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Enhancing crop resilience under excess water stress: Physiological adaptations, management strategies and molecular advances

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Abstract

Recent climatic variability has increased the frequency of waterlogging and flooding events, posing serious threats to crop productivity and food security worldwide. Excess water stress results from prolonged soil saturation, which restricts oxygen availability in the root zone or causes partial to complete plant submergence. This review systematically synthesises current knowledge of the morphological, physiological and biochemical mechanisms associated with crop adaptation to excess water stress, with emphasis on major agricultural crops. Key adaptive responses include adventitious root formation, aerenchyma development, lenticel hypertrophy and shoot elongation, which facilitate internal oxygen transport and plant survival under hypoxic conditions. From a functional perspective, crops generally adopt low-oxygen escape syndrome (LOES) or low-oxygen quiescence syndrome (LOQS) strategies to tolerate oxygen deficiency. Excess water stress also induces oxidative damage through the accumulation of reactive oxygen species, which tolerant plants mitigate through enhanced antioxidant defence systems. In addition to intrinsic adaptive mechanisms, field-level management approaches such as improved drainage, raised-bed cultivation, optimised nutrient management, rescue nutrition, plant growth regulator application, microbial inoculation and climate-smart agronomic practices have shown considerable potential for improving stress resilience and yield stability. Recent advances in molecular breeding, quantitative trait locus (QTL) identification and precision agriculture further support the development of waterlogging-tolerant cultivars and sustainable management strategies. However, large-scale implementation remains constrained by environmental variability, economic limitations and inconsistent field performance. Future research should therefore focus on integrating physiological insights, molecular breeding, precision water management and region-specific agronomic interventions to strengthen crop resilience under increasing flooding and excess water stress scenarios.

Keywords: climate resilience; excess water stress; hypoxia; rescue nutrition; waterlogging tolerance

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Introduction

The escalating pace of climatic variability has become a pressing global issue in recent decades, intensifying multiple forms of abiotic stress that directly influence agricultural output and food security. These environmental pressures include extended dry spells, salinity build-up in soils, temperature fluctuations, accumulation of toxic metals and the increasing occurrence of waterlogging and flooding associated with irregular precipitation patterns (1). Among these stresses, excess water stress, including waterlogging and flooding, is considered one of the most damaging abiotic constraints affecting agricultural productivity worldwide (2).

Climate change is increasing the risk of extreme precipitation and associated excess-water stress in agricultural systems. The IPCC (2023) reported that heavy precipitation events have increased over many land regions and are projected to become more frequent and intense with continued warming. Extreme precipitation intensity is expected to increase by approximately 6–7 % for each 1 °C rise in global mean temperature, increasing the potential for pluvial flooding where rainfall exceeds soil infiltration and drainage capacity. However, changes in river-flood frequency remain regionally variable and depend on rainfall, catchment characteristics, soil moisture and land management. These projected changes highlight the increasing importance of understanding crop responses

and developing effective management strategies for waterlogging and flooding (3).

In India, approximately 30 % of districts and 41 % of the population fall under moderate to very high vulnerability to flooding and waterlogging (4). This increasing exposure is evident from recent flood events in Punjab, which have caused widespread agricultural damage, impacting over 1.92 lakh hectares of cropped area, primarily affecting paddy, followed by cotton and horticultural crops (5). From a physiological standpoint, plant injury under excessive soil moisture largely arises from water-induced stress resulting from persistent soil saturation caused by heavy rainfall, insufficient drainage or elevated groundwater tables. The severity of stress depends on both the duration and extent of soil saturation, manifesting either as waterlogging, where oxygen deficiency is confined mainly to the root zone, or as flooding, during which above-ground plant parts also remain submerged. Partial submergence reduces gas exchange and affects root function, whereas complete flooding exposes the whole plant to low oxygen conditions and severe metabolic disturbance (6) (Fig. 1).

Most cultivated crops exhibit high sensitivity to prolonged submergence. Limited oxygen diffusion under such environments compels plants to redirect energy from growth and reproductive development toward survival-oriented physiological adjustments and defence activation. As a result, yield potential and grain quality are significantly reduced (7). Experimental evidence indicates that excess water conditions reduce grain filling and biomass accumulation, negatively affect key yield components such as ear size, seed weight and plant height and accelerate senescence (8). However, the magnitude of these effects varies considerably with stress intensity, duration, plant developmental stage, genotype and the extent of tissue submergence. Therefore, differences among studies may be due to variations in stress conditions rather than truly conflicting plant responses. To counter the negative consequences of waterlogging, plants display coordinated structural, functional and biochemical adjustments. Prominent structural responses include the initiation of adventitious roots, formation of internal air spaces (aerenchyma) and hyponasty, all of which facilitate improved internal oxygen movement under hypoxic environments (9). The effectiveness of these adaptations, however, depends on the severity and duration of oxygen limitation, with responses that promote acclimation under moderate stress potentially becoming insufficient under prolonged or severe excess water conditions. These responses are closely interconnected, as changes in oxygen availability influence energy metabolism, nutrient acquisition, photosynthetic performance, oxidative balance, growth and ultimately reproductive development.

Particular attention is given to the relationship between oxygen sensing and gene regulation and their downstream effects on plant structure, physiology, metabolism and stress recovery. The review further distinguishes the responses associated with waterlogging from those occurring under flooding, while considering how stress duration and intensity modify the expression and effectiveness of these adaptive mechanisms. Therefore, this review systematically synthesises current evidence on the morphological, physiological, biochemical, molecular and agronomic mechanisms associated with crop adaptation to excess water stress. Particular emphasis is given to recent advances in drainage management, rescue nutrition, microbial interventions, molecular breeding and climate-smart strategies aimed at improving crop resilience under waterlogged and flooded conditions. By integrating these dimensions, the review aims to identify major knowledge gaps and prioritise research and management approaches for improving crop resilience under increasingly variable waterlogging and flooding conditions.

Methodology

Research questions

This systematic review was conducted to address the following research questions:

1. How does excess water stress influence the morphological, physiological and biochemical responses of crop plants?
2. Which agronomic and nutrient-management strategies are effective in improving crop resilience under waterlogged and flooded conditions?
3. What recent advances in molecular breeding and stress-tolerance mechanisms contribute to enhancing crop adaptation to excess water stress?
4. What field-level management approaches show practical potential for minimising yield losses under excess water stress conditions?

Review framework and reporting

The review was structured and reported in accordance with the preferred reporting items for systematic reviews and meta-analyses (PRISMA 2020) framework. The PRISMA framework was used to guide the identification, screening, eligibility assessment and inclusion of relevant literature and to improve transparency in reporting the study-selection process.

Information sources

A systematic literature search was performed using major multidisciplinary and subject-specific electronic databases, including Scopus, Web of Science, Google Scholar, ScienceDirect, SpringerLink, AGRICOLA and Semantic Scholar. These databases were selected to provide broad coverage of the literature in crop science, agronomy, plant physiology, plant nutrition, molecular biology, genetics and environmental stress biology.

The database search was conducted on 13 May 2026. Literature published from January 2000 to 13 May 2026 was considered. In addition to database searching, the reference lists of relevant articles and review papers were screened manually.

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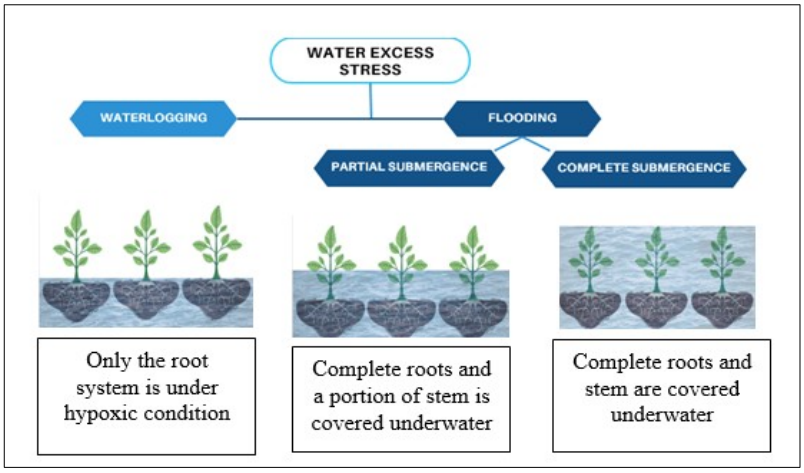


Fig. 1. Major forms and field situations of excess water stress affecting crops.

