PLANT SCIENCE TODAY
Vol x(x): xx–xx
https://doi.org/10.14719/pst.8794

eISSN 2348-1900

REVIEW ARTICLE

Tea (*Camellia sinensis* (L.) O Kuntze) under waterlogging stress: A comprehensive review on adaptation mechanisms and crop improvement opportunities

Md Riyadh Arefin[1,2], Md Ismail Hossain[1], M Abdul Aziz[1], Md Sabibul Haque[2] & A K M Golam Sarwar[2*]

[1]Botany Division, Bangladesh Tea Research Institute, Srimangal 3210, Bangladesh
[2]Department of Crop Botany, Bangladesh Agricultural University, Mymensingh 2202, Bangladesh

*Correspondence email - drsarwar@bau.edu.bd

Received: 10 April 2025; Accepted: 31 August 2025; Available online: Version 1.0: 10 November 2025

Cite this article: Arefin MR, Hossain MI, Aziz MA, Haque MS, Sarwar AKMG. Tea (*Camellia sinensis* (L.) O Kuntze) under waterlogging stress: A comprehensive review on adaptation mechanisms and crop improvement opportunities. Plant Science Today (Early Access). https:/doi.org/10.14719/pst.8794

Abstract

Tea is one of the most consumed beverages worldwide, cultivated in nearly 64 countries. Although a significant amount of water is required for proper growth of tea plant, excessive moisture or waterlogging conditions are detrimental to tea yield and quality. Waterlogged conditions in tea hinder root respiration, accumulate toxic metabolites and alter several physiological descriptors such as leaf yellowing, stomatal closure restricting photosynthesis, leaf senescence, wilting and oxidative damage. Plants immediately respond to waterlogging stress by adapting their morphological structure, such as promoting adventitious root development and aerenchyma formation, or by regulating their defence system, for instance, triggering the accumulation of osmoprotectants and enhancing antioxidant activities to facilitate normal plant functioning. Most of the current research have concentrated on how tea plants respond to waterlogging, but there is a lack of information on the in-depth mechanisms behind the responses. Again, unlike other crop perspectives, crop improvement studies to overcome this issue are also severely insufficient. This review discusses morphological, physiological and biochemical reactions of tea plants to waterlogging stress, with a hypothetical possible mechanism behind the responses. Many possible opportunities are suggested to boost waterlogging tolerance through modern and conventional breeding approaches. This paper also mentions some knowledge gaps, providing future research thrusts with systemic critiques of present studies.

Keywords: crop improvement; energy metabolism; redox homeostasis; tea; waterlogging tolerance

Introduction

Waterlogging is one of the burning issues that affects crop yield. As a consequence of global climate change, lands have become inundated frequently and sometimes it prevails for a longer time. On the contrary, other parts of the globe become drier. Several causes are responsible for creating waterlogging situations, such as changes in rainfall patterns, uneven seasonal distribution, excessive rainfall within a short period, poor drainage, over-irrigation, high water table, etc. (1). Waterlogging replaces air by water in the soil pores, leading to hypoxia (decreased oxygen level) or anoxia (no oxygen) conditions, which are detrimental to crop growth (2, 3). During waterlogging stress, plant root systems are affected primarily due to a lack of sufficient oxygen. Under transient waterlogged conditions, plants temporarily switch to anaerobic respiration; nevertheless, the situation becomes more severe when waterlogging persists for longer periods. In excessive moisture conditions, plants become vulnerable to normal functioning due to anaerobic respiration, producing less energy (ATPs), reducing photosynthesis due to stomatal closure, accumulating toxic metabolites, overproducing reactive oxygen species (ROS), etc. (4–8). Leaf chlorosis, leaf senescence and wilting of plants are also common disorders that could lead to plant death under severe waterlogged conditions or if the plant is susceptible to waterlogging (9, 10).

Tea is one of the major health-beneficial drinks having antioxidant properties and is grown around 64 different countries worldwide from high altitude (Himalayans foothills of Nepal, Darjeeling (India), etc.) to low altitude (Ruhuna of Sri Lanka, Misiones and Corrientes provinces of Argentina, etc.) and flat lands (Northern region of Bangladesh, flat terrain of Kenya, etc.) (11). Several abiotic factors might hinder tea yield, including high or low temperatures, waterlogging, salinity, drought, etc. Sufficient moisture is one of the prerequisites for proper growth and quality green leaf production; yet, tea plants are highly sensitive to prolonged waterlogging (12). Generally, tea is cultivated in sloppy lands to avoid waterlogging, but lands between slopes suffer from serious waterlogging problems due to infiltration or percolation movement of water. Currently, tea is also cultivated in plain lands in many countries where frequent waterlogging persists due to poor drainage or excessive rainfall. Waterlogging is caused by excessive rainfall and has been a primary challenge in recent years, decreasing tea yield in numerous nations, including Bangladesh (13–16). In Bangladesh, waterlogging has affected nearly every tea estate in the Sylhet division to varying degrees (16). It is a major issue in North-East Indian tea plantations, causing the industry to lose 15–25 % of its production each year (17). Heavy rainfall and flooding caused a 10 % reduction in tea yield in Assam and West Bengal (18). In Sri Lanka, a drastic reduction in yield, as well as recovery percentage, was observed after a severe flood in the Ratnapura district (19). Waterlogging stress in tea plants slows down morphological structure (decreased plant height, root length and dry matter as well as increased number of dead leaves, etc.), hinders physiological attributes (decline in stomatal conductance, photosynthesis, transpiration, etc.) and biochemical modulations (proline, antioxidant, wax, flavonoid and phenolic contents) (20, 21). Tea liquor quality decreases (22) while pest and disease infestations increase during excessive moisture stress (23). Waterlogging problem in tea could be solved by proper drainage, cultivation in sloppy lands and controlled irrigation; however, using waterlog-tolerant varieties from a successful breeding program might be the most economical, user-friendly and sustainable solution to mitigate this problem.

The conventional breeding program (mainly hybridization and individual selection) of tea is a complicated one. Tea crop exhibits high self-sterility with a cross-pollinated nature, which leads to huge variations in progenies (24). Again, a plant takes more than 5-7 years to bear flowers with full potential; thus, it also takes longer periods for hybridization program, usually 20-25 years for a new variety (25). Again, individual selection requires natural seedling population for the exploitation of variations. This is also a time-consuming process due to longer and uneven rooting pattern of vegetative cuttings (takes 2-3 years in nursery) (26). Despite these problems, several waterlog-tolerant tea varieties (clones) have been developed through the conventional breeding approach in few countries, such as TV9, SNT-10, MNPR/51/P2, GNGA/31/P3, GNGA/31/P4, DFLGR/34/P8 and Clone-1 of Rupai Plot in India and TRI 2023 in Sri Lanka (19–21, 27, 28). Waterlog-tolerant varieties in many crops have been developed through both conventional and modern breeding approaches; however, advanced strategies regarding varietal development in tea are still scanty (16).

Although the waterlogging problem in tea plants becomes worse day by day, limited research has been conducted regarding tolerance mechanisms and ways of improvement approaches of tea under waterlogging stress. This paper aimed to provide a comprehensive review on the responses of tea plants to waterlogged conditions, along with their adaptive mechanisms and perspectives on approaches to crop improvement, with a key focus on conventional and modern breeding programs. This review also identified some research gaps that may serve as a focus for future research interest for waterlogging in tea.

Waterlogging stress and its classification

When soil is completely or almost fully saturated with water, it is referred to as 'waterlogging' condition of soil. In most cases, the air phase is restricted where anoxic conditions prevail. Several plant developmental processes are hampered by waterlogging, which limits aerobic respiration and reduces growth. The deficiency of oxygen in waterlogged soil can hinder plant root growth, resulting in root rot and inadequate nutrient absorption, which eventually leads to stunted growth, wilting, chlorosis and potentially plant mortality. Waterlogging may be categorized into two types: transient (intermittent) and continuous (2). Transient waterlogging occurs when soil gets momentarily saturated with water, usually following severe rainfall, irrigation, or flooding (1). Transient waterlogging is crucial because of the severe damages, including oxidative damage and this may be worsened when tissues are re-aerated after a stressful event. Depending on the soil type and drainage conditions, excess water typically drains out from the soil and soil recovers to a non-saturated state within few days or weeks (2). Short-term or transient waterlogging raised oxidative stress and fermentation, resulting in limited ATP production in soybean roots (4), reduced growth and yield attributes in mungbean (7), hindered entire flowering and boll formation stage in cotton (8), or 29.0–77.5 % death in *Dalbergia sissoo* in the age of 25–32 years (9). Conversely, continuous waterlogged areas refer to regions that stay submerged in water for prolonged periods, frequently as a result of inadequate drainage, high water tables or persistent water inflow sources. Long-term waterlogging is also harmful to plants. It can induce oxygen depletion and lower the redox potential in the soil, which has a major impact on plant root health and growth (5, 6). Continuous waterlogged situation affects carbohydrate and free amino acids metabolism and ROS scavenging pathways in *Actinidia valvata* (29), hinders growth characteristics, biomasses and mineral contents or even death in *Albizia lebbeck*, *Melia azedarach*, *Morus nigra*, *Pongamia pinnata*, *Salix apanese* and *Taxodium disticum* species (10).

Another classification of waterlogging based on moisture availability in plant root zone is also mentioned in several studies. Three different types of plant root zones, such as normoxia, hypoxia and anoxia, are identified based on gas diffusion under wet conditions (3). Normoxia is referred to as the healthy soil condition for plant growth with proper aeration. When oxygen level is reduced to below optimal level, it turns to hypoxia, which decreases oxygen uptake for respiration, decreases photosynthesis and energy for growth, yield and reproduction as well (9, 29). Anoxia is the phenomenon when soil is completely saturated with water and soil is fully devoid of oxygen, caused by long-term flooding or waterlogging (3). Reduced vessel density, vessel area and vessel diameter were observed in apple during anoxia (long-term waterlogging), while hindering growth, even death, was observed in jackfruit during root hypoxia (3, 10).

Waterlogging problem in plants

In many shrub and tree species, waterlogging has emerged as one of the main abiotic stressors affecting both productivity and quality, such as peach (30), coconut (31), cotton (32), coffee (33), tea (34), etc. Waterlogging on fruit trees causes wilting and scorching leaves, leaf chlorosis and drop, fruit drop, regressive death of the stem and limb dieback and even plant death (35). Waterlogging also affects growth phases of different crops. For instance, a significant decline in number of fruit nodes, boll number, weight of boll, as well as higher boll dropping, rot rates, was observed in cotton with the increase of the duration of excessive moisture stress days (32). Again, it was also found that the development process of plant growth, such as number of leaves, stem growth, root number and others, was greatly affected by high moisture stress conditions (36).

Toxic metabolites (ethanol, aldehydes and lactic acid) due to anaerobic respiration are concentrated and ROS (H_2O_2, O_2^-, etc.) are produced when plants are exposed to waterlogging situations because the O_2 supply in their roots is disrupted and the gaseous exchange of CO_2 is limited (37). Additionally, stomatal closure, caused by waterlogging, directly hinders respiration and photosynthesis, which has a significant effect on plant growth and crop yield (32, 38). The enzymes involved in photosynthesis were inhibited under conditions of prolonged waterlogging; the capacity of leaves to synthesize chlorophyll declined, resulting in senescence, yellowing and peeling; the production of new leaves was delayed and finally, the photosynthetic rate declined, ultimately causing the plants' death (39). Different dynamics of waterlogging effects on different plants are provided in Table 1.

General adaptation strategies of plants to waterlogging

Different plants trigger various morphological, physiological, biochemical and molecular responses to cope with the waterlogging stress. Modification of root cellular structure, like formation of adventitious roots (Ars), aerenchyma and hypertrophic lenticels, is the prime and basic adaptation in many plants (40). In hypoxia or anoxia conditions, where the concentration of O_2 becomes minimum or absent, some plants shift to anaerobic respiration by following ethanol, lactate or alanine fermentation pathways for generating energy in the form of adenosine triphosphate (ATP) (41). Some plants show their potential to increase shoot or root growth (length) to facilitate more gas exchange and nutrient uptake (42). Increased antioxidant capacity may improve stress tolerance, as well as higher antioxidant levels and increased antioxidative enzyme activity, which are thought to be adaptive strategies for combating waterlogging stress circumstances. All aerobic organisms develop a sophisticated antioxidative defense system that resists the detrimental effects of oxygen radicals by either enzymatic or non-enzymatic systems. This system includes synthesis of diverse antioxidative enzymes like superoxide dismutase (SOD), catalase (CAT), peroxidases (POD), glutathione reductase (GR) and ascorbate peroxidase (APX), as well as non-enzymatic antioxidants like ascorbate (AsA), glutathione (GSH), carotenoids and other phenolic compounds (43, 44). Plants tend to induce the synthesis and signalling of several phytohormones to cope with waterlogging stress. For instance, ethylene (ET) helps to promote aerenchyma formation and adventitious roots; abscisic acid (ABA) regulates stomatal closure; jasmonic acid increases phenolic, sugars and flavonoid compounds; and gibberellin helps to elongate internodes and shoot length (37, 45). Some genes, like anaerobic metabolism genes, *ethylene response factor* (*ERF*) and *WRKY* transcription factors, genes affecting symbiotic haemoglobins (*Hb*), have also been identified, which are associated with waterlogging tolerance, such as *SUB1A, OsSD1, OsEIL1a, AtRAP2.12, HvADH4, ZmEREB180, nsHb1* (43). High tolerance is also characterised by quick recovery from flooding stress. Several genes were noticed for fast recovery after stress, such as *RESPIRATORY BURST OXIDASE HOMOLOG D (RbohD), SENESCENCE-ASSOCIATED GENE113 (SAG113)* and *ORESARA1* genes involved in bursting of ROS, synthesis of phytohormones (abscisic acid and ethylene), etc. (46).

