumo et al. 2020). Whereas, some plants like Jerusalem artichoke have cultivated under many stresses like stress low temperatures (Mu et al. 2021), salinity (Shao et al. 2016, 2019; Fang et al. 2018; Luo et al. 2018; Yue et al. 2020; Zou et al. 2020; Zhu et al. 2021), water stress (Ruttanaprasert et al. 2016), drought (Puangbut et al. 2017) and waterlogging (Yan et al. 2018a).

## **Conclusions**

Many crops can grow well under stressful conditions due to their physiological and biochemical properties, which support these plants under stress conditions. The anatomical properties of some grown plants under stress have been reported in many studies, but more investigations are needed. Increasing concern about cultivated plants' histochemical studies under stress has been noticed, including the anatomical parameters such as leaf trichomes, stomatal density, upper epidermal thickness, lignification suberization, and thickening of the endodermis. Further studies are essential to highlight these plants' behavior under stress through the measurement of the anatomical parameters. Therefore, this is a call for publication reviews and original articles related to plants' histological changes under combined stress.

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**TABLE 2. Some published anatomical studies under salinity stress on some cultivated plants**

Plant species	Salinity stress	Anatomical and other findings	Reference
Passion fruit: <i>Passiflora</i> spp.	From 0.3 to 6.3 dS m <sup>-1</sup>	Severe anatomical and morphophysiological changes could be altered under salinity	Moura et al. (2021)
Pennyroyal ( <i>Mentha pulegium</i> L.)	50-150 mM NaCl	For stressed tissues, vibration (100 Hz) induced aerenchyma formation, stele diameter and phloem, a supporting mechanism for inhibition of salt transport to leaves and providing photo-assimilates	Ghalkhani et al. (2020)
Passion fruit ( <i>Passiflora edulis</i> Sims)	150 mM NaCl	A negative effect of salinity for almost evaluated anatomical traits except stomatal density and upper epidermal thickness	Lima et al. (2020)
<i>Eucalyptus urophylla</i>	250 mM NaCl	Applied 24-epibrassinolide supported plants under salinity by increasing spongy parenchyma by 25%, stomatal density by 23%, palisade parenchyma 14%	de Oliveira et al. (2019)
Passion fruit: <i>Passiflora</i> spp.	From 0.3 to 6.3 dS m <sup>-1</sup>	Salinity causes anatomical alterations like greater thicknesses in leaf mesophyll, palisade parenchyma, lower epidermis, upper epidermis and spongy parenchyma	Moura et al. (2019)
Alfalfa ( <i>Medicago sativa</i> cv. Gabès)	150 mM NaCl	Salinity increased lower internodes of stems, the number of lignified phloem fibers also is increased, and their wall thickness is augmented compared to control	Ben Nja et al. (2018)
Sand lily ( <i>Pancreatium maritimum</i> L.)	400 mM NaCl	Egyptian seeds are salt-tolerant than Italian seeds due to high enzymes activities (e.g., amylase, catalase, esterase and peroxidase) and unique spongy, black, thick seed coat which may act as barrier to salt ions	Mohamed et al. (2018)
Olive ( <i>Olea europaea</i> L.)	60 mM NaCl	Salinity induces an increment of total phenols (58%) and an increment of epidermis thickness and scavenging activity in green stage olive, enhanced fruit quality	Moretti et al. (2018)
<i>Salicornia freitagii</i> L.	Saline soils 2.3 – 46.3 dS m <sup>-1</sup>	Stem thickness, length and width of water-storing tissue increased and the diameter of pith in stem under high saline soil, where xylem thickness and diameter of vessels decreased at higher salinity	Akcin et al. (2017)
Soybean ( <i>Glycine max</i> L. Merr.)	2-10 g L <sup>-1</sup> NaCl	Higher NaCl caused smaller root diameter, stele, xylem tissues and cortex thickness; increase the diameter of xylem vessels and ruptured the peripheral layers of roots	Khasanah and Maryani (2017)
Zucchini squash ( <i>Cucurbita pepo</i> L.)	60 mM NaCl	under salinity conditions, anatomical changes in leaves were recorded: increase in palisade, lamina, thickness of spongy parenchyma, intercellular spaces	Rouphael et al. (2017)
Pigeonpea ( <i>Cajanus cajan</i> L. Millsp.)	30 mM NaCl	Under saline-hypoxic (salinity-waterlogging) conditions, pigeon pea forms aerenchyma in roots to be tolerant against this deleterious condition	Duhan et al. (2017c)

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