Search strategy

The search strategy was developed around four major concepts: excess water stress, crop plants, stress responses and tolerance and management or adaptation strategies. Search terms were selected based on terminology commonly used in the literature describing waterlogging, flooding, submergence, hypoxia, anoxia and associated crop responses.

The principal keywords included “waterlogging”, “flooding stress”, “excess water stress”, “submergence”, “hypoxia”, “anoxia”, “crop resilience”, “waterlogging tolerance”, “flood tolerance”, “flooding tolerance”, “nutrient management”, “rescue nutrition”, “fertiliser”, “plant growth regulators”, “antioxidant responses”, “drainage management”, “microbial inoculants”, “precision agriculture”, “molecular mechanisms”, “molecular breeding”, “flood-tolerant cultivars”, “QTL mapping”, “genes” and “abiotic stress adaptation”.

The keywords were combined using Boolean operators AND and OR and truncation symbols and database-specific search syntax were applied where supported. The general search strategy was structured as follows:

(waterlogging OR *flooding* OR *submergence* OR *hypoxia* OR *anoxia* OR *excess water stress)* AND *(crop* OR *plant* OR *cereal* OR *legume* OR *pulse* OR *horticultural crop*) AND (*tolerance* OR *resilience* OR *adaptation* OR *response* OR *management* OR *nutrition* OR *stress tolerance*)

The search strategy was adapted to the search interface and syntax of each database. Searches were restricted to literature published between January 2000 and May 2026. Where applicable, studies published in English and concerning crop plants were prioritised according to the predefined eligibility criteria.

Eligibility criteria

Studies were included if they focused on crop responses, tolerance mechanisms or management practices related to waterlogging, flooding, submergence or excess water stress. Studies were also required to provide clear information on the crop, stress conditions, experimental or field methods and measured responses. Peer-reviewed research articles and relevant review articles addressing physiological, biochemical, molecular, genetic, nutritional or agronomic aspects of crop adaptation and stress management were considered. Studies that were unrelated to crop responses, lacked sufficient methodological information, or did not provide relevant and interpretable findings were excluded.

Duplicate removal

Duplicate records retrieved from multiple databases were identified and removed through manual verification and reference screening.

Inclusion and exclusion criteria

Studies were included when they:

- investigated crop plants exposed to waterlogging, flooding, submergence, hypoxia, anoxia or other forms of excess water stress;
- examined morphological, physiological, biochemical, molecular, genetic, nutritional, agronomic or yield responses to excess water stress;
- evaluated mechanisms or traits associated with crop tolerance, resilience, acclimation, recovery or adaptation to excess water stress;
- investigated agronomic, nutrient-management, drainage, plant-growth-regulator, microbial, breeding, or other interventions intended to alleviate excess-water-induced damage;
- reported sufficient information regarding the crop species, stress conditions, experimental or field methods and relevant outcomes; and
- were published within the predefined literature-search period.
- Studies were excluded when they:
- did not address excess water stress or its consequences for crop plants;
- focused exclusively on drought, salinity, heat, cold or other abiotic stresses without a relevant excess-water component;
- investigated non-crop species without findings directly relevant to crop stress adaptation;

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- lacked sufficient methodological or outcome information;
- were duplicate publications;
- were conference abstracts, opinion pieces, news articles, or other sources lacking sufficient scientific information for evidence synthesis; or
- did not provide findings directly relevant to one or more of the research questions.

Government reports and other authoritative non-peer-reviewed sources were retained only where they provided important contextual information, such as national climate hazards or documented agricultural impacts and were not considered part of the primary evidence base.

Initially, research papers associated with excess water stress, waterlogging tolerance, flooding responses, agronomic management, nutrient interventions and molecular approaches in crops published between 2000 and 2026 were retrieved from different databases. A total of 620 records were identified through database searching, while an additional 35 records were identified through manual cross-referencing. Among the screened studies, 320 articles were excluded because they were unrelated to the review objectives, focused on non-crop systems, lacked sufficient scientific information or addressed unrelated abiotic stresses. The remaining 225 full-text articles were assessed for eligibility. Of these, 108 studies were excluded because of insufficient relevance, overlapping information, incomplete datasets, or lack of direct applicability to crop resilience under excess water stress. Finally, 117 peer-reviewed studies were included in the qualitative synthesis and systematic review.

Study selection

Retrieved records were compiled, duplicates were removed and titles and abstracts were screened against predefined eligibility criteria. Potentially relevant studies were assessed in full text, with reasons for exclusion recorded. The study-selection process is presented in the PRISMA flow diagram (Supplementary Fig. 1).

Reviewer and screening procedure

Title, abstract and full-text screening were performed by a single reviewer according to the predefined eligibility criteria. The screening process was conducted systematically to ensure consistent application of the inclusion and exclusion criteria.

Quality assessment and risk of bias

The methodological quality of included studies was assessed using predefined criteria covering experimental design, stress conditions, controls, replication, outcome measurements, statistical analysis and reporting quality.

Data extraction and synthesis

Information on crop species, stress conditions, experimental methods, morphological, physiological, biochemical, nutritional, molecular, agronomic and yield responses was extracted from eligible studies and organised according to the review objectives. Due to heterogeneity among studies, findings were synthesised qualitatively and organised into morphological and physiological responses, agronomic and nutrient management, molecular mechanisms and field-level management strategies. Contrasting findings, underlying mechanisms, methodological limitations and research gaps were also considered. A quantitative meta-analysis was not performed because of substantial methodological heterogeneity.

Reference-list and citation screening

Reference lists of relevant studies and reviews were screened manually to identify additional eligible publications, which were assessed using the same predefined criteria. The final reference list was checked for duplicates, completeness and relevance.

Plant responses to excess water stress

The severity of excess-water stress generally increases with stress intensity and duration, although the response thresholds vary among crops, genotypes and growth stages (10). Mild or short-term stress may induce reversible responses, whereas prolonged or severe stress can lead to greater impairment of photosynthesis and respiration, carbohydrate depletion, oxidative damage and growth reduction (10, 11). Under prolonged or complete submergence, these effects may progress to tissue injury, metabolic failure and, in susceptible plants, mortality (12). Thus, excess-water stress can be viewed as a continuum from reversible acclimation to irreversible injury, with recovery potential generally declining as stress intensity and duration increase**.**

Morphological responses

Morphological adaptations to waterlogging stress

Waterlogged soils induce several structural modifications that help plants tolerate oxygen-deficient environments by improving internal aeration, sustaining root respiration and maintaining basic metabolic activity. These responses include changes in root structure and architecture, particularly aerenchyma formation, adventitious root development and restriction of radial oxygen loss, which can improve internal oxygen transport and root functioning under prolonged soil saturation. However, the expression and effectiveness of these adaptations vary considerably among species and genotypes, reflecting differences in developmental stage, stress intensity and duration (13). During germination and early seedling establishment, plants are highly vulnerable because of limited root development and restricted carbohydrate reserves, making them less capable of sustaining metabolism under oxygen deficiency (10, 14). In maize (*Zea mays* L.), early vegetative stages are particularly sensitive, with waterlogging causing substantial reductions in growth and yield depending on stress duration. Soybean (*Glycine max* (L.) Merr.) is also sensitive to waterlogging, particularly during reproductive stages, when impaired root function, nodulation and nitrogen fixation can substantially reduce yield (10). Stress intensity further determines the severity of injury. Soil waterlogging restricts oxygen

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diffusion to roots, whereas complete submergence imposes additional limitations on gas exchange, light penetration and photosynthetic carbon assimilation. Oxygen diffusion through water is approximately 10000-fold slower than through air, accelerating oxygen depletion and carbohydrate exhaustion under complete submergence. Similarly, stress duration determines whether plants can acclimate or suffer irreversible injury. Short-term waterlogging may permit recovery following drainage, whereas prolonged exposure progressively increases carbohydrate depletion, oxidative damage, membrane injury and root dysfunction (10, 15).