Waterlogging problem and adaptation mechanisms in Tea

Tea is a perennial crop in which leaves are harvested and widely cultivated in sandy loam soils. The water requirement of tea plants is very high; however, it becomes detrimental to plant growth when soil pore spaces become waterlogged or saturated with water (47). Tea plants suffer from waterlogging conditions during the monsoon rather than winter (48). In the area of the root zone (less than 90 cm depth), waterlogging or a high groundwater table is detrimental, resulting in retarded growth and sometimes being lethal (49). Tea plants cannot thrive in regions with persistent waterlogging, as they are extremely sensitive to stagnant water (12). Waterlogging causes morphological, physiological and biochemical changes in tea plants and tolerant varieties show an accumulation of proline and increased wax content during such conditions (Fig. 1). Detailed changes and adaptation mechanisms are described below.

Morphological changes

Tea bushes that have been waterlogged appear weak; their plucking points are drastically decreased, red rust attacks the stems, their roots become shallow, twisted and bunchy and they have a natural tendency to grow upward, resembling an inverted umbrella. Defoliation and a lack of new leaf production result in weak and sparse canopies, which are the most noticeable characteristics of damaged tea bushes (49). Newly developed roots are generally found to be white and eventually turn brown when aged, whereas delicate black roots signify dead roots during flooding (50). Many crop species experienced a substantial shift in root colour from dark brown to black during waterlogging, such as *Pinus thunbergii* (51). The tips of the roots also tend to die and the lenticels expand, roughening the surfaces, observed in tea plants while subjected to long-term waterlogging conditions (52). Due to their lack of feeder roots, these plants are unable to effectively use the reserve starch, which hinders their ability to recover after pruning and results in poor growth (53).

In case of cotton, the highest reduction in plant height (31.50 %) and leaf area (40.02 %) was observed during squaring and flowering stages respectively, while plants were subjected to 10 days of waterlogged conditions (8). Some yield-related attributes of *Camellia oleifera*, such as number of leaves, plant height, stem base diameter and root-shoot fresh weight, decreased significantly when seedlings were grown in waterlogged conditions than the control (54).

The most unique and successful adaptation strategy of plants during flooding conditions is to develop aerenchyma tissue in roots. Aerenchyma is a specialized spongy type of tissue that has large intercellular spaces, which helps to supply gases (especially atmospheric and photosynthetic O_2) from aerial portions to waterlogged roots, facilitating aerobic respiration (55). During waterlogging, aerenchyma in roots generally develops by two possible ways. The first one is due to the expansions of schizogenous intercellular spaces, while second one is the cortical cells death (lysigeny) (56). The whole process is initiated by the synthesis of ethylene, which is triggered by *APETALA2/ERF* (*AP2/ERF*) domain superfamily genes in adventitious root (57). *AP2/ERF* is one of the largest transcription factor families in plants and the *ERF* gene family is one of its subfamilies, which is responsible for stress tolerance in plants (58). The primary transcription factors controlling the expression of genes linked to waterlogging stress are *Group VII ERFs* (59). Ethylene in various crops is synthesized by different genes during hypoxia or anoxia. ERF and WRKY transcription factors (TF) are responsible for waterlogging-induced changes in sesame (60), while overexpression of RAP2.2 helps to detect low O_2 rapidly in rice (61). Numerous unique genes in *Chrysanthemum morifolium*,

Table 1. Organ-specific morpho-physiological and biochemical disorders of different plants under waterlogging stress

Action	Occurring zone	Occurring reasons	Effect on plants	References
Anaerobic respiration	Root	Lack of O_2	Provide lower energy than aerobic respiration as a temporary solution	(1)
Toxic metabolites (Ethanol/ lactic acid) accumulation	Root	Anaerobic respiration	Cell death and plant senescence	(37)
ROS production	Root	Incomplete electron transport in mitochondria during anaerobic metabolism	Cellular damage, root decay and plant senescence	(29, 37)
Nutrient uptake interruption	Root	Low transpiration (less water movement leads to less nutrient accumulation), root damage, nutrient unavailability	Reduce N, P, K uptake and increase Al^{3+}, Fe^{2+} and Mn^{2+} solubility, leading to toxicity.	(5, 6, 10)
Accumulation of stress hormones (such as Ethylene, ABA, etc.)	Root and leaf	Gene expression and signalling	Stomatal closure, development of root aerenchyma	(29)
Accumulation of stress osmotytes (proline, antioxidants, reducing sugars)	Root and leaf	Gene expression and signalling	Maintain osmotic balance, create immediate stress response to protect cells	(20)
Closure of stomata	Leaf	Decrease xylem water potential, hormonal biosynthesis	Reduced photosynthetic and gas exchange activity, conserve energy and protect against oxidative damage	(21, 32, 38)
Limited Gas Exchange	leaf	Closure of stomata	Disrupted respiration, photosynthesis and nutrient uptake	(3)
Reduction of photosynthesis	leaf	CO_2 deficiency due to stomatal closure, Chlorophyll pigment degradation	Reduced growth and yield, plant senescence	(32, 38)
Leaf chlorosis/ senescence, plant senescence, limited yield or even plant death	Whole plant	All the reasons mentioned above	reduction in growth and yield	(6, 7, 9, 10, 35, 39)

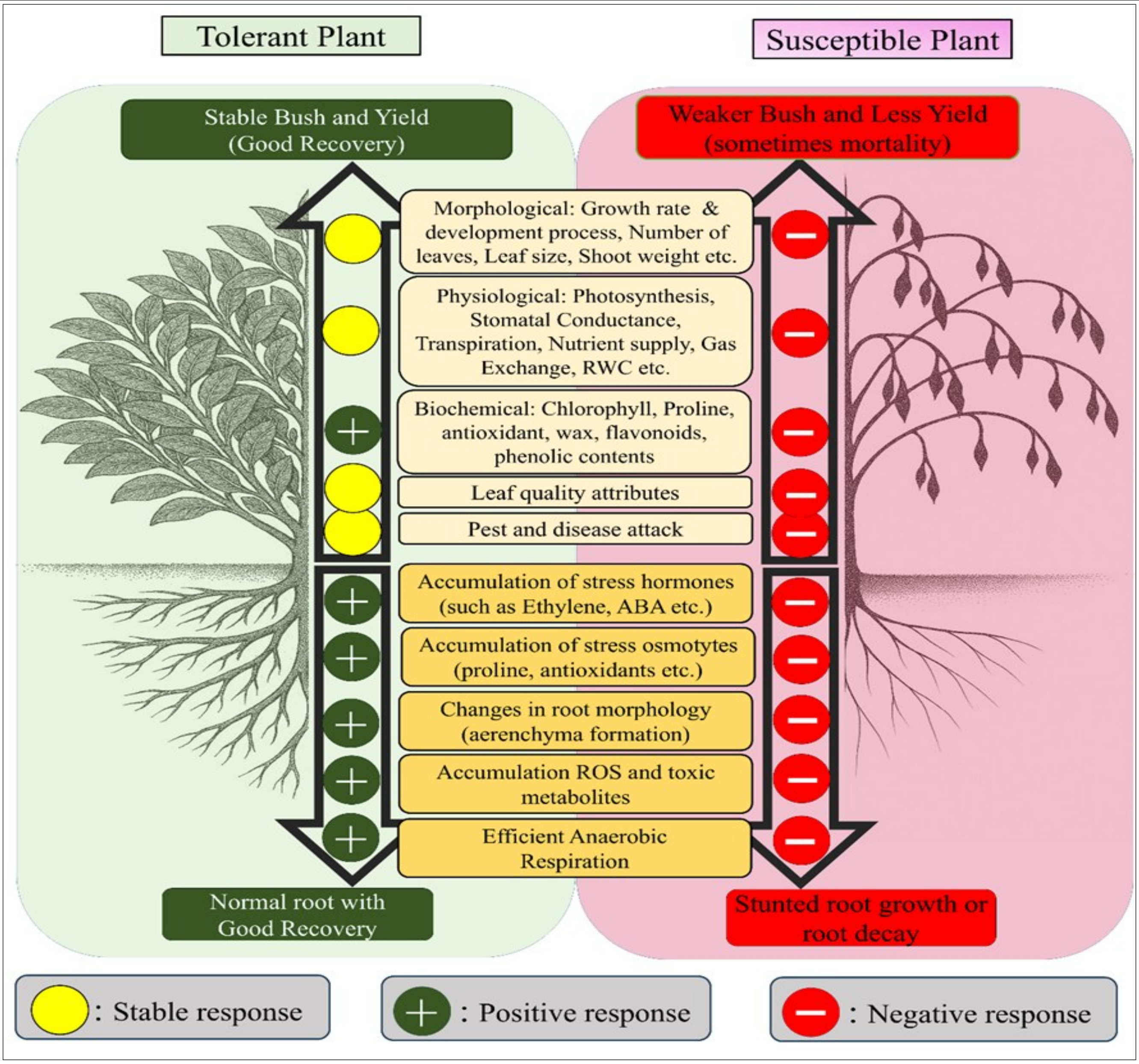

Fig. 1. Response of waterlogging in both susceptible and tolerant tea plant.

such as *Defensin SD2*, *Snakin-2-like*, *HSP83-like*, *ClpB1*, *ATG18a* and *MBF1c*, have also been studied for waterlogged conditions. These *Group VII ERFs* genes expressing 1-aminocyclopropane-1-carboxylic acid synthase (ACS), 1-aminocyclopropane-1-carboxylic acid oxidase (ACO) and other enzymes involved in ethylene production have been demonstrated to be significantly upregulated resulting from waterlogging stress (62). The genome of the tea plant contains 178 *AP2/ERF* genes (*CsAP2/ERFs*) and these genes have a wide contribution to face biotic and abiotic stresses. For example, 9 candidate *CsAP2/ERFs* genes in tea were found to be associated with spring bud break in various light and temperature combined treatment experiments (63). Another study found that tea plant growth was regulated by 90 *CsERF* genes, some of which also contributed to its growth for cold stress tolerance (64). Again, anthracnose disease of tea was successfully tackled by *CsERF105,* a nuclear-localized transcription factor located in qARChr1 locus (65). Aerenchyma tissue was observed in the roots of tolerant tea plants after 45 days of flooding stress (66). Although aerenchyma plays a crucial role in plant adaptation to hypoxic conditions in tea plants, detailed regulatory mechanisms governing its formation are still insufficiently understood and need to be explored thoroughly.

Physiological responses

Long-term exposure to excessive water in the soil causes a series of successive physiological problems in tea plants. It ultimately generates reduced photosynthesis, chlorophyll pigment degradation, decreased leaf water potentials, chlorosis of leaves, blackening of the roots, poor absorption of nutrients, plant senescence and even plant death (67). Generally, during waterlogging stress conditions, leaf chlorophylls (chlorophyll a and b) are found to be decreased; on the contrary, anthocyanin contents are detected to accumulate by UDP-glycosyltransferase (*UGT*) gene family in leaves as stress indicators (68, 69). Several research studies have been conducted to solve abiotic stress problems, but research on the waterlogging problem in tea is very much insufficient (14). Genotypes MNPR/51/P2, GNGA/31/P3, GNGA/31/P4 and DFLGR/34/P8 were identified as highly tolerant to waterlogging stress after total root zone submergence (21). Reduced amount of chlorophyll content, inducing leaf chlorosis, leaf water potential and abscission of leaf were observed due to a longer period of waterlogging. They also observed that waterlogging affected stomatal conductance (gs), transpiration (E) and photosynthesis (Pn) in a declining manner. Degree of tolerance against excessive water stress among some TRA garden series clones like Sanyasithan 8 (SNT-8), Sanyasithan 9 (SNT-9), Sanyasithan 10 (SNT-10) and Sanyasithan 27 (SNT-27) was also assessed by some scientists (17). They found that, after full root zone submergence stress, photosynthesis (Pn), transpiration (E), water use efficiency (WUE), stomatal conductance (gs), leaf potential and chlorophyll contents (Ch a and b) significantly decreased, except for the tolerant clone SNT-10. Waterlogging-tolerant tea variety SNT-10 showed less decrease of transpiration (43.8 %) while SNT-8 and SNT-9 varieties decreased 59.6 % and 50.6 % respectively, indicating waterlogging susceptibility. In drought susceptible tea plants, the overexpression of *CsProDH1* gene reduced the efficiency of photosynthesis; in contrast, silencing this gene increased the adaptive capability by enhancing photosynthesis with increased proline synthesis and neutralised the ROS in Pro-P5C cycle (70). Stomatal behaviour plays a crucial role in photosynthesis by regulating gaseous exchange (stomatal conductance) between plants and environment. During excess moisture conditions, stomatal conductance decreases to preserve internal moisture, resulting in minimal photosynthesis, transpiration, leaf relative water content (RWC) and ultimately crop yield (71). In tea, *CsEPF1* and *CsYODAs* genes have negative correlation with stomatal behaviour (72). The behaviour of stomata is also regulated by abscisic acid (ABA), an important phytohormone (73), which has a critical role during flooding stress (74). The accumulation of ABA in tolerant tea plants under excessive water stress of 45 days was found to be maximum, i.e. three times higher than control (66). Myeloblastosis (*MYB*), WRKY, basic helix-loop-helix (*bHLH*), etc. transcription factors were found responsible for ABA synthesis during stress conditions, i.e. flooding in many crops (75). Although ABA plays a crucial role in mediating adaptive responses to hypoxic stress, the mechanism controlling its biosynthesis in tea under waterlogged conditions is still unclear. Further investigation is needed to establish the regulatory networks of ABA production and signalling in tea during waterlogging stress.

