



REVIEW ARTICLE

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

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## 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 apianese* 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<sub>2</sub> supply in their roots is disrupted and the gaseous exchange of CO<sub>2</sub> 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<sub>2</sub> 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 bunched 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).

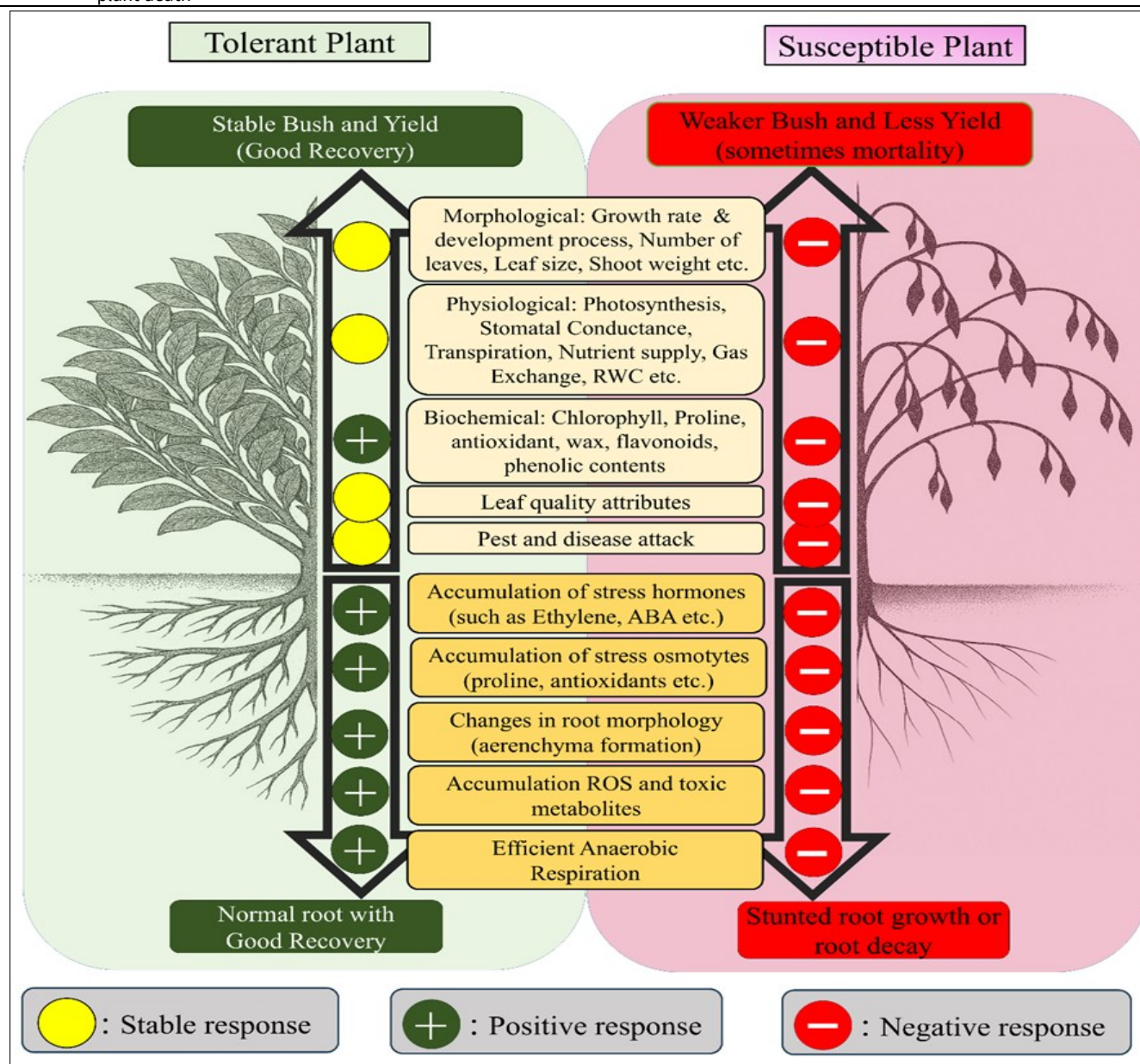
In case of cotton, the highest reduction in plant height (31.50 %) and leaf area (40.02 %) was observed during squaring and flowering stages respectively, while plants were subjected to 10 days of waterlogged conditions (8). Some yield-related attributes of *Camellia oleifera*, such as number of leaves, 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<sub>2</sub>) 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<sub>2</sub> 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 <sub>2</sub>                                                                                            | 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 <sup>3+</sup> , Fe <sup>2+</sup> and Mn <sup>2+</sup> 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 <sub>2</sub> 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 ( $O_2^{\bullet-}$ ), hydrogen peroxide ( $H_2O_2$ ) and hydroxyl radicals ( $\bullet OH$ ), while indirectly reducing ROS by activating the enzymes like SOD, CAT and POD (77). Antioxidant enzymes like SOD transforms  $O_2^{\bullet-}$  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  $\mu mol g^{-1}$  of fresh weight (FW), while the leaf proline content varied between 0.01 to 3.78  $\mu mol g^{-1}$  of FW after 45 days of flooding. It was noticed a five to six-fold increase in proline content (0.7 to 3.7  $\mu mol g^{-1}$  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  $\mu\text{g cm}^{-2}$  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 *FaSnRK1 $\alpha$*  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 *Phytophthium*, *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 (*Creilus 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 characterized 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<sub>2</sub> and some structural modifications such as aerenchyma formation. Genes related to *ERFs*, 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 trials 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