Aerenchyma formation: Aerenchyma formation is one of the most important structural adaptations associated with waterlogging tolerance. Under hypoxic conditions, cortical cells undergo programmed cell death, producing interconnected air spaces that facilitate oxygen transport from shoots to submerged roots and assist in the removal of toxic gases. Two major forms of aerenchyma development are recognised: schizogenous and lysigenous. Schizogenous aerenchyma develops through separation of neighbouring cells without cell death, whereas lysigenous aerenchyma develops through programmed cell death and subsequent breakdown of cortical cells (16, 17). In crops such as maize, flooding-induced hypoxia stimulates lysigenous aerenchyma formation, thereby improving root aeration and plant survival under prolonged soil saturation (17, 18). However, the contribution of aerenchyma to tolerance depends on the plant's capacity to maintain oxygen transport from aerial tissues to submerged roots. Thus, aerenchyma formation may confer greater benefit when shoots remain exposed to air, whereas its effectiveness can be constrained when shoot tissues are also submerged (19). Although aerenchyma formation involves cellular and anatomical changes within the root cortex, it is considered a morphological adaptation in this review because it substantially alters root structure and creates a continuous internal pathway for gas movement (19, 20).

Reduction of radial oxygen loss: Alongside aerenchyma formation, numerous wetland-adapted crops develop protective outer root barriers that limit radial oxygen loss (ROL). Radial oxygen loss describes the outward diffusion of oxygen from root tissues into oxygen-poor surrounding soils. Research indicates that deposition of lignin or suberin layers in the external cortex restricts this oxygen leakage, thereby preserving oxygen supply for actively growing root tips where respiratory demand is greatest (21). Comparable findings in *Juncus effusus* L. showed that strengthened lignified and suberised layers markedly reduce oxygen permeability in outer root tissues (22). Thus, restriction of ROL complements aerenchyma formation by retaining oxygen within the root and directing it towards metabolically active tissues. However, this adaptation is particularly relevant to plants capable of maintaining an internal oxygen supply from shoots; its protective value may therefore decline as submergence increasingly restricts shoot gas exchange (23).

Morphological adaptations to flooding stress

Flooding imposes additional structural constraints when aerial tissues become partially or completely submerged. Accordingly, morphological responses involving shoot position, shoot elongation and submerged-leaf gas exchange become particularly important under flooding, whereas root adaptations such as aerenchyma formation and ROL restriction are shared with waterlogging.

Shoot elongation: In rice (*Oryza sativa* L.) and various wetland plants, rapid extension of stems, petioles, leaf sheaths and coleoptiles facilitates access to atmospheric oxygen and carbon dioxide, thereby sustaining respiration and photosynthesis during inundation. During submerged germination, rice commonly shows pronounced coleoptile extension, allowing the shoot tip to approach or reach the water surface and improving seedling survival under hypoxic conditions. The speed and extent of elongation differ significantly among genotypes, reflecting strong genetic regulation of flooding tolerance mechanisms (24). This response can be advantageous when elongation enables submerged tissues to regain contact with the atmosphere; however, excessive elongation may increase respiratory and carbohydrate costs. Therefore, the adaptive value of shoot elongation depends on the depth and duration of submergence and the plant's ability to balance escape growth with energy conservation.

Formation of adventitious roots: The emergence of adventitious roots (ARs) constitutes another important morphological adjustment under extended flooding. Adventitious root formation is promoted by coordinated hormonal signalling, particularly ethylene and auxin, under oxygen-deficient conditions. When primary root systems become damaged or insufficient to meet water and nutrient requirements, new roots can develop closer to the soil–water interface. Investigations on lowland and deepwater rice varieties in eastern and northeastern India indicate that AR development supports survival, sustains physiological processes and hastens recovery after de-submergence by rebuilding functional root networks (25). Similar observations in *J. effusus* and *Rumex palustris* Sm. reveal that adventitious roots can partly replace injured root systems, ensure continued physiological activity and facilitate post-flood recovery (18). Importantly, this response can also occur under waterlogging and should therefore be regarded as a shared root adaptation rather than a flooding-specific trait (19, 20).

Gas film formation: Certain aquatic and semi-aquatic species maintain a delicate gas layer on the leaf surface which acts as a physical interface between the submerged leaf and surrounding water, reducing the diffusion barrier for gases and facilitating the movement of carbon dioxide (CO_2) into the leaf and oxygen (O_2) out of the photosynthetic tissues. This can sustain underwater photosynthesis and contribute to internal oxygen availability during submergence. Experimental removal of this layer in rice has been shown to reduce

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underwater photosynthetic efficiency by nearly 80 %, highlighting its significance during submergence (22). Leaf gas films also permit nocturnal O_2 entry, preventing stem oxygen deficiency and promoting elongation of submerged shoots (26). Unlike root-based adaptations, gas-film formation directly improves gas exchange at submerged leaf surfaces and is therefore particularly relevant to partial or complete shoot submergence. Its effectiveness, however, depends on the persistence of the gas film under prolonged immersion and the physical characteristics of the leaf surface.

Hyponasty: Hyponasty refers to the upward curvature of petioles and serves as an adaptive movement that improves exposure to air and light in flooded settings. This response is driven by ethylene-mediated unequal cell expansion, where the lower side of the petiole base grows more rapidly than the upper side. As a result, leaf tips rise above the water surface, enhancing both oxygen diffusion and light capture. By improving access to atmospheric gases and light, hyponasty can help sustain photosynthetic activity and reduce shoot oxygen limitation. Experimental evidence in *Arabidopsis* Heynh. and wetland species such as *R. palustris* confirms that hyponastic movement significantly contributes to plant endurance under hypoxic stress (27). Its adaptive value is therefore greatest when shoot tissues are submerged but remain capable of reaching the water surface.

Waterlogging and flooding represent different levels of excess-water stress, with the spatial extent of oxygen limitation influencing which morphological adaptations become most important. Under waterlogging, where the shoot remains exposed to air, root-based traits such as aerenchyma formation, restriction of radial oxygen loss and adventitious root development can improve internal aeration and root functioning. Under partial or complete submergence, these root adaptations may remain important, but additional constraints on shoot gas exchange and light availability favour responses such as shoot elongation, hyponasty and gas-film formation.

Importantly, the effectiveness of these traits is not uniform across crops. Genotypic differences, stress duration, water depth, developmental stage and the capacity to maintain carbohydrate and oxygen supply can determine whether a particular adaptation improves survival or becomes insufficient under severe stress. Thus, morphological tolerance should be viewed as an integrated response in which root and shoot adaptations interact rather than as a set of independent traits.

Physiological responses

Physiological responses to waterlogging stress

Waterlogged soils create pronounced oxygen limitation in the root zone, initiating a series of physiological disturbances in plants. Insufficient oxygen availability restricts normal root respiration, resulting in ATP shortage and metabolic imbalance. The severity of these effects depends on the duration and intensity of oxygen limitation and the capacity of the plant to adjust its metabolism.