Biochemical changes

Several biochemical changes can be noticed during waterlogging in plants. One of the key indicators of stress tolerance against waterlogging is the rise of leaf proline and leaf wax production. Proline is a key solute in plants, synthesized in stress conditions *via* glutamate pathway, where the enzyme pyrroline-5-carboxylate synthetase (P5CS) plays a vital role (76). The hydrophilic nature of proline allows it to maintain osmotic balance by regulating cellular water content or turgidity. Biochemically, proline directly scavenges the superoxide radicals (O_2•-), hydrogen peroxide (H_2O_2) and hydroxyl radicals (•OH), while indirectly reducing ROS by activating the enzymes like SOD, CAT and POD (77). Antioxidant enzymes like SOD transforms O_2•- to less harmful H_2O_2 and O_2, meanwhile CAT and POD convert H_2O_2 into water, thus reducing the effects of ROS (78). During defense mechanism, the oxidation of proline generates NADH and $FADH_2$ by glutamate pathway occurs in mitochondria *via* proline dehydrogenase (ProDH) and pyrroline-5-carboxylate dehydrogenase (P5CDH) (79). This phenomenon reduces ROS leakage by supplying electrons to the mitochondrial electron transport chain during stress conditions and promotes ATP synthesis at low oxygen levels in tea (70). The genotypic variation in proline accumulation was found to be highly significant during waterlogging in tea (21). Before induction of flooding, the tea leaf proline accumulation among the genotypes varied between 0.681 to 0.937 μ mol g^{-1} of fresh weight (FW), while the leaf proline content varied between 0.01 to 3.78 μ mol g^{-1} of FW after 45 days of flooding. It was noticed a five to six-fold increase in proline content (0.7 to 3.7 μ mol g^{-1} of FW) in tea during 45 days of waterlogging compared to control (20). Also, it was recorded highest accumulation of proline (78 % increase over the control) in SNT-10 variety under 0 to 45 days of full root zone submergence (17).

Aerial parts of plants are known to experience water deficits during waterlogging conditions and preserving this finite amount of internal water is essential for survival (80). During hypoxic conditions, root suffers from oxidative stress and faces dehydration due to root dysfunction (67). The wax layer of leaf surface acts as an impermeable barrier which prevents the loss of internal water (81). Several genes were found responsible for accumulation of wax layers during stress conditions, such as transgenic *Arabidopsis* plants with elevated leaf epidermal wax formation was observed due to overexpression of the ERF-related genes *SHN* and *WIN1* (82). Waterlogging-tolerant tea plants were observed to accumulate more wax content to prevent water loss during stress conditions. It was found that wax content among selected germplasm varies between 78.54 to 130.92 µg cm^{-2} after 45 days of submergence (21). They identified four genotypes, *viz*. MNPR/51/P2, GNGA/31/P3, GNGA/31/P4 and DFLGR/34/P8, which are more tolerant to waterlogging and showed highest accumulation of waxes during stress conditions. High water use efficiency was observed (20), while a tolerant variety (TRA/D/SNT10/P3) synthesizes more leaf wax under severe waterlogged conditions. It was noticed highest (17.5 %) increase of wax content in variety SNT-10 during 45 days of higher moisture stress (17). Although the *CsKCS3* and *CsKCS18* are highly responsible for cuticular wax formation in tea leaves (83), the wax formation pattern during waterlogging by these genes still needs to be properly explored.

A wide range of flavonoids, such as flavanones, flavonols and flavanols, may be generated by tea plants during different abiotic stress conditions. Flavonoids are crucial secondary metabolites, found in tea plants that have significant impact both on the water stress response and quality of tea (84). On the other hand, the most common secondary metabolites in plants that can scavenge ROS particles are phenolic compounds. The overall flavonoid content of tea plants can rise as a result of drought stress because it can prevent the accumulation of Flavanone 3-hydroxylase (F3H) enzyme, which is involved in flavonoid production (85). Interestingly, phenolic compounds were found to vary among the tea genotypes and stress conditions in different studies (86).

Tea is one of the greatest sources of antioxidants and enzymes and the beneficial health effects of tea are directly linked with its antioxidant properties. During waterlogging, plants switch their respiration from aerobic to anaerobic. Overexpression of *FaSnRK1α* gene acts as a pivotal precursor for increasing anaerobic respiration rate during flooding stress in many crops, such as strawberry (87). An important enzyme named Alcohol dehydrogenase (ADH) also plays a vital role in anaerobic metabolism by converting acetaldehyde into ethanol and increasing ADH synthesis denotes higher waterlogging tolerance (88). Waterlogging-tolerant tea plants synthesised around 2.5 times more ADH after 45 days of flooding than non-stressed plants, indicating more effective anaerobic respiration under excess moisture (66). Langaroudi and his co-workers (89) identified DG 39 and DN varieties more tolerant to moisture deficit stress, which showed better activities of antioxidant enzymes (CAT, POD), carotenoid and polyphenol content. It was reported that four tea varieties (TV-1, TV-20, TV-29 and TV-30) were able to withstand water deficit stress for 20 days, followed by a period of rehydration (90). They observed that the tea plant suffered oxidative damage from the stress, which reduced its antioxidant capacity and altered several physiological and biochemical processes. In another study, two varieties of *Camellia oleifera* (CoH1 and CoH2) were used to examine their developmental process and leaf characterisation under waterlogged stress (WL) and also applied exogenous Spermidine (SPD) to alleviate waterlogging damages by a group of researchers (54). It was also found that both varieties can withstand waterlogged conditions a little, but applying SPD significantly increases their tolerance level against waterlogging by regulating antioxidant enzymatic activities (POD, SOD, CAT, AOX and GSH-PX), photosynthesis, osmoprotectants and several activities in root zone. Although several studies cover the antioxidant enzymatic activities in different crops under different stresses, there is a serious lack of studies for tea; therefore, an in-depth investigation is needed on biochemical changes of different antioxidative enzymes (SOD, CAT, POD, APX, GR, AOX, GSH-PX, etc.), antioxidants (AsA, GSH), phenolic and flavonoid compounds during excess moisture stress.

Liquor quality deterioration

Waterlogging or flooding conditions decrease the gallic acid and caffeine concentrations in tea plants with a significant reduction of epitheaflavic acid, epitheaflavic acid-3′-gallate and theaflavic acid, which ultimately affect the liquor quality (22). Tea leaves under low soil moisture stress showed less accumulation of polyphenols and vulnerable varieties showed this decline far more quickly than tolerant varieties (91). The liquor quality of made tea mostly depends on the concentrations of gallic acid, caffeine, catechin and phenylalanine ammonialyase (PAL). PAL, a leading substrate for polyphenol oxidase, also plays a crucial role in the biosynthesis of flavanols. It was reported different biochemical changes during low and high moisture stress with UPASI-2 (Assam), UPASI-8 (Camboid) and UPASI-9 (China), where UPASI-2 and UPASI-9 were found to be drought-tolerant and UPASI-8 was drought-susceptible (22). They also observed that all genotypes were greatly affected by drought and waterlogging stress, with fluctuations in PAL activities. The varietal and treatment interactions were also more significant than the controls, while a 40 % reduction of gallic acid concentrations was observed in waterlogging stress conditions. This reduction ultimately affected the level of theaflavins and thearubigins; hence, the liquor quality was compromised. It was observed that the Epigallocatechin (EGC), Epicatechin (EC), Epicatechin gallate (ECG), Epigallocatechin gallate (EGCG) and their total content (TC) were increased, meanwhile, the catechin content was decreased during excess moisture stress of the growing season (92).

Disease and pest infestations

Flooding has a great impact on plant defense mechanisms, which also increases their vulnerability to several diseases and pests. Waterlogging leads to anaerobic respiration, where ethanol, carbohydrates and amino acids are synthesised and these metabolites ultimately increase pathogen inoculation (93). Incursion of fungal diseases, causal organisms like *Phytopythium*, *Pythium*, *Phytophthora* and *Fusarium*, was increased during an excess moisture situation. For instance, infestations of root rot disease by *Phytophthora cambivora*, *P. cactorum* and *P. cryptogea* in apple plants were increased during waterlogging (94). Waterlogging is also responsible for pest infestation in many plants. For example, the degree of infestation by the pest psyllid (*Creiis lituratus*) was found to be increased in *Eucalyptus dunnii* plants (95). Tea bushes are severely affected by waterlogging, causing stunted growth and reducing plants' immunity against diseases and pests. Several diseases like epiphytic red rust, grey blight, dieback, etc. and many pests like *Ectropis obliqua*, tea mosquito bug (*Helopeltis*), red spider mites, trips, etc. can attack plants under waterlogged conditions. Polyphenols are natural antioxidants that enhance tea quality, which are found to accumulate less during stress conditions (91). Polyphenol content in leaves has a strong relation with tea mosquito bug infestation, *i.e.* less polyphenol content induces the attack of tea mosquito bugs (96). The severe attack of tea mosquito bug also induces frequent necrotic areas or lesions in tender shoots, which ultimately leads to die-back disease, causing blackening of young shoots (97). Waterlogging weakens the tea bush by hampering its physiological processes and reducing its natural defense capability. This weak defense system leads to high vulnerability to attack by red rust disease, which creates a serious injury to leaves and ultimately reduces the photosynthesis (49). From above findings, it can be summarized that waterlogging causes less polyphenol synthesis in leaves, which indirectly increases pest and disease susceptibility in tea. Previous researches reported that green leaf volatiles (GLVs) play a crucial role in tea plant's defense mechanism against insect infestation during stress conditions. In several stress conditions, such as drought and low-temperature situations, tea plant activates *CsCHAT1* gene, which encodes an enzyme, namely BAHD acyltransferase to release Z-3-hexenyl acetate (Z-3-HAC). This Z-3-HAC is an organic GLV compound that increases resistance from *E. obliqua* by enhancing carbohydrate (starch and sucrose) metabolism in stress conditions (98, 99). Waterlogging in tea nurseries also causes surface rooting, club callusing (no root formation of nodal cuttings), stunted growth and vulnerability to many diseases and pests (23). However, review on direct relation of waterlogging and pest-disease infestation in tea is very limited; therefore, a detailed and deep investigation is required to identify above relationships with proper mechanisms and controlling dynamics.

Hypothetical key gene pathways of waterlogging-tolerant tea plant

Flooding stress is one of the major abiotic stresses limiting water and nutrient uptake, disrupts root metabolism, reduces photosynthetic efficiency, ultimately reducing both yield and quality of made tea. As tea is regarded as sensitive to excessive soil moisture, very few cultivars exist worldwide to face waterlogging stress. Among these cultivars, the SNT-10 cultivar has emerged as a relatively tolerant genotype, showing sustained growth and productivity even under conditions of prolonged soil saturation. Previous studies reported that this tolerance was charaterised by higher photosynthesis rate, more water use efficiency, lower decrease of transpiration rate, minimum decrease of stomatal conductance, accumulation of epicuticular wax content, higher proline synthesis, greater ABA accumulation, lower leaf drop, minimal decreases of leaf pigment (chlorophyll a and b), higher ADH activity in root, higher total soluble protein content in leaf and finally development of aerenchyma tissue in roots (66). Maximum proline accumulation helped to reduce ROS and minimize oxidative stresses. Again, synthesis of ABA and wax content facilitated the stomatal conductance and maintain inner moisture respectively, which assisted efficient photosynthesis. Finally, the SNT-10 could develop aerenchyma in roots with higher ADH activity, which is a better morphological adaptation against waterlogging. Till now, only few studies have reported the response of tea plant during excess moisture. Therefore, future research on detailed mechanisms and signalling pathways with responsible genes is required to understand the causes behind the responses.

During hypoxia or anoxia, several signalling pathways were detected to withstand the stress. High tolerance may be comprised of several pathways or steps, such as activation of hormones or genes, initiation of quick anaerobic respiration, bringing morphological changes in plants and lastly fast recovery after stress. Excessive water-tolerant tea is hypothesized to be regulated by a complex interplay of gene networks and a series of metabolic pathways which is graphically illustrated with possible actions of genes, enzymes or TFs, assumed from the above discussions (Fig. 2). These may include enhanced antioxidant defense, hormonal regulation (particularly abscisic acid and ethylene), efficient carbohydrate (starch and sucrose) metabolism under low O_2 and some structural modifications such as aerenchyma formation. Genes related to *ERF*s, proline accumulation, wax biosynthesis, increased photosynthetic efficiency with leaf pigment (anthocyanin) accumulation and stomatal regulation are likely to play pivotal roles in this adaptive response. Moreover, the tolerant plant has to balance reactive oxygen species (ROS) production against oxidative stress with quick recovery from stress by a rapid and fast stress-signalling mechanism. Although there is a serious lack of knowledge for the adaptive mechanism of tea against waterlogging, this hypothetical key gene pathways not only provides insights into the genetic basis of waterlogging tolerance but also will be a guideline for developing climate-resilient cultivars.