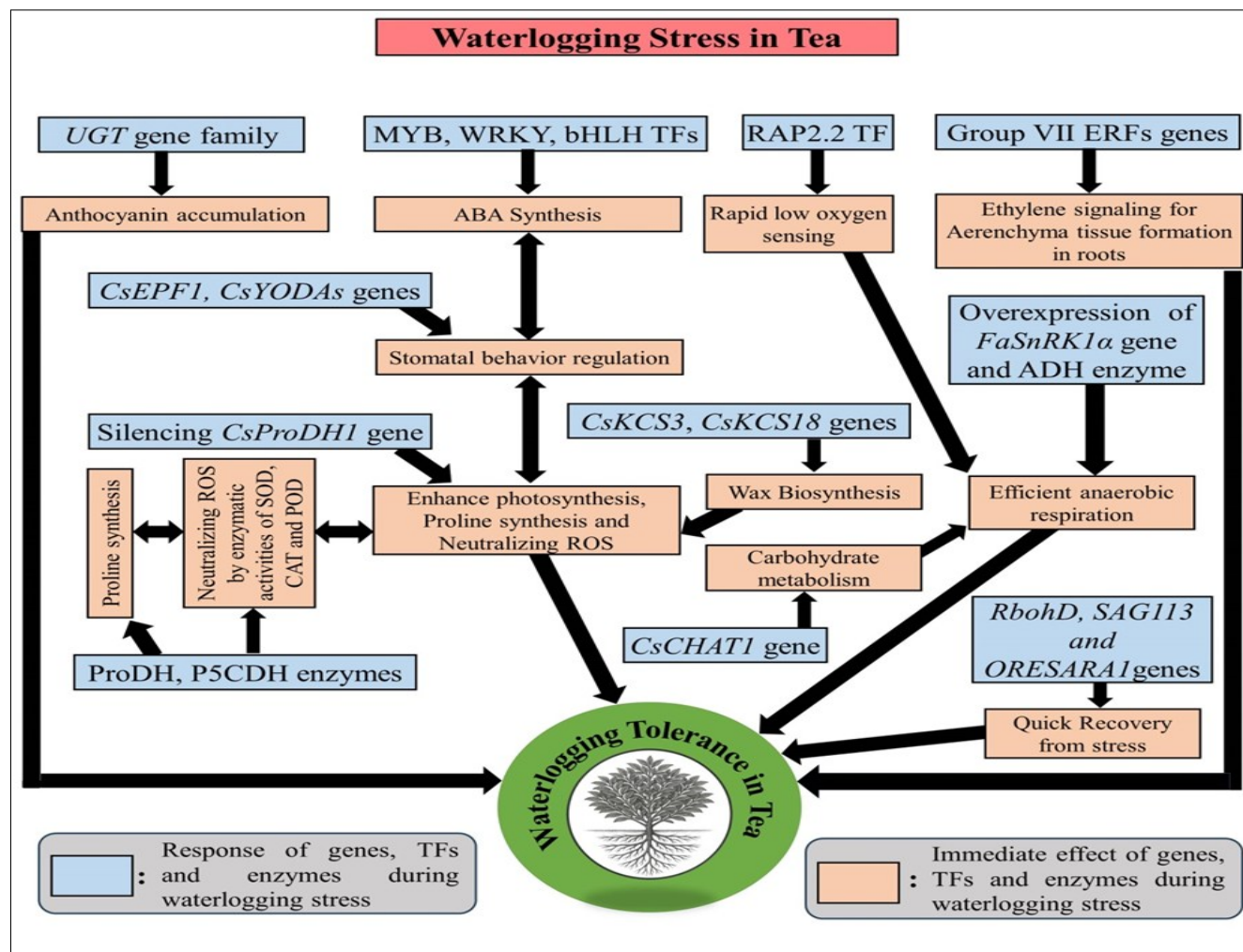
| Name of variety/<br>Accession | Country    | Special Character                                  | Breeding method                                         | References   |
|-------------------------------|------------|----------------------------------------------------|---------------------------------------------------------|--------------|
| 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 ( <i>assamica</i> - <i>cambod</i> hybrid) | (102)        |
| KTRI 895/7                    | Kenya      | Moderately high polyphenol content                 | Hybridization ( <i>assamica</i> - <i>cambod</i> 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 <i>assamica</i> )    | (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)        |