Effects on respiratory activity: During hypoxic or anoxic exposure, a lack of oxygen markedly suppresses mitochondrial respiration and oxidative phosphorylation, leading to cellular energy deficits and disruption of metabolic equilibrium (28). To sustain a minimal ATP supply, plants temporarily activate anaerobic metabolic routes such as glycolysis and ethanol fermentation. This metabolic shift provides a short-term source of ATP by allowing glycolysis to continue when mitochondrial respiration is restricted. However, fermentation produces considerably less ATP than aerobic respiration, making prolonged dependence on this pathway energetically unsustainable (10).

Although these mechanisms enable short-term persistence, they are energetically inefficient and generate harmful metabolites, including lactic acid, ethanol, aldehydes and related anaerobic compounds that weaken membrane stability and cellular performance (29). Extended waterlogging promotes the accumulation of these toxic products, such as acetaldehyde and organic acids in plant tissues and surrounding soil, ultimately causing cellular injury, growth inhibition and irreversible tissue damage leading to cell death (30). Thus, anaerobic metabolism represents an important short-term acclimation mechanism, but its effectiveness is limited when oxygen deprivation persists. The transition from adaptive metabolic adjustment to metabolic injury therefore depends largely on the duration and severity of stress and the plant's capacity to maintain energy balance.

Effects on photosynthetic activity: Photosynthesis, which depends on adequate light and carbon dioxide availability, becomes severely restricted during prolonged soil saturation. Oxygen deficiency around the roots interferes with chlorophyll synthesis while accelerating pigment degradation, causing premature yellowing, early senescence and reduced leaf development, thereby lowering photosynthetic efficiency and crop productivity (31). In *Sesamum indicum* L., waterlogging has been reported to significantly reduce levels of chlorophyll a, chlorophyll b, total chlorophyll and carotenoids, producing proportional declines in photosynthetic capacity (32). These findings indicate that photosynthetic decline under waterlogging can arise from both pigment loss and indirect effects of impaired root function and carbon metabolism. However, the extent of photosynthetic inhibition may vary among genotypes according to their ability to maintain root aeration and recover after stress removal.

Physiological responses to flooding

Under extended submergence, plants typically adopt two contrasting survival modes: the Low-Oxygen Escape Strategy (LOES) and the Low-Oxygen Quiescence Strategy (LOQS). These adaptive pathways are governed by ethylene-responsive transcription regulators such as SNORKEL1 (SK1), SNORKEL2 (SK2) and SUB1A, which coordinate hormonal balance and structural adjustments during oxygen limitation (33).

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In the LOES pathway, rapid elongation of stems and petioles helps plants re-establish contact with the atmosphere. In deep-water rice, SK1 and SK2 stimulate gibberellin biosynthesis, promoting internode extension and enhancing tolerance to flooding. This strategy is advantageous when floodwater is gradually rising and sufficient carbohydrate reserves are available to support rapid growth. However, excessive elongation is metabolically expensive and may accelerate carbohydrate depletion when plants remain completely submerged for prolonged periods (33). Thus, LOES is most effective when escape growth can restore atmospheric contact before carbohydrate reserves become critically depleted.

Conversely, the LOQS pathway focuses on conserving energy during deep or transient submergence. The SUB1A regulator suppresses excessive ethylene synthesis, restricts gibberellin-driven elongation and stabilises hormonal equilibrium, thereby improving survival under short-duration floods. By limiting unnecessary shoot growth, LOQS reduces carbohydrate consumption and preserves energy reserves for maintenance during submergence and subsequent recovery. Therefore, the relative advantage of LOES and LOQS depends on flood depth, duration, carbohydrate availability and genotype (34). Collectively, these contrasting strategies demonstrate the considerable physiological flexibility of plants when adapting to excess water conditions.

Experimental evidence in rice demonstrates this context dependence. Deep-water rice cultivars activate SK1 and SK2 and promote rapid internode elongation under progressively rising floodwaters, whereas SUB1A-containing varieties restrict elongation and conserve carbohydrate reserves during transient complete submergence (35). Although rice provides the best-characterised genetic model for these strategies, comparable physiological responses have also been reported in wheat (*Triticum aestivum* L.) suggesting that contrasting escape and conservation responses may occur beyond rice (36, 37).

Biochemical responses to excess water

Excess water stress enhances the production of reactive oxygen species (ROS), such as superoxide radicals, hydrogen peroxide and hydroxyl radicals, leading to oxidative damage to lipids, proteins and nucleic acids. Reactive oxygen species accumulation occurs partly because oxygen limitation disrupts normal electron transport and cellular redox balance, while rapid reoxygenation after stress removal can further enhance ROS production. To minimise oxidative injury, plants activate antioxidant defence systems involving enzymes such as superoxide dismutase, catalase and peroxidases. Tolerant genotypes often exhibit stronger antioxidant activity and improved redox regulation compared with susceptible cultivars, thereby enhancing stress tolerance under prolonged flooding conditions. Superoxide dismutase converts superoxide radicals into hydrogen peroxide, which is subsequently detoxified mainly by catalase and peroxidases. This coordinated antioxidant response limits membrane lipid peroxidation and protects proteins and cellular membranes, thereby supporting recovery after stress.

However, stronger antioxidant activity alone should not be interpreted as definitive evidence of tolerance, because ROS also function as signalling molecules during stress adaptation. The balance between ROS production and detoxification, rather than ROS elimination itself, is therefore important for maintaining cellular homeostasis under excess water stress (38–42).

Molecular responses to excess water stress

Excess water stress induces coordinated molecular responses involving stress perception, hormonal signalling, oxygen sensing, transcriptional regulation and energy homeostasis. Ethylene acts as an early signal during submergence and, in rice, interacts with regulatory pathways involving *SNORKEL1* (*SK1*), *SNORKEL2* (*SK2*) and *SUB1A*, which contribute to contrasting responses depending on genotype and flooding conditions (10–12).

Oxygen sensing is mediated largely through the N-degron pathway, which regulates the stability of *ERF-VII* transcription factors. Under hypoxia, reduced activity of plant cysteine oxidases (PCOs) stabilises *ERF-VII* proteins, promoting the expression of hypoxia-responsive genes such as *PDC*, *ADH* and *SUS* that support glycolytic ATP production (43, 44). Phytoglobin 1 (PGB1) also contributes by regulating nitric oxide levels and *ERF-VII* stability. However, prolonged reliance on anaerobic metabolism remains energetically inefficient and may contribute to metabolic injury (45, 46).

Comparative responses among crops

Morphological and physiological adaptations to excess water vary considerably among crops and genotypes (10). Rice generally exhibits strong structural plasticity through aerenchyma formation, adventitious rooting and, in some genotypes, shoot elongation, whereas maize develops inducible aerenchyma and crown roots (11, 47). Wheat (*Triticum aestivum* L.) generally shows weaker structural adaptation and greater sensitivity to prolonged waterlogging, while soybean, cowpea and alfalfa may experience reduced root growth, nodulation and photosynthetic performance (48–50). These differences indicate that tolerance depends on the combined maintenance of root aeration, energy status, photosynthesis and redox balance rather than on a single adaptive trait (Table 1).

Molecular regulation also shows both conserved and crop-specific features. In rice, *SUB1A*, *SK1* and *SK2* regulate contrasting responses to submergence, while *ZmEREB180* in maize and *TaERFVII.1* and *PRT6*/ERF-VII pathways in wheat and barley contribute to hypoxia responses (47, 58). In soybean, *GLB1* and *GLB2* contribute to nitric oxide homeostasis, whereas *Sporamin A* is associated with stress responses in sweet potato (*Ipomoea batatas* (L.) Lam.) (49–50, 59). Thus, although core oxygen-sensing mechanisms are partly conserved, their downstream regulation and

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phenotypic outcomes vary among crops, highlighting the importance of crop- and genotype-specific mechanisms in excess-water tolerance.