Opportunities for crop improvement under waterlogging stress

Tea varieties with desirable characteristics have developed through conventional or modern breeding strategies in various nations (Table A1). One of the major drawbacks of the breeding methods of tea is the self-sterility, longer life span, lack of regeneration tendency during callusing and complex tree morphology (100). Very few numbers of waterlog-tolerant varieties were developed in some countries by following a conventional strategy (individual selection). Here, some possible crop improvement strategies to cope with waterlogging problem are illustrated in Fig. 3 and briefly described below.

Individual Selection

Tea is a cross-pollinated crop; hence, huge potential variations amongst traits can be observed naturally. Individual selection is used to identify potential germplasm in many crops (101), especially in tea (102). The success of the selection program mostly depends on the highly heritable traits and low genotype x environment interactions (103). The collection, conservation, appraisal and assessment of tea germplasms have received a lot of attention and effort over the last 50 years, especially in the last two decades, to fully use the abundant tea germplasms, breed more novel varieties with desirable characters and support the Chinese tea industry (104). Almost all tea-growing countries follow individual selection methodology in crop improvement programs, which has major steps like selection in seedling plantations, characterization of germplasms, nursery and field trials, etc. Waterlogging-tolerant varieties may be developed from waterlog-prone areas by the collection of potential germplasms, evaluation of germplasms based on yield and quality, artificial or field trials of the collected germplasms to qualify their waterlogging tolerance ability and finally adaptation trails in different local or regions.

Appendix

Table A1. List of some tea varieties or accessions with their special character and breeding methods around the world

Name of variety/ Accession	Country	Special Character	Breeding method	References
Sundaram	India	High yield and quality	Polyploidy method (Triploid)	(28)
UPASI 20	India	Moderate yield, highly tolerant to drought	Polyploidy method (Triploid)	(28)
TV 29	India	High quality	Polyploidy method (Triploid)	(28)
HS 10A	Sri Lanka	Cold resistant	Polyploidy method (Triploid)	(28)
TRI 3069	Sri Lanka	High yield, drought tolerant	Polyploidy method (Tetraploid)	(28)
TRFK 306	Kenya	Anthocyanin-rich	Hybridization (*assamica– cambod* hybrid)	(102)
KTRI 895/7	Kenya	Moderately high polyphenol content	Hybridization (*assamica– cambod* hybrid)	(102)
TTL-1	India	High-yield, moderate quality, drought-tolerant	Hybridization (UPASI 9 X TRI-2025)	(28)
TTL-4	India	High yielder, easy rooter, good quality	Hybridization (UPASI-10 X TRI-2025)	(28)
TRI 777	Sri Lanka	High-quality-made tea	Hybridization (Open pollination)	(102)
TRI 2022	Sri Lanka	Stem canker tolerant	Hybridization (Open pollination)	(102)
TRI 2024	Sri Lanka	Nematode tolerant	Hybridization (Open pollination)	(102)
TRI 2025	Sri Lanka	Drought and canker tolerant	Hybridization (Open pollination)	(102)
TRI 2043	Sri Lanka	Blister blight tolerant, silver tip-making quality	Hybridization (Open pollination)	(102)
TRI 3016	Sri Lanka	Nematode tolerant	Hybridization (Controlled pollination)	(102)
TRI 3018	Sri Lanka	High yield	Hybridization (Controlled pollination)	(102)
TRI 3022	Sri Lanka	Drought tolerant	Hybridization (Controlled pollination)	(102)
Zhongcha 703	China	Green tea	Hybridization (Open pollination)	(102)
Fuming 2	China	Green, black, oolong tea	Hybridization (Open pollination)	(102)
Mingguancha	China	Green, black, white tea	Hybridization (Open pollination)	(102)
Zhenong 701	China	Green tea	Hybridization (Controlled pollination)	(102)
Zhongcha 128	China	Green tea	Hybridization (Controlled pollination)	(102)
Jinzhi	China	Green, black tea	Hybridization (Controlled pollination)	(102)
Kanaemaru	Japan	Japanese green tea	Hybridization (Kanaya F 183 × Kanaya No. 13)	(102)
Danshin 37	Japan	Japanese green tea	Hybridization (Saemidori × Yumeakari)	(102)
Sun Rouge	Japan	Red coloured-liquid tea	Hybridization (Open pollination)	(102)
Benifuki	Japan	Black tea	Hybridization (Benihomare × MakuraCd86)	(102)
Minekaori	Japan	Pan-fried green tea	Hybridization (Yabukita × Unkai)	(102)
BT6	Bangladesh	High quality	Hybridization	(100)
BT15	Bangladesh	High quality	Hybridization	(100)
BT17	Bangladesh	Moderate drought tolerant	Hybridization	(100)
Sainomidori	Japan	Japanese green tea	Individual Selection	(102)
Okuyutaka	Japan	Japanese green tea	Individual Selection (seedlings of Yutakamidori)	(102)
Izumi	Japan	Pan-fired green tea	Individual Selection (seedlings of Benihomare)	(102)
Indo	Japan	Black tea	Individual Selection (seedlings of *assamica*)	(102)
TTL-2	India	Average yield, excellent quality	Individual Selection	(28)
TV9	India	Waterlogging tolerant	Individual Selection	(28)
SNT-10	India	Waterlogging tolerant	Individual Selection	(17, 20, 21)
MNPR/51/P2	India	Waterlogging tolerant	Individual Selection	(21)
GNGA/31/P3	India	Waterlogging tolerant	Individual Selection	(21)
GNGA/31/P4	India	Waterlogging tolerant	Individual Selection	(21)
DFLGR/34/P8	India	Waterlogging tolerant	Individual Selection	(21)
Clone-1 of Rupai Plot	India	Waterlogging tolerant	Individual Selection	(24)
TRI 2023	Sri Lanka	Waterlogging tolerant	Individual Selection	(19)
CH13	Sri Lanka	Blister blight and drought tolerant	Individual selection from old landraces	(102)
CY 9	Sri Lanka	Drought tolerant	Individual selection from old landraces	(102)
DN	Sri Lanka	Drought and shot hole borer tolerant	Individual selection from old landraces	(102)
H 1/58	Sri Lanka	Blister blight tolerant, high quality	Individual selection from old landraces	(102)
KP 204	Sri Lanka	Canker and low country live wood termite tolerant	Individual selection from old landraces	(102)
PK 2	Sri Lanka	Canker and blister blight tolerant, high quality	Individual selection from old landraces	(102)
Zhongcha Xicha 3	China	Green tea	Individual selection from old landraces	(102)
Taizicha 1	China	Black, Green tea	Individual selection from old landraces	(102)

Sanhua 1951	China	Black, Green, white, dark tea	Individual selection from old landraces	(102)
Tianfucha 1	China	Black, Green, white tea	Individual selection from old landraces	(102)
BT2	Bangladesh	Drought tolerant, Darjeeling flavour	Individual selection	((100)
BT4	Bangladesh	High quality	Individual selection	(100)
BT10	Bangladesh	High yield	Individual selection	(100)
BT12	Bangladesh	High yield	Individual selection	(100)
BT19	Bangladesh	White and Yellow tea	Individual selection	(100)
BT23	Bangladesh	Golden tips tea	Individual selection	(100)
Chuanmu 217	China	Green tea	Bud mutation	(102)
Zhongcha Huangya 5	China	Green tea	Bud mutation	(102)
Zhongcha 108	China	Green tea	Radiation mutation	(102)
Qianfu 4	China	Green, white tea	Radiation mutation	(102)
Zhongcha 601	China	Green tea	Bud mutation	(102)

List of abbreviations or symbols with their elaborations

Abbreviations or symbols	Elaboration
µ	Micro
ABA	Abscisic acid
ACO	1-aminocyclopropane-1-carboxylic acid oxidase
ACS	1-aminocyclopropane-1-carboxylic acid synthase
ADH	Alcohol dehydrogenase
AFLP	Amplified Fragment Length Polymorphism
ARs	Adventitious roots
AsA	Ascorbate
ATP	Adenosine triphosphate
bHLH	basic helix-loop-helix
BT	Bangladesh Tea
CAPS	Cleaved Amplified Polymorphic Sequence
Cas9	*CRISPR-associated protein 9*
CAT	Catalase
CHS	*Chalcone synthase*
CRISPR	*Clustered Regularly Interspaced Short Palindromic Repeats*
Cs	*Caffeine synthase*
E	Transpiration
EC	Epicatechin
ECG	Epicatechin gallate
EGC	Epigallocatechin
EGCG	Epigallocatechin gallate
ERF	Ethylene-Responsive Factors
et al.	Et alia and others
F3H	*Flavanone 3-hydroxylase*
FW	Fresh weight
Gs	Stomatal conductance
GSH	*Glutathione*
GWAS	Genome-wide association study
H_2O_2	Hydrogen peroxide
Hb	Hemoglobins
ISSR	Inter-Simple Sequence Repeat
MAS	Marker-assisted Selection
mol	Mole
nsHb1	*Non-symbiotic hemoglobin*
•OH	Hydroxyl radical
O_2•-	Superoxide radical
OsEIL1a	*Ethylene Insensitive3-Like Gene 1a*
P5CDH	Pyrroline-5-carboxylate dehydrogenase
P5CS	Pyrroline-5-carboxylate synthetase
PAL	Phenylalanine ammonia-lyase
Pn	Photosynthesis
ProDH	Proline dehydrogenase
POD	Peroxidases
QTL	Quantitative trait loci
RAPD	Random Amplified Polymorphic DNA
RFLP	Restriction Fragment Length Polymorphism
ROS	Reactive oxygen species
RWC	Leaf Relative Water Content
SNT	Sanyasithan
SOD	Superoxide dismutase
SPD	Spermidine
SSR	Simple Sequence Repeat
SUB1A	*Submergence 1A*
TC	Total content
TF	Transcription factors
TR	Thearubigins
TRI	Tea Research Institute
TV	Tocklai Vegetative
UGT	UDP-glycosyltransferase
UPASI	The United Planters' Association of Southern India
WL	Waterlogging
WUE	Water use efficiency

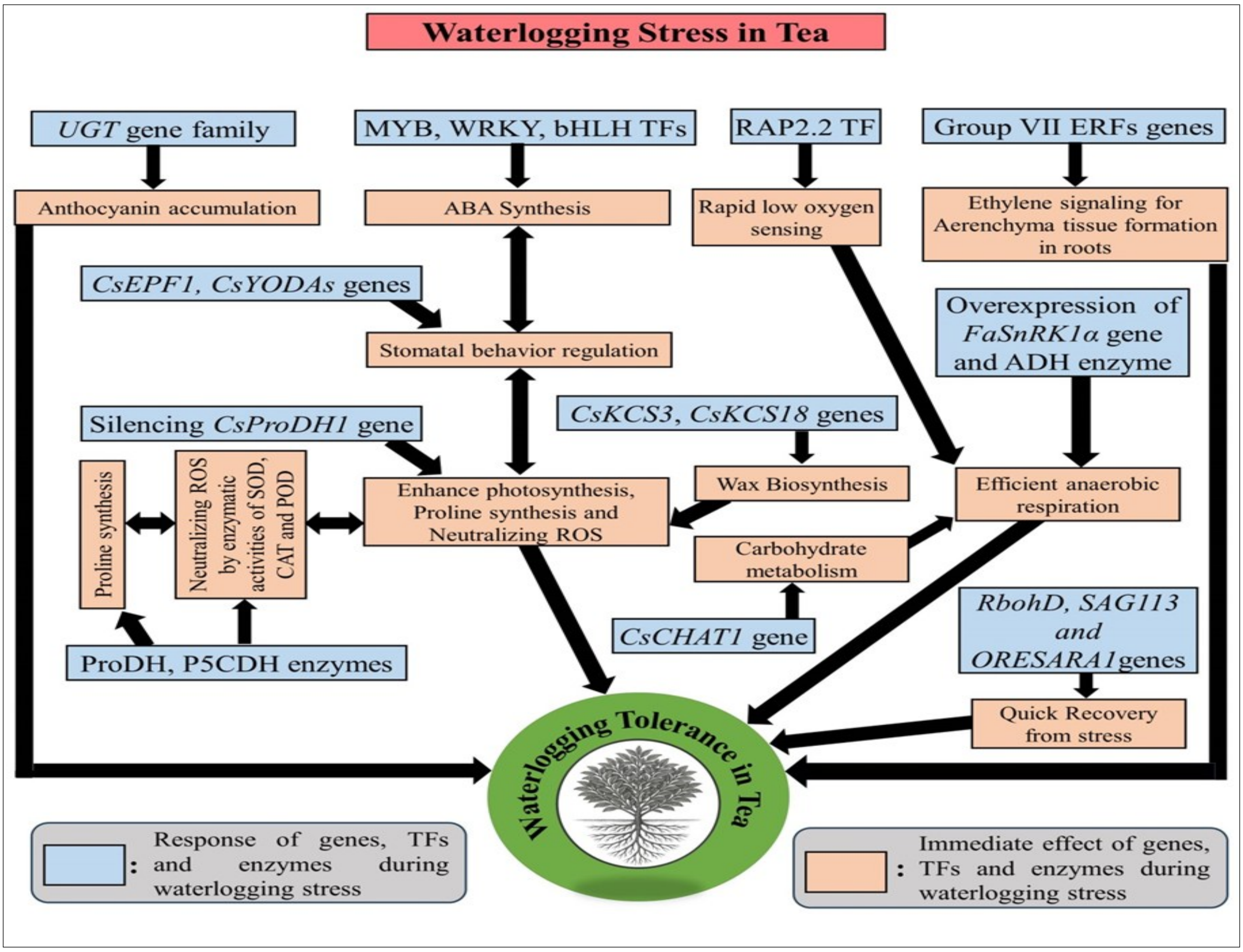

Fig. 2. Hypothetical key gene pathways for waterlogging tolerance in tea.