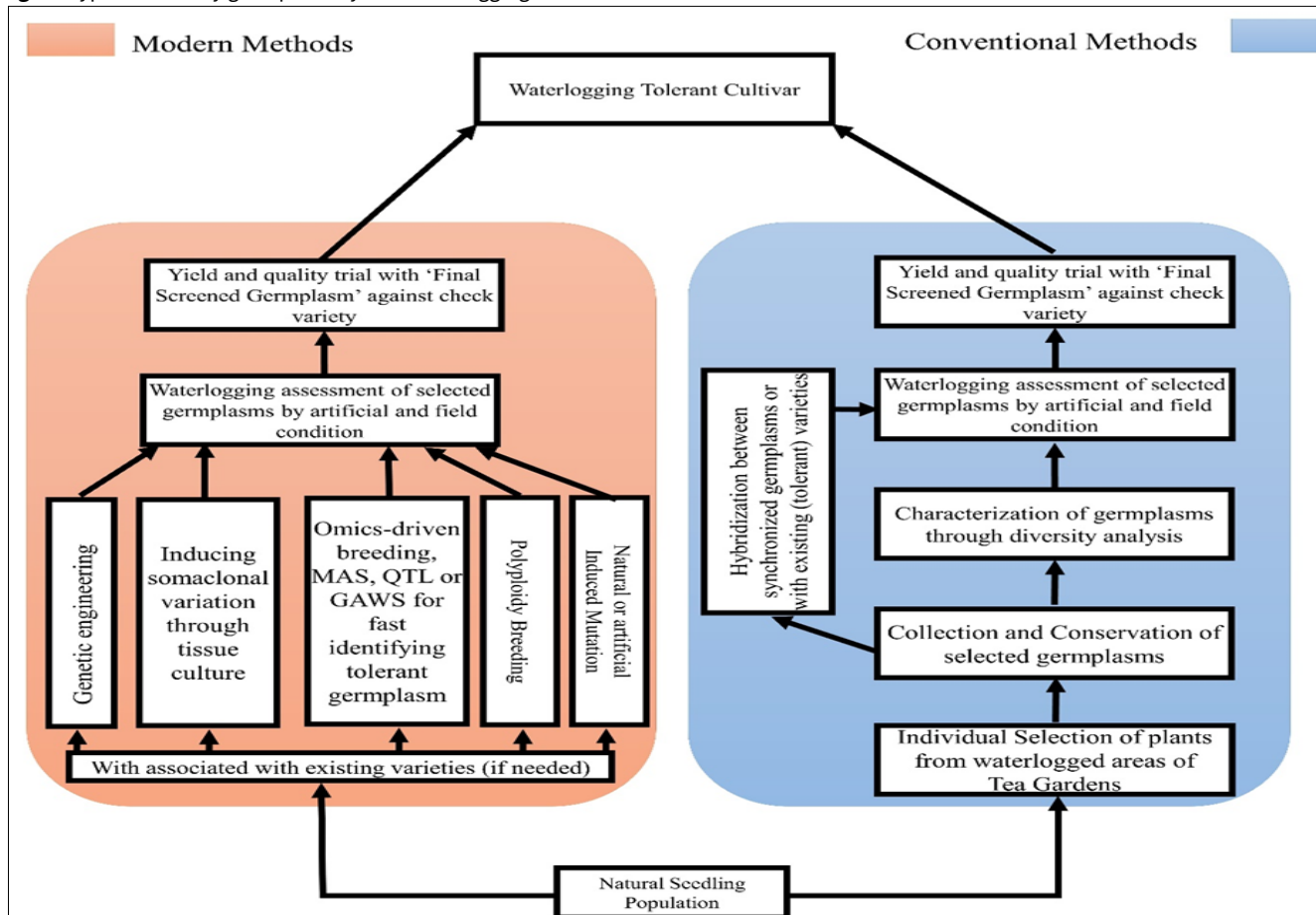
|                    |            |                                      |                                         |        |
|--------------------|------------|--------------------------------------|-----------------------------------------|--------|
| Sanhua 1951        | China      | Black, Green, 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                                                      |
|-------------------------------|------------------------------------------------------------------|
| $\mu$                         | 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                           |
| <i>Cas9</i>                   | <i>CRISPR-associated protein 9</i>                               |
| CAT                           | Catalase                                                         |
| <i>CHS</i>                    | <i>Chalcone synthase</i>                                         |
| <i>CRISPR</i>                 | <i>Clustered Regularly Interspaced Short Palindromic Repeats</i> |
| <i>Cs</i>                     | <i>Caffeine synthase</i>                                         |
| E                             | Transpiration                                                    |
| EC                            | Epicatechin                                                      |
| ECG                           | Epicatechin gallate                                              |
| EGC                           | Epigallocatechin                                                 |
| EGCG                          | Epigallocatechin gallate                                         |
| ERF                           | Ethylene-Responsive Factors                                      |
| et al.                        | Et alia and others                                               |
| <i>F3H</i>                    | <i>Flavanone 3-hydroxylase</i>                                   |
| FW                            | Fresh weight                                                     |
| Gs                            | Stomatal conductance                                             |
| <i>GSH</i>                    | <i>Glutathione</i>                                               |
| GWAS                          | Genome-wide association study                                    |
| H <sub>2</sub> O <sub>2</sub> | Hydrogen peroxide                                                |
| <i>Hb</i>                     | Hemoglobins                                                      |
| ISSR                          | Inter-Simple Sequence Repeat                                     |
| MAS                           | Marker-assisted Selection                                        |
| mol                           | Mole                                                             |
| <i>nsHb1</i>                  | <i>Non-symbiotic hemoglobin</i>                                  |
| •OH                           | Hydroxyl radical                                                 |
| O <sub>2</sub> •-             | Superoxide radical                                               |
| <i>OsEIL1a</i>                | <i>Ethylene Insensitive3-Like Gene 1a</i>                        |
| 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                                           |
| <i>SUB1A</i>                  | <i>Submergence 1A</i>                                            |
| 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  $\gamma$ -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 (GWAS)

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*, *tmmas*, *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 culture and 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.

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## 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

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