The physiological and biochemical responses to excess water stress are closely interconnected rather than acting independently. Oxygen limitation restricts mitochondrial respiration and ATP production, promoting anaerobic metabolism, while prolonged energy deficiency can impair photosynthesis, nutrient acquisition, growth and reproduction. Changes in redox balance during stress and reoxygenation further activate antioxidant responses. Thus, plant performance depends on the ability to coordinate energy conservation, carbon assimilation, redox regulation and recovery.

No single physiological or biochemical trait is sufficient to define excess-water tolerance. Instead, tolerance results from the coordinated action of complementary mechanisms, whose effectiveness varies with crop species, genotype, developmental stage, stress intensity, duration and recovery conditions. The major morphological, physiological and biochemical mechanisms contributing to excess-water tolerance and their interactions are summarised in Fig. 2. Therefore, tolerance should be evaluated by considering interactions among morphological adaptation, metabolic adjustment, antioxidant regulation and recovery capacity rather than individual traits alone.

Integrated strategies for enhancing crop resilience to excess water stress

Improving crop resilience under waterlogging and flooding requires an integrated approach combining genetic improvement with climate-smart agronomic management. Together, these strategies enhance internal aeration, maintain metabolic stability, reduce yield losses and improve adaptation under oxygen-deficient environments.

Waterlogging- and flood-tolerant varieties

Development of waterlogging- and flood-tolerant cultivars remains one of the most effective long-term strategies for reducing crop losses under excess water stress. At the M.S. Swaminathan Rice Research Station, Moncompu, rice lines KAUM 179-1 and KAUM 180-2 developed through pedigree selection for the flood-prone Kuttanad region, exhibit submergence tolerance, lodging resistance and improved adaptability under below sea level cultivation conditions (60).

Globally, breeding programmes have successfully incorporated major flood-tolerance loci such as *SUB1A*, *SNORKEL1 (SK1)* and *SNORKEL2 (SK2)* into elite rice germplasm, leading to the development of improved flood-resilient cultivars (34). Despite this, the effectiveness of these genetic improvements varies with flood duration, crop species and environmental conditions, highlighting the need for broader multi-crop validation and region-specific breeding strategies.

Adjustment of planting dates

Modifying sowing time serves as a cost-efficient agronomic intervention for reducing crop exposure to excessive soil moisture. Aligning planting schedules with favourable weather windows allows sensitive growth stages to avoid peak rainfall periods, thereby lowering the likelihood of waterlogging injury (61).

Crops such as wheat, barley and rapeseed generally demonstrate greater tolerance during early vegetative phases than during reproductive development (62). Early sowing can therefore help crops complete critical growth stages before severe flooding occurs. In addition, practices such as seed priming, precision planting, conservation tillage and the use of tolerant cultivars further improve crop establishment and resilience under variable moisture conditions (62). Therefore, calendar-based crop planning represents a practical and sustainable means of mitigating waterlogging risk.

Use of cover crops

Cover cropping improves soil structure, aggregation, infiltration capacity and drainage efficiency, thereby reducing the severity of waterlogging stress. Continuous cover crop use can lower soil compaction and enhance soil aeration under saturated conditions (63). Reed canary grass (*Phalaris arundinacea* L.), for example, has been reported to reduce soil moisture and water-table depth through enhanced evapotranspiration, improving root-zone aeration in poorly drained soils (64).

Table 1. Morphological responses of important crops under waterlogging stress

Crop species	Key morphological effects	Reference
Gossypium hirsutum L.	Reduced vegetative growth and lint yield; development of root aerenchyma	51
Zea mays L.	Reduced plant height, leaf number and total leaf area	52
Glycine max (L.) Merr.	Reduced shoot and root dry weight, nodulation and pod number; enhanced aerenchyma formation	53
Allium cepa L.	Reduced plant height, leaf area, bulb weight and marketable yield	54
Sorghum bicolor (L.) Moench	Reduced leaf area and biomass under early waterlogging	55
Triticum aestivum L.	Reduced leaf area and grain yield under prolonged waterlogging	56
Vigna unguiculata (L) Walp.	Reduced plant height, leaf number and leaf area; adventitious root formation under severe stress	57

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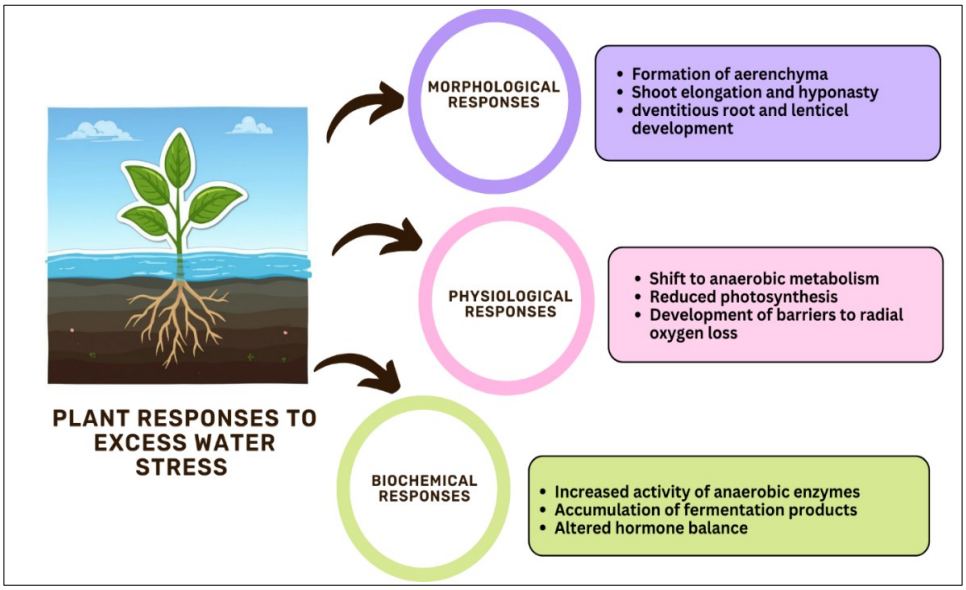


Fig. 2. Integrated adaptive responses of plants to excess water stress at morphological, physiological and biochemical levels.

Although reports suggest that the performance of cover crops varies with species selection, soil texture, climatic conditions and management intensity, unsuitable combinations may yield limited or even adverse effects (63). Careful selection and scheduling are therefore essential for maintaining optimal soil-water balance in flood-prone regions.

Nutrient management to mitigate excess water stress

Excess moisture substantially disrupts nutrient dynamics by reducing availability, uptake efficiency and utilisation due to root-zone oxygen limitation. Suppressed root respiration limits active ion transport and microbial processes, restricts root proliferation and alters the shoot-to-root balance, ultimately causing nutrient disequilibrium (65). Well-planned nutrient strategies can counter these limitations by sustaining metabolic processes and accelerating recovery once stress subsides.

Role of macronutrients: Nitrogen (N) is particularly vulnerable under saturated soil conditions. Moderate nitrogen supplementation following waterlogging has been shown to enhance photosynthetic recovery, stimulate root regrowth and restore plant vigour, as observed in cotton (*Gossypium hirsutum* L.) (66). In pulse crops, flooding severely disrupts root nodulation and symbiotic nitrogen fixation, resulting in acute nitrogen deficiency. For instance, in *G. max*, flooding strongly reduces nitrogen fixation in nodules; however, N metabolism can partially recover after drainage, with the rate of recovery depending on the duration of waterlogging. Providing external nitrogen sources, such as nitrate, during or after flooding can partially compensate for the loss of biological nitrogen fixation, thereby improving chlorophyll content, biomass accumulation and post-flood growth recovery (67). Conversely, excess nitrogen application under saturation often leads to a decline in nitrate availability due to leaching and denitrification losses, thereby limiting its effectiveness in stress recovery (68).