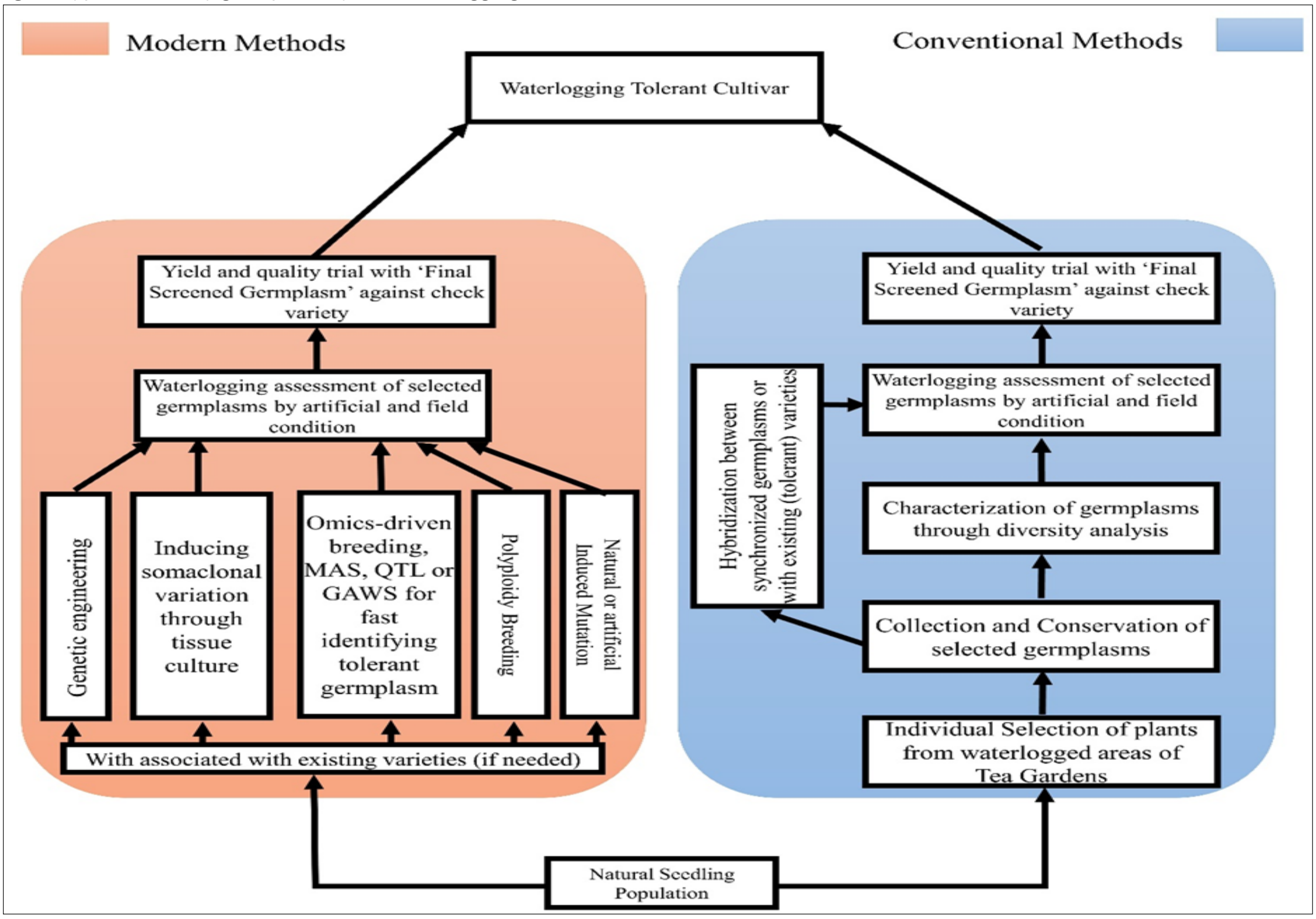

Fig. 3. Possible crop improvement strategies to mitigate waterlogging problem in tea.

Hybridization

Hybridization, one of the most commonly practised breeding methods, has been used in many crops to obtain genetic variation, desirable traits and hybrid vigour. In tea, the hybridization technique between improved varieties/landraces is carried out to achieve potential traits or characters of special interest. For instance, two hybrid progenies, later released as commercial varieties in Bangladesh, named BT6 and BT15 (Table A1), having superior liquor quality, were obtained from crossing two established varieties, BT1 and TV1 (100). Interspecific hybridization in genus *Camellia* (*C. irrawadiensis, C. taliensis, C. japonica* and *C. kissi*) has been practised in many countries to seek desirable traits, where progeny with no caffeine content was observed in *C. irrawadiensis* and *C. taliensis* hybrids (105). Hybrids of several crops were found to show tolerance against waterlogging, such as maize (106), pigeon pea (107), etc. Artificial or natural hybridization between improved varieties and waterlog-tolerant varieties can be a possible way to get more tolerance or other desirable characteristics in tea.

Mutation breeding

Mutations can be obtained chemically or physically to obtain some genetic variations, but genetic changes through mutation must be heritable. Mutants in various crops have been observed with waterlogging-tolerant potentials, such as mutation of *ZmDIR5* in maize (108). In tea generally, gamma radiation (Co60 *y* -ray) or chemicals are used to induce mutations. In China, the varieties 'Zhongcha 108' (anthracnose resistance) and 'Zhongcha 601' (high yield and quality with early sprouting) were obtained through gamma mutation of 'Longjing 43' (109). Further research on mutation breeding can lead to fulfilling the goal of a waterlogging-tolerant variety.

Polyploidy breeding

The cultivated tea plant has the genome of 2n=30, however, triploid, tetraploid, pentaploid or even aneuploid forms were found in tea, though artificially or naturally (110). Generally, leaves of polyploids have more weight; hence, the main concern of polyploidy breeding is yield boosting. Different tea-growing nations have already established their polyploids for commercial cultivation, which have some unique capabilities, for instance, Sundaram (natural triploid, high yield and quality), UPASI 20 (natural triploid, moderate yield and quality, drought tolerant) and TV 29 (natural triploid, high quality) in India. Kenya has developed '382/1' variety, which is natural triploid with high-yielding potential, whereas Sri Lanka has created HS 10A (natural triploid and cold resistant), GF 5/01 (natural triploid and high yielding), TRI 3069 (artificial tetraploid and drought tolerant) tea varieties (28). An increase in ploidy level or hybridization between the polyploids may induce tolerance against waterlogging in tea.

Omics-driven breeding, Marker-assisted selection (MAS), Quantitative trait loci (QTL) mapping and Genome-wide association study (GAWS)

Omics-driven breeding generally refers to the application of 'omics' technologies such as genomics, transcriptomics, proteomics, etc., for crop improvement (111). This is a new speed breeding technology, allows more precise selection of desirable traits, which facilitates faster development of new varieties by analyzing the complete set of genes (genomics), RNA transcripts (transcriptomics), proteins (proteomics), etc. (112, 113). A wide dimension of research was reported on the '-omics'-related works against different abiotic stresses including waterlogging in many crops. A total of 28 differentially expressed proteins (DEPs) were identified during waterlogging stress in cotton, among which 24 were up-regulated and four were down-regulated proteins (114). In soybean, up-regulated expression of luminal-binding protein 5 was detected, while arabinogalactan protein 2 and methyltransferase PMT2 were found down-regulated during excess moisture condition (115). A recent study reported that drought tolerance in tea was characterized by synthesis of lignin, flavonoids and fatty acids. This phenomenon was driven by 4789 proteins, in which 11 were found up-regulated and 100 were down -regulated (85). Again, nearly 7263 proteins were investigated, where 14 differentially accumulated proteins (DAPs) were found responsible for better cellular membrane integrity, providing tolerance against low temperature and shading stress in tea (116). Under waterlogging stress, total soluble protein was observed more in tolerant tea plants than the susceptible plants and the synthesis was lower in stress condition than non-stress environment (66). The quantity of total protein was measured during waterlogging stress, however, the behaviour, especially up-/down-regulation pattern of responsible proteins, is still unknown, which should be identified and recommended for future interest.

Conventional tea breeding is very time-consuming and laborious because it generally takes one to three decades to establish a new variety with potential traits. Different types of markers, *viz.* morphological markers, biochemical markers, isozyme markers, metallic markers, cytological markers, molecular markers, etc., exist in tea which are used for characterization of germplasm, parental identification, constructing genetic mapping and identifying the genotypes of special characters (109). By monitoring the inheritance of particular genes or DNA sequences linked to the traits of interest, molecular markers are effective tools for improving plant breeding efficiency through marker-assisted selection. Currently, various molecular markers, such as Restriction Fragment Length Polymorphism (RFLP), Random Amplified Polymorphic DNA (RAPD), Cleaved Amplified Polymorphic Sequence (CAPS), Amplified Fragment Length Polymorphism (AFLP), Simple Sequence Repeat (SSR), Inter-Simple Sequence Repeat (ISSR), have been adopted and widely applied in the tea plant. Molecular markers are also utilised to accelerate selection breeding, diversity analysis, identify genes, etc. For example, in India, cDNA-AFLPs were used to identify genes expressed in drought, SSRs were utilised in Japan and China to detect caffeine-less tea, ISSRs in China, Japan and Kenya for the assessment of genetic diversity and genetic relationship and other (117).

Finding the markers connected to important genes that underlie desired qualities is essential since the success of MAS breeding is mostly dependent on the relationship between molecular markers and desired phenotypes. QTL (quantitative trait loci) and GWAS (genome-wide association studies) analysis are typically used for genetic mapping to facilitate MAS breeding. High-density genetic linkage maps are generated using informative molecular (DNA) markers to identify the quantitative trait locus (QTL) of significant characteristics, such as yield and quality traits, resistance to disease and pests and tolerance to different abiotic stresses. It was studied the performance of forty-two genotypes for QTL identification by AFLP, SSR and RAPD markers (118). One QTL (EST-SSR073) was identified by using SSR markers for blister blight disease resistance in 'TRI 2043' and 'TRI 2023' cross (119), while another QTL (AFLP_CS_87) was for drought tolerance in the 'TV-19' × 'TV-20' cross (120). GWAS is another strong analytical approach, based on the linkage disequilibrium principle, which is mostly utilized to uncover genetic loci linked to particular attributes. More gene enhancement, editing, or altering can be possible by GWAS because it contains more alleles than QTLs (121). It was recognized 10 Single Nucleotide Polymorphisms (SNPs) within the *F3'5'H* gene from 202 tea germplasms, while one SNP within chalcone synthase (*CHS*) gene was discovered from 176 tea accessions by GWAS for catechin content (122). MAS breeding is very sophisticated, yet it is globally used for different biotic or abiotic stress tolerance in tea (119) as well as to overcome waterlogging problems in rice (*Sub1* gene), barley (*tfy1.1-3, tfsur-2 tfsur-1, tfy1.1-1, tfmas, tfy2.1-2* gene), soybean (*Rps* gene), etc. (123). So, future research should be conducted to mine the waterlogging tolerance genes in tea to withstand this stress.

Somaclonal variation through tissue culture

Plant tissue culture is a rapid multiplication method that is used in many crops. However, sometimes variations can be observed in callus, protoplast, tissue, or even in plants due to uncertain mutations, which are known as somaclonal variations. Somaclonal variants are tolerant to many stresses, including waterlogging conditions in many crops (124). Five somaclonal variants, which were low-temperature stress tolerant and thus suitable for cultivation in higher altitudes, were developed from somatic embryos of variety UPASI-10 and characterised by 'membrane stability index' (125). Another study found that a white tea variety named 53KA10 showed most somaclonal variation amongst 12 genotypes using 8 SSR markers (126). Further study is recommended to establish a valid protocol for somaclonal variation through tissue culture against waterlogging tolerance.

Genetic engineering

Genetic engineering, or creating transgenic plants, is one of the major, fast and very sophisticated breeding strategies to create variations, to induce tolerance, or to attain resistance against different biotic or abiotic stressors. Inserting or editing tolerant genes in targeted crops may increase the adaptability to many adverse environments. Successful progress was found in many studies for *Agrobacterium*-mediated gene transfer in tea plants. For example, blister blight resistance was obtained by *chitinase* gene and *1,3-β-glucanase* gene from potato into tea plant, where efficiency was found 2.2 % and 1.97 % respectively (127). It was adopted *A. rhizogenes*-mediated protocol for *CsMYB73* gene transformation to regulate theanine biosynthesis in tea (128). Particle bombardment protocol was optimized (129) with the introduction of gene, while a caffeine-free transgenic plant was obtained (130) through *A. tumefaciens*-mediated protocol with *caffeine synthase* (*Cs*) gene in tea. Genetic transformation or engineering techniques are being utilized in many crops to mitigate waterlogging problems. For instance, waterlogging tolerance capability was enhanced by the transformation of the *CabHLH18* gene in hot pepper (131) and by transfer of ascorbate peroxidase (APX) cDNA from the *Solanum melongena* to rice (132). Recently, CRISPR (Clustered Regularly Interspaced Short Palindromic Repeats) technology, in conjunction with the CRISPR-associated protein 9 (*Cas9*), has transformed the domain of genetic engineering since its identification as a bacterial adaptive immunological mechanism. It has been used in tea breeding to develop disease-resistant plants and improve tea quality through precise genetic alterations (133-135). Although genetic engineering has not yet achieved any success in increasing tolerance levels against waterlogging in tea, further research can facilitate the solution.

Conclusion

Waterlogging is a major constraint to sustainable tea production, hampering morphological, physiological and biochemical activities, which causes serious crop loss and quality deterioration. The generic responses of tea plants under flooding stress have been reported by several short-term studies. However, the real-time response in field conditions, interaction of soil water-nutrient cycle during hypoxia or anoxia and recovery mechanism after stress conditions, are still remain unexplored. In-depth future study is recommended to unveil the background phenomenon with genomic study regarding the tolerance mechanism for waterlogging stress of tea, highlighting the activity of antioxidants, ROS production, proline and wax accumulation, development of aerenchyma, pest-disease relationship, etc. Breeding strategies for tea are still constrained by flowering habit, perennial nature, lack of precise screening tools and so on. Systemic studies on molecular markers, genomics selection, transcriptomics, proteomics, tissue cultureand genetic engineering for tolerance mechanisms are scarce till now. Therefore, future investigations should be concentrated on developing precise, robust selection indices, exploiting wild germplasms for desirable genes and applying modern biotechnological tools to accelerate the crop improvement program for waterlogging tolerance in tea.

Acknowledgements

The first author (MRA) is thankful to the Ministry of Science and Technology, Government of the People's Republic of Bangladesh (https://most.gov.bd/) for the National Science and Technology Fellowship (memo no: 39.00.0000.012.02.009.24.24, date: 30.01.2025) during the study period.

Authors' contributions

MRA participated in data collection and writing the original draft manuscript. MIH and MAA did resources and editing. MSH conceptualised, visualisation of data and editing. AKMGS did conceptualisation, editing, formatting and finalizing the manuscript. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interest to declare.

Ethical issues: None

References

1. Kyu KL, Taylor CM, Douglas CA, Malik AI, Colmer TD, Siddique M, et al. Genetic diversity and candidate genes for transient waterlogging tolerance in mungbean at the germination and seedling stages. Front Plant Sci. 2024;15. https://doi.org/10.3389/fpls.2024.1297096

2. Morales-Olmedo M, Ortiz M, Sellés G. Effects of transient soil waterlogging and its importance for rootstock selection. Chil J Agr Res. 2015;75(Suppl. 1):45–56. https://doi.org/10.4067/S0718-58392015000300006

3. Zahra N, Hafeez MB, Shaukat K, Wahid A, Hussain S, Naseer R, et al. Hypoxia and anoxia stress: plant responses and tolerance mechanisms. J Agron Crop Sci. 2021;207(2):249–84. https://doi.org/10.1111/jac.12471

4. *da*-Silva CJ, do Amarante L. Short-term nitrate supply decreases fermentation and oxidative stress caused by waterlogging in soybean plants. Environ Exp Bot. 2020;176:104078. https://doi.org/10.1016/j.envexpbot.2020.104078

5. Luo H, Liu S, Song Y, Qin T, Xiao S, Li W, et al. Effects of waterlogging stress on root growth and soil nutrient loss of winter wheat at seedling stage. Agronomy. 2024;14(6):1247–57. https://doi.org/10.3390/agronomy14061247

6. Malik AI, Colmer TD, Lambers H, Setter TL, Schortemeyer M. Short-term waterlogging has long-term effects on the growth and physiology of wheat. New Phytol. 2002;153(2):225–36. https://doi.org/10.1046/j.0028-646X.2001.00318.x

7. Naher N, Alam AKMM, Zannat O. Short-term waterlogging effect on growth and yield of mungbean. J Sher-e-Bangla Agric Univ. 2022;13 (1&2):41–48. https://saulibrary.edu.bd/sauj/jsau/v-13-n-1-2/v-13-n-1-2-a-5.pdf

8. Wang H, Chen Y, Hu W, Wang S, Snider JL, Zhou Z. Carbohydrate metabolism in the subtending leaf cross-acclimates to waterlogging and elevated temperature stress and influences boll biomass in cotton (*Gossypium hirsutum*). Physiol Plant. 2017;161(3):339–54. https://doi.org/10.1111/ppl.12592

9. Basak SR, Basak AC, Rahman MA. Impacts of floods on forest trees and their coping strategies in Bangladesh. Weather Clim Extrem. 2015;7:43–48. https://doi.org/10.1016/j.wace.2014.12.002

10. Khamis MH, Hariri MF. Effect of prolonged waterlogging on growth and mineral content of different forest tree species. In: XIV World Forestry Congress. Durban, South Africa; 2015. p. 1–11. https://foris.fao.org/wfc2015/api/file/55168b3a75ecfcd11a935ad2/contents/6bd8ea6e-eab0-4e18-803d-60068cb74b11.pdf

11. FAO. Crops and livestock products [Internet]. Food and Agriculture Organization of the United Nations. 2023 [cited 2025 Apr 6]. https://www.fao.org/faostat/en/#data/QCL

12. Mukhopadhyay M, Mondal TK. Cultivation, improvement and environmental impacts of tea. In: Oxford Research Encyclopedia of Environmental Science; 2017. https://doi.org/10.1093/acrefore/9780199389414.013.373

13. Wijeratne MA, Anandacoomaraswamy A, Amarathunga MKSLD, Ratnasiri J, Basnayake BRSB, Kalra N. Assessment of impact of climate change on productivity of tea (*Camellia sinensis* L.) plantations in Sri Lanka. J Natl Sci Found Sri. 2007;35(2):119. https://doi.org/10.4038/jnsfsr.v35i2.3676

14. Duncan JMA, Saikia SD, Gupta N, Biggs EM. Observing climate impacts on tea yield in Assam, India. Appl Geogr. 2016;77:64–71. https://doi.org/10.1016/j.apgeog.2016.10.004

15. Lou W, Sun K, Zhao Y, Deng S, Zhou Z. Impact of climate change on inter‐annual variation in tea plant output in Zhejiang, China. Int J Climatol. 2020;41(S1). https://doi.org/10.1002/joc.6700

16. Arefin MR, Haque MS, Sarwar AKMG. Characterization and genetic diversity of tea (*Camellia sinensis* (L.) O. Kuntze) genotypes for waterlogging tolerance. Phyton-Int J Exp Bot. 2024;93(12):3411–42. https://doi.org/10.32604/phyton.2024.058893

17. Borah D, Deka DK, Lahon T, Baruah U, Barman TS. Water logging tolerant clone for cultivation in marginal land. Sci Cult. 2011;77(9-10):419–24.

18. Ghosal S. Tea production down by more than 10 percent due to heavy rain, flooding in Assam and West Bengal. The Economic Times [Internet]. 2020 Jul 20 [cited 2025 Mar 31].

19. Mahindapala KGJP, Jayarathna SPAPK. Impact of flood for production of tea small holdings: A case study at 2017 floods in the tea small holdings in Kaluganga River Basin of Ratnapura district, Sri Lanka. In: Seventh Symposium on plantation Crop Research. Colombo, Sri Lanka; 2019. p. 1–30.

20. Barman TS, Baruah U, Deka DK, Borah D, Lahon T, Saikia JK. Selection and evaluation of waterlogging tolerant tea genotypes for plantation in marginal land. Two Bud. 2011;58:33–38.

21. Deka DK, Borah D, Lahon T, Baruah U, Handique AK, Barman TS. Selection of waterlogging tolerant tea (*Camellia sinensis* L.) genotypes. J Plant Crops. 2011;39(1):203–09.

22. Jeyaramraja PR, Pius PK, Kumar RR, Jayakumar D. Soil moisture stress-induced alterations in bio constituents determining tea quality. J Sci Food Agric. 2003;83(12):1187–91. https://doi.org/10.1002/jsfa.1440

23. Hossain MI. Techsoi Cha Nursery Bebosthapona (Sustainable Tea Nursery Management). Sreemangal, Moulvibazar-3210: Bangladesh Tea Research Institute; 2024. pp. 1–26.

24. Azka NA, Taryono, Wulandari RA. Assessment of tea plant (*Camellia sinensis* L.) accessions for pollen sources in natural crossing by using microsatellites. SABRAO J Breed Genet. 2021;53(4):673–84. https://doi.org/10.54910/sabrao2021.53.4.10

25. Ranjith K, Victor R, Ilango J. Influence of top working on growth and flowering of tea clones. Sci Hortic. 2018;235:47–52. https://doi.org/10.1016/j.scienta.2018.02.008

26. Shehasen MZ. Tea plant (*Camellia sinensis*) breeding mechanisms role in genetic improvement and production of major producing countries. Int J Res Stud Sci Eng Technol. 2019;6(11):10–20. https://ijrsset.org/pdfs/v6-i11/2.pdf

27. Das S, Das S, Hazarika M. Breeding of the tea plant (*Camellia sinensis*) in India. In: Chen L, Apostolides Z, Chen ZM, editors. Advanced Topics in Science and Technology in China. Berlin:Springer; 2012. p. 69–124. https://doi.org/10.1007/978-3-642-31878-8_3

28. Mondal TK. Breeding and biotechnology of tea and its wild species. New Delhi, India: Springer; 2014. https://doi.org/10.1007/978-81-322-1704-6

29. Li Z, Bai D, Zhong Y, Lin M, Sun L, Qi X, et al. Full-length transcriptome and RNA-Seq analyses reveal the mechanisms underlying waterlogging tolerance in Kiwifruit (*Actinidia valvata*). Int J Mol Sci. 2022;17;23(6):3237–47. https://doi.org/10.3390/ijms23063237

30. Insausti P, Gorjón S. Floods affect physiological and growth variables of peach trees (*Prunus persica* (L.) Batsch), as well as the postharvest behavior of fruits. Sci Hort. 2013;152:56–60. https://doi.org/10.1016/j.scienta.2013.01.005

31. Medeiros WJF de, Oliveira FÍF de, Lacerda CF de, Sousa CHC de, Cavalcante LF, Silva ARA da, et al. Isolated and combined effects of soil salinity and waterlogging in seedlings of “Green Dwarf” coconut. Semin Ciênc Agrár. 2018;39(4):1459. https://doi.org/10.5433/1679-0359.2018v39n4p1459

32. Zhang Y, Li Y, Liang T, Yuan Y, Li Z, Xu S, et al. Field-grown cotton shows genotypic variation in agronomic and physiological responses to waterlogging. Field Crops Res. 2023;302:109067. https://doi.org/10.1016/j.fcr.2023.109067

33. Silveira HR de O, Santos M de O, Alves JD, Souza KRD de, Andrade CA, Alves RGM. Growth effects of water excess on coffee seedlings (*Coffea arabica* L.). Acta Sci Agr. 2014;36(2):211–21. https://doi.org/10.4025/actasciagron.v36i2.17557

34. Rao NR, Kapoor M, Sharma N, Venkateswarlu K. Yield prediction and waterlogging assessment for tea plantation land using satellite image -based techniques. Int J Remote Sens. 2007;28(7):1561–76. https://doi.org/10.1080/01431160600904980

35. Topali C, Antonopoulou C, Chatzissavvidis C. Effect of waterlogging on growth and productivity of fruit crops. Hortic. 2024;10(6):623–33. https://doi.org/10.3390/horticulturae10060623

36. León-Burgos AF, Unigarro CA, Balaguera-López HE. Soil waterlogging conditions affect growth, water status and chlorophyll "a", fluorescence in coffee plants (*Coffea arabica* L.). Agron. 2022;12 (6):1270. https://doi.org/10.3390/agronomy12061270

37. Manghwar H, Hussain A, Alam I, Khoso MA, Ali Q, Liu F. Waterlogging stress in plant: unraveling the mechanisms and impacts on growth, development and productivity. Environ Exp Bot. 2024;224:105824–34. https://doi.org/10.1016/j.envexpbot.2024.105824

38. Azrai M, Efendi R, Muliadi A, Aqil M, Suwarti N, Zainuddin B, et al. Genotype by environment interaction on tropical maize hybrids under normal irrigation and waterlogging conditions. Front Sustain Food Syst. 2022;6. https://doi.org/10.3389/fsufs.2022.913211

39. Voesenek LACJ, Colmer TD, Pierik R, Millenaar FF, Peeters AJM. How plants cope with complete submergence. New Phytol. 2006;170 (2):213–26. https://doi.org/10.1111/j.1469-8137.2006.01692.x

40. Eysholdt-Derzsó E, Sauter M. Hypoxia and the group VII ethylene response transcription factor *HRE2* promote adventitious root elongation in *Arabidopsis*. Plant Biol J. 2019;21:103–08. https://doi.org/10.1111/plb.12873

41. Evans DE, Gladish DK. Plant responses to waterlogging. In: Thomas B, Murray BG, Murphy DJ, editors. Encyclopedia of Applied Plant Sciences. 2nd edition. Oxford: Acad Press; 2017. p. 36–39. https://doi.org/10.1016/B978-0-12-394807-6.00083-6

42. Pan J, Sharif R, Xu X, Chen X. Mechanisms of waterlogging tolerance in plants: research progress and prospects. Front Plant Sci. 2021;11. https://doi.org/10.3389/fpls.2020.627331

43. Xu Z, Ye L, Shen Q, Zhang G. Advances in studies on waterlogging tolerance in plants. J Integr Agric. 2023;23(9). https://doi.org/10.1016/j.jia.2023.12.028

44. Garnczarska M. Response of the ascorbate–glutathione cycle to re-aeration following hypoxia in lupine roots. Plant Physiol Bioch. 2005;43(6):583–90. https://doi.org/10.1016/j.plaphy.2005.05.003

45. Hartman S, Liu Z, van Veen H, Vicente J, Reinen E, Martopawiro S, et al. Ethylene-mediated nitric oxide depletion pre-adapts plants to hypoxia stress. Nature Commun. 2019;10(1):4020. https://doi.org/10.1038/s41467-019-12045-4

46. Yeung E, Van Veen H, Vashisht D, Sobral Paiva AL, Hummel M, Rankenberg T, et al. A stress recovery signaling network for enhanced flooding tolerance in *Arabidopsis thaliana*. Proc Natl Acad Sci USA. 2018;115(26). https://doi.org/10.1073/pnas.1803841115

47. Kamau DM. Productivity and resource use in ageing tea plantations [PhD Thesis]. Wageningen: Wageningen University; 2008. p. 1–140. https://edepot.wur.nl/121950

48. Li S, Lu J, Pope E, Golding N, Zhou T, Li F, et al. Influence of multi-timescale precipitation indices on primary tea production in Baoshan, Yunnan, China. Environ Res Commun. 2022;4(2):025009–19. https://doi.org/10.1088/2515-7620/ac5087

49. Amarathunga MKSLD. Remedial measures to improve the productivity of low-lying tea lands. Tea Bull. 2004;19:15–17.

50. Wingfield MJ. Pathology- Diseases of Forest Trees. In: Burley J, editor. Encyclopedia of Forest Sciences. Singapore: Elsevier; 2004. p. 744–50 https://doi.org/10.1016/B0-12-145160-7/00061-2

51. Fujita S, Noguchi K, Tange T. Root responses of five Japanese afforestation species to waterlogging. Forests. 2020;11(5):552–62. https://doi.org/10.3390/f11050552

52. Sarma KC. Waterlogging: disease of tea and associated crops in North East India. India: Tocklai Tea Research Institute; 1960. p. 56.