Potassium (K) and calcium (Ca) play central roles in osmotic regulation, membrane stabilisation and stress signalling during hypoxic stress. Adequate K supply in cotton increases antioxidant enzyme activities, such as catalase (CAT) and superoxide dismutase (SOD), reduces reactive oxygen species accumulation and improves recovery and yield. In rice, it supports carbohydrate retention, chlorophyll preservation and reduced senescence and lodging (69, 70). Calcium enhances tolerance by stabilising membrane-associated ATPase activity, facilitating abscisic-acid-mediated stomatal regulation and improving nutrient transport, as demonstrated in pepper under hypoxic soils (71). Magnesium contributes to chlorophyll formation and photosynthetic efficiency; magnesium oxide (MgO) pretreatment in papaya (*Carica papaya* L.) mitigated waterlogging-induced decline in photosynthesis and improved biomass accumulation and leaf area (72). Overall, balanced macronutrient management enhances metabolic stability, maintains carbon assimilation and improves crop recovery under excess water stress.

Role of micronutrients: Although direct experimental validation for zinc (Zn), manganese (Mn), copper (Cu) and boron (B) under waterlogging remains limited, their physiological roles indicate potential contributions to stress resilience. Zinc participates in enzyme activation and oxidative stress mitigation during post-flood recovery (73). Moreover, Mn supports enzymatic reactions involved in reactive oxygen detoxification (74). Copper functions as a cofactor for ROS-scavenging enzymes, while boron contributes to cell wall integrity and carbohydrate transport, indirectly aiding plant stability when micronutrient balance is maintained (73). Collectively, these micronutrients may strengthen plant endurance and post-stress recovery.

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Waterlogging exerts negative consequences on crop growth and productivity by disrupting micronutrient dynamics across species. In onion (*Allium cepa* L.), prolonged soil saturation significantly reduced the availability and plant uptake of Fe, Cu, Mn and B, which was closely associated with impaired bulb development and yield reduction (73). Similarly, in cotton (*G. hirsutum*), waterlogging altered micronutrient distribution in leaves, stems and roots, leading to nutrient imbalance under extended flooding conditions and contributing to stress-induced physiological dysfunction (74). These findings underscore that maintaining micronutrient homeostasis is a critical component of crop tolerance to waterlogging stress and a key determinant of sustained growth and yield under hypoxic soil conditions.

Role of essential and beneficial nutrients: Essential nutrients such as Fe and beneficial elements like silicon (Si) further improve tolerance to excess water stress by supporting antioxidant activity, root regeneration, chlorophyll maintenance and internal aeration. Iron application has been reported to alleviate hypoxia-induced chlorosis in cotton, whereas Si supplementation enhances aerenchyma formation, stomatal conductance, chlorophyll retention and root hydraulic conductivity under saturated soil conditions (75, 76).

Adaptive nutrient management strategies: Nutrient management in flood-susceptible fields requires flexible approaches to minimise nutrient losses and improve crop recovery. Waterlogging following fertiliser application often causes substantial N depletion through leaching and denitrification. Application of “rescue N” after restoration of soil aeration has been shown to improve crop recovery, photosynthetic activity and yield stability (77). Split N application further helps maintain nutrient availability throughout crop growth and reduces loss under saturated conditions. In maize, post-flood N supplementation has improved N redistribution and grain formation following transient flooding (78).

Enhanced efficiency fertilisers (EEFs): Enhanced efficiency fertilisers help synchronise N release with crop demand while reducing losses under waterlogged conditions. Urease inhibitors (e.g. NBPT) delay urea hydrolysis and minimise ammonia volatilisation, although extended inhibition may temporarily increase urea concentration (79). Slow- and controlled-release fertilisers including polymer or sulfur-coated urea and urea-formaldehyde provide a gradual nutrient supply that limits leaching and gaseous emissions (80). Nitrification inhibitors such as nitrapyrin, dicyandiamide (DCD) and 3,4-dimethylpyrazole phosphate (DMPP) restrict ammonium-to-nitrate conversion, reducing nitrate loss, while newer DMS-based inhibitors offer prolonged effectiveness in saturated soils (81). Overall, EEFs enhance N-use efficiency and facilitate crop recovery following excess water exposure.

Collectively, these findings highlight the importance of balanced and adaptive nutrient management for improving crop resilience under excess water stress. Additionally, the effectiveness of nutrient interventions remains highly dependent on crop species, developmental stage, stress duration and soil redox conditions, emphasising the need for integrated nutrient- and water-management strategies tailored to flood-prone agroecosystems.

The contrasting outcomes of nutrient interventions indicate that their success depends on the timing and severity of stress. For example, rescue nitrogen is more effective after restoration of soil aeration, whereas excessive N application during prolonged saturation may be ineffective because of leaching and denitrification losses. Thus, nutrient management should be synchronised with drainage and crop recovery rather than applied uniformly throughout the stress period.

Role of plant growth regulators in waterlogging tolerance

Plant tolerance to excess water stress is strongly regulated by hormonal signalling networks that coordinate stress perception, growth regulation and metabolic adaptation under hypoxic conditions. Hormones including ethylene, abscisic acid (ABA), auxins, gibberellins (GAs), brassinosteroids (BR), jasmonic acid (JA), salicylic acid (SA) and melatonin play important roles in regulating adaptive responses during waterlogging and flooding stress (82). The major functions of these plant growth regulators (PGRs) are summarised in Table 2.

Table 2. Role of plant growth regulators in mitigating waterlogging stress

Plant growth regulator	Crop	Effect	Reference
Ethylene	*Glycine max* (L.) Merr. (Soybean)	Exogenous ethephon (50–200 µM) enhanced ethylene release, adventitious root formation and root surface area under waterlogging	83
Abscisic acid (ABA)	*Glycine max* (L.) Merr. (Soybean)	Waterlogging reduced ABA levels within 24 hr, while aerenchyma formation occurred after 72 hr; exogenous ABA inhibited aerenchyma development	84, 85
Auxin	*Oryza sativa* L. (Rice)	Inhibition of auxin transport reduced adventitious root formation, indicating the importance of auxin signalling during flooding	86
	Cucumis sativus L. (Cucumber)	Active auxin transport was essential for adventitious root induction under hypoxic conditions	87

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Gibberlins (GA)	*Brassica napus* L. (Rape)	Exogenous GA reduced lipid peroxidation, stabilised membranes and improved waterlogging tolerance	88
Jasmonic acid (JA)	*Glycine max* (L.) Merr. (Soybean)	JA altered proteomic responses associated with glycolysis, fermentation and cell-wall metabolism, improving stress recovery	89
Brassinosteroids (BR)	*Cucumis sativus* L. (Cucumber)	24-epibrassinolide enhanced adventitious root formation, carbohydrate transport, antioxidant activity and reduced ROS accumulation	90
Salicylic acid (SA)	*Prunus persica* (L.) Mill. (Peach)	Exogenous SA increased antioxidant enzyme activity, proline accumulation and membrane stability under waterlogging	91
Melatonin	*Medicago sativa* L.	Melatonin increased polyamine accumulation, reduced ethylene biosynthesis, stabilised membranes and delayed senescence	92

Use of anti-ethylene agents to withstand hypoxia

Ethylene plays a central role in plant adaptation to flooding and hypoxic environments by regulating structural and physiological responses. Moderate ethylene accumulation promotes adaptive traits such as adventitious root formation and aerenchyma development, whereas prolonged exposure may suppress growth and reduce yield potential (93).

Anti-ethylene compounds including 1-methylcyclopropene (1-MCP), aminoethoxyvinylglycine (AVG), aminooxyacetic acid (AOA), 1-aminocyclopropane-1-carboxylate (ACC) inhibitors and silver or cobalt ions reduce ethylene-induced injury by inhibiting ethylene biosynthesis or receptor activity (94). In cotton, application of 1-MCP and AVG improved seed and lint yield under waterlogged conditions, particularly when AVG was applied during the early reproductive stages (95). However, the effectiveness of anti-ethylene treatments remains highly dependent on crop species, stress duration, growth stage and application timing.