53. Barman TS, Saikia JK, Pathak SK. Starch reserve and growth of tea. Two Bud. 1998;45:14–18.

54. Cisse EHM, Huang JF, Li DD, Miao LF, Xiang LS, Yang F. Exogenous spermidine alleviated waterlogging damages in two varieties of *Camellia oleifera*. Forests. 2023;14(1):91–101. https://doi.org/10.3390/f14010091

55. Bailey-Serres J, Voesenek LACJ. Flooding stress: acclimations and genetic diversity. Annu Rev Plant Biol. 2008;59(1):313–39. https://doi.org/10.1146/annurev.arplant.59.032607.092752

56. *da*-Silva CJ, do Amarante L. Nitric oxide signaling in plants during flooding stress. In: Singh VP, Singh S, Tripathi DK, Romero-Puertas MC, Sandalio LM, editors. Nitric Oxide in Plant Biology. Oxford: Academic Press; 2022. p. 241–60. https://doi.org/10.1016/B978-0-12-818797-5.00009-1

57. Manik SMN, Quamruzzaman M, Zhao C, Johnson P, Hunt I, Shabala S, et al. Genome-wide association study reveals marker trait associations (MTA) for waterlogging-triggered adventitious roots and aerenchyma formation in barley. Int J Mol Sci. 2022;23(6):3341. https://doi.org/10.3390/ijms23063341

58. Wan L, Wu Y, Huang J, Dai X, Lei Y, Yan L, et al. Identification of ERF genes in peanuts and functional analysis of *AhERF008* and *AhERF019* in abiotic stress response. Funct Integr Genomics. 2014;14(3):467–77. https://doi.org/10.1007/s10142-014-0381-4

59. Bashar KK, Tareq MZ, Islam MS. Unlocking the mystery of plants' survival capability under waterlogging stress. Plant Sci Today. 2020;7 (2):142–53. https://doi.org/10.14719/pst.2020.7.2.663

60. Wang L, Dossa K, You J, Zhang Y, Li D, Zhou R, et al. High-resolution temporal transcriptome sequencing unravels ERF and WRKY as the master players in the regulatory networks underlying sesame responses to waterlogging and recovery. Genomics. 2021;113(1):276–90. https://doi.org/10.1016/j.ygeno.2020.11.022

61. Hinz M, Wilson IW, Yang J, Buerstenbinder K, Llewellyn D, Dennis ES, et al. *Arabidopsis* RAP2.2: an ethylene response transcription factor that is important for hypoxia survival. Plant Physiol. 2010;153(2):757–72. https://doi.org/10.1104/pp.110.155077

62. Zhao N, Li C, Yan Y, Cao W, Song A, Wang H, et al. Comparative transcriptome analysis of waterlogging-sensitive and waterlogging-tolerant *Chrysanthemum morifolium* cultivars under waterlogging stress and reoxygenation conditions. Int J Mol Sci. 2018;19(5):1455. https://doi.org/10.3390/ijms19051455

63. Liu Y, Chen S, Chen J, Wang J, Wei M, Tian X, et al. Comprehensive analysis and expression profiles of the *AP2/ERF* gene family during spring bud break in tea plant (*Camellia sinensis*). BMC Plant Biol. 2023;23(1):206. https://doi.org/0.1186/s12870-023-04221-y

64. Zhang T, Cai J, Wang S, Lv L, Yuan D, Zeng X, et al. Identification and expression analysis of the ethylene response factor gene family in tea plant (*Camellia sinensis*). Agronomy. 2023;13(7):1900. https://doi.org/10.3390/agronomy13071900

65. Zhang C, Li H, Mei P, Ye Y, Liu D, Gong Y, et al. QTL detection and candidate gene analysis of the anthracnose resistance locus in tea plant (*Camellia sinensis*). J Integr Agric. 2025;24(6):2240–50. https://doi.org/10.1016/j.jia.2025.02.015

66. Deka DK. Physiological, biochemical and molecular characterization of some waterlogging tolerant tea [*Camellia sinensis* (L) O. Kuntze] germplasm of Brahmaputra valley. [PhD Thesis]. India: Gauhati University; 2013. p. 1–235.

67. Sharma S, Sharma J, Soni V, Kalaji HM, Elsheery NI. Waterlogging tolerance: A review on regulative morpho-physiological homeostasis of crop plants. J Water Land Dev. 2021;16–28. https://doi.org/10.24425/jwld.2021.137092

68. Enkhbat G, Ryan MH, Foster KJ, Nichols PGH, Kotula L, Hamblin A, et al. Large variation in waterlogging tolerance and recovery among the three subspecies of *Trifolium subterranean* L. is related to root and shoot responses. Plant Soil. 2021;464(1–2):467–87. https://doi.org/10.1007/s11104-021-04959-0

69. Kamal KA, Shah FA, Zhao Y, Chen Z, Fu S, Zhu Z, et al. Genome-wide identification of the *UGT* genes family in *Acer rubrum* and role of

ArUGT52 in anthocyanin biosynthesis under cold stress. BMC Plant Biol. 2025;25(1):288. https://doi.org/10.1186/s12870-024-06043-y

70. Deng D, Gao Q, Zeng R, Jiang J, Shen Q, Ma Y, et al. The *Proline Dehydrogenase* gene *CsProDH1* regulates homeostasis of the Pro-P5C cycle under drought stress in tea plants. Int J Mol Sci. 2025;26(7):3121. https://doi.org/10.3390/ijms26073121

71. Tian L, Li J, Bi W, Zuo S, Li L, Li W, et al. Effects of waterlogging stress at different growth stages on the photosynthetic characteristics and grain yield of spring maize (*Zea mays* L.) Under field conditions. Agric Water Manag. 2019;218:250–58. https://doi.org/10.1016/j.agwat.2019.03.054

72. Li P, Lin J, Zhu M, Zuo H, Shen Y, Li J, et al. Variations of stomata development in tea plant (*Camellia sinensis*) leaves in different light and temperature environments and genetic backgrounds. Hortic Res. 2023;10(2):278. https://doi.org/10.1093/hr/uhac278

73. Rai GK, Khanday DM, Choudhary SM, Kumar P, Kumari S, Martínez-Andújar C, et al. Unlocking nature's stress buster: Abscisic acid's crucial role in defending plants against abiotic stress. Plant Stress. 2024;11:100359. https://doi.org/10.1016/j.stress.2024.100359

74. Zhao Y, Zhang W, Abou-Elwafa SF, Shabala S, Xu L. Understanding a mechanistic basis of ABA involvement in plant adaptation to soil flooding: the current standing. Plants. 2021;10(10):1982. https://doi.org/10.3390/plants10101982

75. De Ollas C, González-Guzmán M, Pitarch Z, Matus JT, Candela H, Rambla JL, et al. Identification of ABA-mediated genetic and metabolic responses to soil flooding in tomato (*Solanum lycopersicum* L. Mill). Front Plant Sci. 2021;12:613059. https://doi.org/10.3389/fpls.2021.613059

76. Hayat S, Hayat Q, Alyemeni MN, Wani AS, Pichtel J, Ahmad A. Role of proline under changing environments: a review. Plant Signal Behav. 2012;7(11):1456–66. https://doi.org/10.4161/psb.21949

77. Sorkheh K, Shiran B, Khodambashi M, Rouhi V, Mosavei S, Sofo A. Exogenous proline alleviates the effects of H_2O_2-induced oxidative stress in wild almond species. Russ J Plant Physiol. 2012;59(6):788–98. https://doi.org/10.1134/S1021443712060167

78. Ying Z, Fu S, Yang Y. Signaling and scavenging: unraveling the complex network of antioxidant enzyme regulation in plant cold adaptation. Plant Stress. 2025;16:100833. https://doi.org/10.1016/j.stress.2025.100833

79. Zheng Y, Cabassa-Hourton C, Planchais S, Crilat E, Clément G, Dacher M, et al. Pyrroline-5-carboxylate dehydrogenase is an essential enzyme for proline dehydrogenase function during dark-induced senescence in *Arabidopsis thaliana*. Plant Cell Environ. 2023;46(3):901–17. https://doi.org/10.1111/pce.14529

80. Yang WC, Lin KH, Wu CW, Chang YJ, Chang YS. Effects of waterlogging with different water resources on plant growth and tolerance capacity of four herbaceous flowers in a Bioretention Basin. Water. 2020;12(6):1619. https://doi.org/10.3390/w12061619

81. Kosma DK, Bourdenx B, Bernard A, Parsons EP, Lü S, Joubès J, et al. The impact of water deficiency on leaf cuticle lipids of *Arabidopsis*. Plant Physiol. 2009;151(4):1918–29. https://doi.org/10.1104/pp.109.141911

82. Broun P, Poindexter P, Osborne E, Jiang CZ, Riechmann JL. WIN1, a transcriptional activator of epidermal wax accumulation in *Arabidopsis*. Proc Natl Acad Sci USA. 2004;101(13):4706–11. https://doi.org/10.1073/pnas.0305574101

83. Mo L, Yao X, Tang H, Li Y, Jiao Y, He Y, et al. Genome-wide investigation and functional analysis reveal that *CsKCS3* and *CsKCS18* are required for tea cuticle wax formation. Foods. 2023;12(10):2011. https://doi.org/10.3390/foods12102011

84. Dong F, Hu J, Shi Y, Liu M, Zhang Q, Ruan J. Effects of nitrogen supply on flavonol glycoside biosynthesis and accumulation in tea leaves (*Camellia sinensis*). Plant Physiol Biochem. 2019;138:48–57. https://doi.org/10.1016/j.plaphy.2019.02.017

85. Gu H, Wang Y, Xie H, Qiu C, Zhang S, Xiao J, et al. Drought stress triggers proteomic changes involving lignin, flavonoids and fatty acids in tea plants. Sci Rep. 2020;10(1). https://doi.org/10.1038/s41598-020-72596-1

86. Rahimi M, Kordrostami M, Mohamadhasani F, Chaeikar SS. Antioxidant gene expression analysis and evaluation of total phenol content and oxygen-scavenging system in tea accessions under normal and drought stress conditions. BMC Plant Biol. 2021;21(1). https://doi.org/10.1186/s12870-021-03275-0

87. Luo J, Yu W, Xiao Y, Zhang Y, Peng F. Strawberry *FaSnRK1α* regulates anaerobic respiratory metabolism under waterlogging. Int J Mol Sci. 2022;23(9):4914. https://doi.org/10.3390/ijms23094914

88. Gao M, Gai C, Li X, Feng X, Lai R, Song Y, et al. Waterlogging tolerance of *Actinidia valvata* dunn is associated with high activities of pyruvate decarboxylase, alcohol dehydrogenase and antioxidant enzymes. Plants. 2023;12(15):2872. https://doi.org/10.3390/plants12152872

89. Langaroudi IK, Piri S, Chaeikar SS, Salehi B. Evaluating drought stress tolerance in different *Camellia sinensis* L. cultivars and effect of melatonin on strengthening antioxidant system. Sci Hort. 2023;307:111517. https://doi.org/10.1016/j.scienta.2022.111517

90. Upadhyaya H, Panda SK, Dutta BK. Variation of physiological and antioxidative responses in tea cultivars subjected to elevated water stress followed by rehydration recovery. Acta Physiol Plant. 2008;30(4):457–68. https://doi.org/10.1007/s11738-008-0143-9

91. Cheruiyot EK, Mumera LM, Ng'etich WK, Hassanali A, Wachira FN. Polyphenols as potential indicators for drought tolerance in tea (*Camellia sinensis* L.). Biosci Biotechnol Biochem. 2007;71(9):2190–97. https://doi.org/10.1271/bbb.70156