This context dependence may explain differences among reported responses, as ethylene can promote adaptive responses such as adventitious rooting at appropriate levels, but prolonged or excessive ethylene signalling may restrict growth. Therefore, treatment effectiveness depends on achieving an appropriate balance between stress signalling and growth regulation.

Combined application of fertilisers and growth regulators

Integrated application of nutrients and PGRs provides a complementary strategy for mitigating waterlogging damage. Nutrient supplementation supports metabolic recovery, whereas PGRs improve photosynthetic activity, antioxidant defence and hormonal balance under hypoxic conditions. In cotton, foliar application of urea and potassium chloride (KCl) combined with PGRs such as brassinolide and diethyl aminoethyl hexanoate enhanced chlorophyll retention, membrane stability, adventitious root formation and post-waterlogging recovery (75). These findings highlight the potential of integrated nutrient–hormonal management strategies for improving crop resilience under prolonged soil saturation.

Pretreatment with hydrogen peroxide

Although hydrogen peroxide (H_2O_2) is commonly recognised as a reactive oxygen species, it also functions as an important signalling molecule involved in stress acclimation. Exogenous H_2O_2 application can prime plants for improved tolerance by enhancing antioxidant activity and metabolic preparedness prior to waterlogging exposure (95). Studies have shown that H_2O_2 pretreatment reduces oxidative damage while improving root growth, chlorophyll retention, biomass accumulation and photosynthetic performance under excess moisture conditions (96).

In soybean, H_2O_2 seed priming enhanced seedling survival and recovery under waterlogged conditions, indicating its potential as a practical early-stage stress-management strategy (28).

Role of microbes in mitigating waterlogging stress

Beneficial microbial inoculants, particularly the endophytic fungus *Serendipita indica*, have shown considerable potential in improving plant tolerance to waterlogging by enhancing root function, rhizosphere activity and stress defence mechanisms (97). In waterlogged peach seedlings, *S. indica* reduced oxidative damage and improved antioxidant activity, thereby enhancing stress tolerance (98). Similar protective effects involving activation of the ascorbate-glutathione cycle have also been reported in white clover (99).

Co-inoculation of *S. indica* with the arbuscular mycorrhizal fungus *Funneliformis mosseae* further improved root growth, nutrient uptake and antioxidant responses in peach under hypoxic conditions (98). In sugar beet systems, flooding has also been associated with increased populations of beneficial rhizobacteria such as *Pseudomonas*, which contribute to improved rhizosphere functioning and nutrient cycling (100). Collectively, these findings highlight microbial interventions as promising biological tools for strengthening crop resilience under excess water stress. Nevertheless, field-scale evidence and long-term validation of microbial approaches remain limited.

Biodrainage

Biodrainage is increasingly recognised as an environmentally sustainable approach for managing excess water stress in flood-prone regions. Tree species such as *Eucalyptus* L'Hér., *Populus* L., *Casuarina* L., *Dalbergia* L.f., *Syzygium* Gaertn., *Acacia* Mill., *Prosopis* L. and *Leucaena* Benth. exhibit high transpiration capacity, enabling substantial reductions in groundwater levels under waterlogged conditions (101).

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In the Indira Gandhi Nahar Project of Rajasthan, plantations of *Eucalyptus*, *Acacia* and *Dalbergia* significantly reduced canal-induced waterlogging and soil salinity, lowering groundwater tables by nearly 15 m within six years despite limited plantation coverage (102, 103).

Raised seedbeds to alleviate waterlogging

Raised-bed cultivation is an effective agronomic strategy for reducing soil saturation and improving crop performance under waterlogged conditions, particularly in semi-arid and poorly drained regions (104). Elevating planting beds above the soil surface improves drainage, reduces root-zone oxygen deficiency and enhances nutrient uptake. Crops grown on raised beds frequently exhibit improved growth and yield compared with conventional flat planting systems (105). In Punjab, raised-bed wheat cultivation increased grain yield and nitrogen-use efficiency by more than 10 % relative to traditional methods (106). However, adoption may be limited by equipment requirements and field-management constraints.

Precision agriculture for managing excess water stress

Precision agriculture technologies are increasingly being integrated into excess water management to address spatial variability in soil saturation and crop response (107). Tools such as remote sensing, geographic information system (GIS)-based terrain analysis, unmanned aerial vehicle (UAV) imagery and crop simulation models enable identification of poorly drained areas and support site-specific drainage and nutrient-management decisions. Satellite platforms including Sentinel-1 and Sentinel-2, combined with machine-learning approaches have shown strong potential for mapping waterlogged zones and predicting yield losses in cereal systems under excess moisture conditions (108, 109). Similarly, UAV-based multispectral imaging enables early detection of flooding-induced physiological stress, facilitating timely agronomic intervention (110).

Despite their potential, the large-scale adoption of precision technologies remains constrained by cost, technical expertise, environmental variability and limited validation across diverse agroecological regions.

Genetic and biotechnological approaches for improving tolerance to excess water stress

Genetic and molecular approaches have emerged as important strategies for improving crop tolerance to flooding, waterlogging and submergence stress. Recent advances in molecular-marker studies, QTL mapping, genomic selection and functional genomics have accelerated the identification of genes and regulatory pathways associated with hypoxia tolerance and adaptive responses under oxygen-deficient environments.

Major quantitative trait loci such as *SUB1A*, *SNORKEL1 (SK1)* and *SNORKEL2 (SK2)* have been successfully incorporated into elite rice cultivars to improve survival under submergence and flooding conditions (34). In addition, genome-wide association studies and multi-omics approaches have identified candidate genes associated with anaerobic metabolism, carbohydrate regulation, adventitious root formation, aerenchyma development, antioxidant activity and stress signalling. In sweet corn, integrative omics analyses identified candidate genes such as *Zmhpc1* associated with improved anaerobic metabolism and stress adaptation (111).

Functional genomics studies have further highlighted the role of ethylene-responsive factor (*ERF-VII*) transcription factors, alcohol dehydrogenase (*ADH*), pyruvate decarboxylase (*PDC*) and hypoxia-responsive signalling pathways in regulating flooding tolerance (112–114). In barley, overexpression of *HvERF2.11* enhanced antioxidant defence and anaerobic metabolism, improving plant tolerance under saturated soil conditions (113). Integration of transcriptomics, proteomics, metabolomics and other multi-omics tools has significantly improved understanding of molecular networks associated with flooding adaptation. These approaches have revealed differential regulation of genes involved in carbohydrate metabolism, hormonal crosstalk, calcium signalling, mitochondrial respiration and oxidative stress regulation during hypoxic stress (114–116).

Recent advances in clustered regularly interspaced short palindromic repeats (CRISPR)/CRISPR-associated protein (Cas)-mediated genome editing and genomic selection also provide promising opportunities for targeted manipulation of genes controlling root architecture, stress signalling and excess-water tolerance. Despite this, field-level deployment of flood-tolerant cultivars remains constrained by genotype-environment interactions, variable flooding intensity and limited multi-location validation (117). Therefore, integration of molecular breeding with precision phenotyping and climate-smart agronomic management will be essential for developing resilient crop varieties under increasingly erratic flooding conditions.

However, direct comparisons among management studies are constrained by methodological differences in stress duration, water depth, soil conditions, crop growth stage, treatment dose and experimental environment. A considerable proportion of the available evidence is derived from pot, greenhouse or controlled experiments, while field-scale validation remains limited for several approaches. For example, microbial interventions have shown promising effects on antioxidant defence and root function, but their long-term field performance remains insufficiently validated. Therefore, results obtained under controlled conditions should be interpreted cautiously when developing field recommendations.