92. Wang LY, Wei K, Jiang YW, Cheng H, Zhou J, He W, et al. Seasonal climate effects on flavanols and purine alkaloids of tea (*Camellia sinensis* L.). Eur Food Res Technol. 2011;233(6):1049–55. https://doi.org/10.1007/s00217-011-1588-4

93. Tyler BM. Molecular basis of recognition between *Phytophthora* pathogens and their hosts. Annu Rev Phytopathol. 2002;40(1):137–67. https://doi.org/10.1146/annurev.phyto.40.120601.125310

94. Browne GT, Mircetich SM. Effects of flood duration on the development of *Phytophthora* root and crown rots of apple. Phytopathol. 1988;78(6):846. https://doi.org/10.1094/phyto-78-846

95. Stone C, Chesnut K, Penman T, Nichols D. Waterlogging increases the infestation level of the pest psyllid *Creiis lituratus* on *Eucalyptus dunnii*. Aust For. 2010;73(2):98–105. https://doi.org/10.1080/00049158.2010

96. Shilpa S, J. S. M, Rakesh G, B. S, Joseph J, H. P. M, et al. Deciphering the role of polyphenol in defence mechanism against tea mosquito bug (*Helopeltis theivora* Waterhouse.) in cocoa (*Theobroma cocoa* L.). PLoS ONE. 2022;17(10):e0271432. https://doi.org/10.1371/journal.pone.0271432

97. Sireesha U, Borah R, Ramdam DS, Modak B, Pradhan B. Review on destructive pest tea mosquito bug, *Helopeltis theivora* of tea (*Camellia sinensis*). Int J Entomol Res. 2020;5(6):222–28. Availabe from: https://www.entomologyjournals.com/assets/archives/2020/vol5issue6/5-6-24-632.pdf

98. Gu H, Li J, Qiao D, Li M, Yao Y, Xie H, et al. A defensive pathway from NAC and TCP transcription factors activates a BAHD acyltransferase for (Z)-3-hexenyl acetate biosynthesis to resist herbivore in tea plant (*Camellia sinensis*). New Phytol. 2025;245(3):1232–48. https://doi.org/10.1111/nph.20283

99. Wang S, Gu H, Chen S, Li Y, Shen J, Wang Y, et al. Proteomics and phosphoproteomics reveal the different drought-responsive mechanisms of priming with (Z)-3-hexenyl acetate in two tea cultivars. J Proteomics. 2023;289:105010. https://doi.org/10.1016/j.jprot.2023.105010

100. Arefin MR, Hossain MI. Present status and future prospects of tea production and research on varietal improvement in Bangladesh. Turkish J Agric Food Sci Technol. 2022;10(12):2324–33. https://doi.org/10.24925/turjaf.v10i12.2324-2333.5259

101. Lebedev VT, Lebedeva TN, Chernodubov A, Shestibratov KA. Genomic selection for forest tree improvement: methods, achievements and perspectives. Forests. 2020;11(11):1190–100. https://doi.org/10.3390/f11111190

102. Chen L, Chen JD, editors. The tea plant genome. Singapore: Springer Nature; 2024. https://doi.org/10.1007/978-981-97-0680-8

103. White TL, Adams WT, Neale DB. Phenotypic mass selection – genetic gain, choice of traits and indirect response. CABI Publisher; 2007. https://doi.org/10.1079/9781845932855.0329

104. Chen L, Zhou ZX, Yang YJ. Genetic improvement and breeding of tea plant (*Camellia sinensis*) in China: from individual selection to hybridization and molecular breeding. Euphytica. 2006;154(1-2):239–48. https://doi.org/10.1007/s10681-006-9292-3

105. Kamunya SM, Wachira FN, Pathak RS, Muoki RC, Sharma RK. Tea Improvement in Kenya. In: Chen L, Apostolides Z, Chen ZM, editors. Global Tea Breeding. Berlin, Heidelberg: Springer; 2012. p. 177–226. https://doi.org/10.1007/978-3-642-31878-8_5

106. Muliadi A, Effendi R, Azrai dan M. Tolerance level of several hybrid maize genotypes to waterlogging stress. IOP Conf Ser: Earth Environ Sci. 2020;484(1):012002–12. https://doi.org/10.1088/1755-1315/484/1/012002

107. Belliappa SH, Bomma N, Pranati J, Soregaon CD, Hingane AJ, Basavaraj PS, et al. Breeding for water-logging tolerance in pigeon pea: current status and future prospects. CABI Agric Biosci. 2024;5(1). https://doi.org/10.1186/s43170-024-00299-y

108. Zhao Z, Qin T, Zheng H, Guan Y, Gu W, Wang H, et al. Mutation of *ZmDIR5* reduces maize tolerance to waterlogging, salinity and drought. Plants. 2025;14(5):785–95. https://doi.org/10.3390/plants14050785

109. Ma JQ, Kamunya SM, Yamaguchi S, Ranatunga MAB, Chen L. Classic genetics and traditional breeding of tea plant. In: Chen L, Chen JD, editors. The tea plant genome. Singapore: Springer; 2024. p. 79–120. https://doi.org/10.1007/978-981-97-0680-8_5

110. Hembree WG, Ranney TG, Jackson BE, Weathington M. Cytogenetics, Ploidy and Genome Sizes of *Camellia* and Related Genera. Hortic Sci. 2019;54(7):1124–42. https://doi.org/10.21273/hortsci13923-19

111. Dai X, Shen L. Advances and trends in omics technology development. Front Med. 2022;9:911861. https://doi.org/10.3389/fmed.2022.911861

112. Naqvi RZ, Mahmood MA, Mansoor S, Amin I, Asif M. Omics-driven exploration and mining of key functional genes for the improvement of food and fiber crops. Front Plant Sci. 2024;14:1273859. https://doi.org/10.3389/fpls.2023.1273859

113. Raza A, Bashir S, Khare T, Karikari B, Copeland RGR, Jamla M, et al. Temperature-smart plants: a new horizon with omics-driven plant breeding. Physiol Plant. 2024;176(1):e14188. https://doi.org/10.1111/ppl.14188

114. Zhang H, Xie Z, Tu X, Liu A, Chen J, He Y, et al. Morphological and proteomic study of waterlogging tolerance in cotton. Sci Rep. 2024;14(1):14550. https://doi.org/10.1038/s41598-024-64322-y

115. Komatsu S, Kuji R, Nanjo Y, Hiraga S, Furukawa K. Comprehensive analysis of endoplasmic reticulum-enriched fraction in root tips of soybean under flooding stress using proteomics techniques. J Proteomics. 2012;77:531–60. https://doi.org/10.1016/j.jprot.2012.09.032

116. Zaman S, Shen J, Wang S, Song D, Wang H, Ding S, et al. Effect of shading on physiological attributes and proteomic analysis of tea during low temperatures. Plants. 2023;13(1):63. https://doi.org/10.3390/plants13010063

117. Li JW, Li H, Liu ZW, Wang YX, Chen Y, Yang N, et al. Molecular markers in tea plant (*Camellia sinensis*): Applications to evolution, genetic identification and molecular breeding. Plant Physiol Biochem. 2023;198:107704–14. https://doi.org/10.1016/j.plaphy.2023.107704

118. Kamunya SM, Wachira FN, Pathak RS, Korir R, Sharma V, Kumar R, et al. Genomic mapping and testing for quantitative trait loci in tea (*Camellia sinensis* (L.) O. Kuntze). Tree Genet Genomes. 2010;6(6):915–29. https://doi.org/10.1007/s11295-010-0301-2

119. Karunarathna KHT, Mewan KM, Weerasena OVDSJ, Perera N, Edirisinghe ENU. A functional molecular marker for detecting blister blight disease resistance in tea (*Camellia sinensis* L.). Plant Cell Rep. 2020;40(2):351–59. https://doi.org/10.1007/s00299-020-02637-6

120. Bali S, Raina SN, Bhat V, Aggarwal RK, Goel S. Development of a set of genomic microsatellite markers in tea (*Camellia* L.) (Camelliaceae). Mol Breed. 2013;32(3):735–41. https://doi.org/10.1007/s11032-013-9902-4

121. Wang Z, Huang R, Moon DG, Ercisli S, Chen L. Achievements and prospects of QTL mapping and beneficial genes and alleles mining for important quality and agronomic traits in tea plant (*Camellia sinensis*). Bev Plant Res. 2023;3(1):1–12. https://doi.org/10.48130/bpr-2023-0022

122. Jiang CK, Ma JQ, Liu YF, Chen JD, Ni DJ, Chen L. Identification and distribution of a single nucleotide polymorphism responsible for the catechin content in tea plants. Hortic Res. 2020;7(1). https://doi.org/10.1038/s41438-020-0247-y

123. Ahmed F, Rafii MY, Ismail MR, Juraimi AS, Rahim HA, Asfaliza R, et al. Waterlogging tolerance of crops: breeding, mechanism of tolerance, molecular approaches and future prospects. Biomed Res Int. 2013:1–10. https://doi.org/10.1155/2013/963525

124. Iacona C, Cirilli M, Zega A, Frioni E, Silvestri C, Muleo R. A somaclonal myrobalan rootstock increases waterlogging tolerance to peach cultivar in controlled conditions. Sci Hortic. 2013;156:1–8. https://doi.org/10.1016/j.scienta.2013.03.014

125. Thomas J, Vijayan D, Joshi SD, Lopez SJ, Kumar RR. Genetic integrity of somaclonal variants in tea (*Camellia sinensis* (L.) O Kuntze) as revealed by inter simple sequence repeats. J Biotechnol. 2005;123(2):149–54. https://doi.org/10.1016/j.jbiotec.2005.11.005

126. Eminoğlu A, İzmirli Şg, Beriş Fş, Dinçer D, Yazici K. Detection of somaclonal variation in tissue-cultured Turkish tea genotypes using SSR markers. In: 7th International Anatolian agriculture, food, environment and biology congress. Turkey: Turkish Science and Technology Publishing; 2024. p. 85.

127. Singh HR, Hazarika P, Agarwala N, Bhattacharyya N, Bhagawati P, Gohain B, et al. Transgenic tea over-expressing *Solanum tuberosum Endo-1,3-beta-d-glucanase* gene conferred resistance against blister blight disease. Plant Mol Biol Rep. 2018;36(1):107–22. https://doi.org/10.1007/s11105-017-1063-x

128. Ma H, Liu N, Sun X, Zhu M, Mao T, Huang S, et al. Establishment of an efficient transformation system and its application in regulatory mechanism analysis of biological macromolecules in tea plants. Int J Biol Macromol. 2023;244:125372–82. https://doi.org/10.1016/j.ijbiomac.2023.125372

129. Saini U, Kaur D, Bhattacharya A, Kumar S, Singh RD, Ahuja PS. Optimising parameters for biolistic gun-mediated genetic transformation of tea [*Camellia sinensis* (L.) O. Kuntze]. J Hortic Sci Biotech. 2012;87(6):605–12. https://doi.org/10.1080/14620316.2012.11512919

130. Mohanpuria P, Kumar V, Ahuja PS, Yadav SK. Agrobacterium-mediated silencing of caffeine synthesis through root transformation in *Camellia sinensis* L. Mol Biotechnol. 2010;48(3):235–43. https://doi.org/10.1007/s12033-010-9364-4

131. Tian H, Fan G, Xiong X, Wang H, Zhang S, Geng G. Characterization and transformation of the *CabHLH18* gene from hot pepper to enhance waterlogging tolerance. Front Plant Sci. 2024;14. https://doi.org/10.3389/fpls.2023.1285198

132. Chiang CM, Chen LFO, Shih SW, Lin KH. Expression of eggplant ascorbate peroxidase increases the tolerance of transgenic rice plants to flooding stress. J Plant Biochem Biotech. 2014;24(3):257–67. https://doi.org/10.1007/s13562-014-0265-7

133. Yuwei T, Liping L, Ruoxian W, Yuhong C, Zhonghua L, Shuoqian L. Development of a CRISPR/Cas9 constructed for genome editing of caffeine synthase in *Camellia sinensis*. J Tea Sci. 2016;36(4):414–26. (in Chinese with English summary)

134. Huang J, Chen HM. CRISPR revolution: precision breeding for enhanced tea quality and disease resistance. J Tea Sci Res. 2024;14(3):160–68. https://doi.org/10.5376/jtsr.2024.14.0015

135. Nivetha DK, Manikanda BN, Shobhana VG, Ehab AAS, Ramya SN, Dinesh KG. Exploring pioneering efforts in tea breeding and genetic transformation and designing driving innovative strategies for better brewing. Plant Sci Today. 2024;11(4):1723–38. https://doi.org/10.14719/pst.3543

Additional information

Peer review: Publisher thanks Sectional Editor and the other anonymous reviewers for their contribution to the peer review of this work.

Reprints & permissions information is available at https://horizonepublishing.com/journals/index.php/PST/open_access_policy

Publisher's Note: Horizon e-Publishing Group remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Indexing: Plant Science Today, published by Horizon e-Publishing Group, is covered by Scopus, Web of Science, BIOSIS Previews, Clarivate Analytics, NAAS, UGC Care, etc
See https://horizonepublishing.com/journals/index.php/PST/indexing_abstracting

Publisher information: Plant Science Today is published by HORIZON e-Publishing Group with support from Empirion Publishers Private Limited, Thiruvananthapuram, India.