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Future Perspectives and Conclusion

The severity of plant responses depends not only on the occurrence of excess water but also on stress intensity, duration, water depth, crop species, genotype and developmental stage. Increasing stress duration and severity generally intensify reductions in root respiration, photosynthesis, nutrient uptake, biomass accumulation and yield (6, 10). Short-term waterlogging may induce reversible responses such as anaerobic metabolism, aerenchyma formation and adventitious root development, whereas prolonged or severe stress can result in carbohydrate depletion, oxidative damage, membrane injury and irreversible tissue damage. Thus, tolerance should be considered a dose-dependent response rather than a fixed trait. Comparative evidence across crops indicates that tolerant genotypes generally maintain better root aeration, carbohydrate availability, antioxidant capacity and post-stress recovery than susceptible genotypes. However, these responses are not universally consistent (36, 50, 53). For example, rapid shoot elongation may facilitate escape from shallow or deep-water flooding in some rice genotypes, whereas growth quiescence may be more advantageous when carbohydrate reserves are limited (19, 31). Such contrasting strategies indicate that the effectiveness of a tolerance mechanism is strongly dependent on flood depth, duration, crop genotype and environmental context**.** Direct dose–response comparisons remain limited because studies differ considerably in stress duration, water depth, growth stage and experimental conditions.

The reviewed literature also highlights important methodological limitations. A substantial proportion of waterlogging studies have been performed under controlled or pot conditions using single genotypes, relatively uniform stress treatments and short experimental periods (10, 27, 53). Such approaches may not adequately capture the spatial and temporal heterogeneity of field waterlogging. Moreover, differences in the definitions and severity of waterlogging, partial flooding and complete submergence complicate comparisons among studies. Many investigations focus on individual physiological, biochemical or molecular responses without simultaneously relating these traits to recovery and final yield (10, 27, 36). Consequently, a trait that responds strongly to waterlogging is not necessarily a reliable predictor of field-level tolerance. Development of standardised stress protocols, common phenotyping criteria and integrated measurements of stress response, recovery and yield would substantially improve the comparability and practical value of waterlogging research.

Agronomic management provides an important complementary approach to genetic tolerance. Improved drainage, raised-bed cultivation and suitable land configuration can reduce the duration of soil saturation and improve root-zone aeration (101–106). Nutrient management can also influence crop recovery following waterlogging. Biological approaches are receiving increasing attention as complementary strategies for improving crop resilience. Beneficial microorganisms and root-associated symbionts may enhance nutrient acquisition, antioxidant defence, root development and recovery under waterlogging (97–100). However, the performance of microbial inoculants can vary with host genotype, soil properties, microbial establishment and environmental conditions. Future research should therefore move beyond the evaluation of individual inoculants towards the identification of stable, crop-specific and environment-specific microbial consortia capable of functioning under oxygen-deficient soil conditions.

Advances in molecular breeding and multi-omics approaches provide further opportunities to improve waterlogging tolerance. Comparative transcriptomic, metabolomic and proteomic analyses have further demonstrated the complexity of stress-responsive networks and their dependence on genotype and tissue type (29, 50, 111, 116). These approaches can facilitate the identification of candidate genes, molecular markers and biomarkers associated with stable tolerance across developmental stages. Genome-editing technologies such as CRISPR/Cas additionally provide opportunities for targeted manipulation of genes associated with oxygen sensing, hormonal signalling, aerenchyma formation and metabolic acclimation; however, potential pleiotropic effects, genotype dependence, regulatory requirements and possible yield penalties under non-waterlogged conditions must be carefully evaluated before deployment.

Digital agriculture and artificial intelligence provide emerging opportunities to improve the spatial and temporal assessment of waterlogging stress. The UAV-based multispectral, hyperspectral and thermal sensing can provide rapid, non-destructive information on crop growth, canopy condition and stress-related changes over large areas (108–110). Coupling remote sensing with hydrological and flood-prediction models could further support early-warning systems for crop protection. Nevertheless, reliable AI-based prediction requires large, well-curated and geographically diverse datasets, robust ground-truth observations and validation across different crops and agroecological environments.

Climate change is expected to increase the frequency and intensity of extreme precipitation and other hydrological disturbances in many agricultural regions, further emphasising the need for integrated waterlogging management (3). Under these conditions, biodrainage and landscape-scale water management may provide additional options for reducing persistent water tables and improving the sustainability of affected production systems (101–103). However, the suitability and economic feasibility of such approaches depend strongly on soil properties, climate, topography, farm size, available infrastructure and local management capacity.

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Overall, excess-water tolerance is a multilevel, interactive and dose-dependent phenomenon governed by coordinated structural, physiological, biochemical, molecular and microbial responses. Future crop improvement should therefore move beyond identifying individual tolerance traits towards integrating complementary mechanisms with efficient drainage, adaptive nutrient management, tolerant genotypes, genome editing, microbiome-based interventions and climate-smart digital technologies. A comparative assessment of these major strategies, including their potential advantages, limitations and field applicability, is presented in Table 3. Combining AI-enabled phenotyping, flood prediction, multi-omics and field-based decision-support systems with economically feasible agronomic practices could improve the precision, reliability and scalability of excess-water management. Such an integrated approach can improve the economic feasibility and field applicability of strategies for sustaining crop productivity under increasingly variable waterlogging and flooding conditions.

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Authors' contributions

VN, SA, MS[1], NK and KAJ contributed to the literature search, data collection and preparation of the first draft of the manuscript. SK analysed the manuscript and provided continuous guidance and assistance throughout the revision and finalisation process. KS, PSP, PRS and MS[2] reviewed and edited the manuscript. MA critically reviewed the manuscript and contributed to its revision and refinement. All authors read and approved the final version of the manuscript [MS[1] stands for M Salma and MS[2] for M Sreeja].

Table 3. Comparative assessment of major strategies for improving crop resilience to excess water stress

Strategy	Major advantages	Key limitations	Future potential
Improved drainage	Rapid removal of excess water; improves root aeration	Infrastructure and maintenance costs	Integrated farm-scale water management
Raised-bed cultivation	Improves drainage and root aeration	Labour and establishment costs	Site-specific land configuration
Nutrient management	Supports recovery and nutrient acquisition	Timing and dose are critical	Stress-responsive nutrient management
Rescue N application	Can improve post-waterlogging recovery	Risk of N loss if poorly timed	Precision, stage-specific N management
Silicon/biostimulants	May enhance antioxidant defence and recovery	Variable field responses	Crop- and stress-specific formulations
Plant growth regulators	Can modify root growth and stress responses	Dose-dependent effects and cost	Targeted physiological regulation
Microbial inoculation	Potentially improves nutrient uptake and stress defence	Field consistency may be low	Microbiome engineering and microbial consortia
Conventional breeding/QTL	Produces heritable tolerance	Time-consuming and genotype dependent	Gene pyramiding and climate-resilient cultivars
Microbial inoculation	Potentially improves nutrient uptake and stress defence	Field consistency may be low	Microbiome engineering and microbial consortia
Conventional breeding/QTL	Produces heritable tolerance	Time-consuming and genotype dependent	Gene pyramiding and climate-resilient cultivars
CRISPR/Cas genome editing	Precise modification of candidate genes	Regulatory, pleiotropic and genotype constraints	Targeted multi-trait flood tolerance
UAV/AI phenotyping	Rapid, non-destructive, large-scale assessment	Requires datasets, sensors and technical expertise	Automated stress detection and phenotyping
Flood prediction/ML	Enables early warning and targeted intervention	Requires reliable weather, soil and field data	Real-time decision-support systems
Multi-omics	Identifies complex tolerance networks and biomarkers	High cost and analytical complexity	Integrated biomarker-assisted breeding
Biodrainage	Long-term water-table management	Site-specific effectiveness and establishment time	Integrated landscape water management

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Compliance with ethical standards

Conflict of interest

Authors do not have any conflict of interests to declare.

Ethical issues

None

Declaration of generative AI and AI-assisted technologies in the writing process

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