



International Journal of Research in Agronomy

E-ISSN: 2618-0618
P-ISSN: 2618-060X
© Agronomy
NAAS Rating (2026): 5.20
www.agronomyjournals.com
2026; SP-9(9): 01-07
Received: 02-06-2026
Accepted: 08-07-2026

Navya V
PG Scholar, Department of
Agronomy, College of Agriculture
Vellayani, Kerala Agricultural
University, Thiruvananthapuram,
Kerala, India

Sreelakshmi K
Assistant Professor, Department of
Agronomy, College of Agriculture,
Vellayani, Kerala Agricultural
University, Thiruvananthapuram,
Kerala, India

Aswathy S
PG Scholar, Department of
Agronomy, College of Agriculture
Vellayani, Kerala Agricultural
University, Thiruvananthapuram,
Kerala, India

Nayana Krishnan
PG Scholar, Department of
Agronomy, College of Agriculture
Vellayani, Kerala Agricultural
University, Thiruvananthapuram,
Kerala, India

Salma M
PG Scholar, Department of
Agronomy, College of Agriculture
Vellayani, Kerala Agricultural
University, Thiruvananthapuram,
Kerala, India

Corresponding Author:

Navya V
PG Scholar, Department of
Agronomy, College of Agriculture
Vellayani, Kerala Agricultural
University, Thiruvananthapuram,
Kerala, India

Root morphological and anatomical adaptations of grain and forage legumes to waterlogging stress

Navya V, Sreelakshmi K, Aswathy S, Nayana Krishnan and Salma M

DOI: <https://www.doi.org/10.33545/2618060X.2026.v9.i9Sa.6455>

Abstract

Waterlogging is a major abiotic stress that adversely affects crop growth, productivity and yield stability by restricting oxygen availability in the soil and disrupting root respiration, nutrient acquisition and overall plant metabolism. Grain and forage legumes are particularly vulnerable because of their high respiratory demand and dependence on functional root systems for water and nutrient uptake and biological nitrogen fixation. However, legumes exhibit considerable variation in their ability to withstand waterlogged conditions through coordinated morphological and anatomical adaptations. This review synthesizes current knowledge on the structural mechanisms that enable grain and forage legumes to acclimate to waterlogging stress. Morphological adaptations include adventitious root formation, modification of root system architecture, changes in lateral root development, root hair responses and alterations in root-to-shoot biomass allocation. Anatomical adaptations include lysigenous and schizogenous aerenchyma formation, secondary aerenchyma development, hypertrophic lenticel formation, regulation of radial oxygen loss and modification of apoplastic barriers through suberin and lignin deposition. These adaptations collectively facilitate oxygen transport to submerged root tissues, improve exploitation of relatively oxygenated soil layers and regulate resource allocation under oxygen deficiency. Considerable interspecific and genotypic variation exists in the expression of these traits, highlighting their potential value for identifying waterlogging-tolerant germplasm. Understanding the structural basis of waterlogging tolerance can contribute to the development of reliable phenotypic screening criteria and support breeding strategies aimed at improving the resilience and yield stability of legume crops under increasingly variable water regimes. The review also identifies major knowledge gaps concerning the integration of root morphological and anatomical traits and their application in breeding and crop improvement programmes.

Keywords: Waterlogging tolerance, root architecture, aerenchyma, adventitious roots, anatomical adaptation

Introduction

Waterlogging is a major abiotic constraint that substantially limits crop growth and productivity worldwide. It develops when excess water saturates the soil profile and fills air-filled pore spaces, resulting in a rapid decline in soil oxygen availability and diffusion. Oxygen diffusion through water is several orders of magnitude slower than through air, causing a rapid depletion of oxygen in the rhizosphere and the development of hypoxic or anoxic conditions ^[1, 2]. Grain legumes, including economically and nutritionally important crops such as soybean (*Glycine max* L.) and cowpea (*Vigna unguiculata* (L.) Walp.), are particularly vulnerable to excess soil moisture. The adverse effects are especially pronounced during early vegetative growth, when oxygen deprivation restricts root respiration, nutrient acquisition, root development and biological nitrogen fixation ^[3-5].

Under prolonged waterlogging, oxygen deficiency disrupts mitochondrial respiration and severely restricts energy production in the primary root system, leading to impaired root growth, cellular injury and, under severe conditions, root deterioration and decay ^[6, 7]. In response to these adverse hydrological conditions, plants employ a range of structural, physiological and metabolic adaptations that enable continued functioning under oxygen-deficient conditions ^[8, 9]. Among these responses, modifications of the root system are particularly important because they can partially restore water and nutrient acquisition and improve internal oxygen transport.

One of the most prominent morphological adaptations is the formation and elongation of adventitious roots from submerged or basal stem tissues. These roots can replace or supplement the function of the damaged primary root system and may possess anatomical characteristics that facilitate oxygen transport under waterlogged conditions [8, 10, 11]. In parallel, anatomical modifications such as aerenchyma formation increase the internal porosity of roots and stems, thereby facilitating relatively low-resistance diffusion of oxygen from aerial tissues towards submerged root tissues [12–14].

Aerenchyma may develop through different developmental pathways. Wetland and aquatic plants commonly possess constitutive or inducible primary aerenchyma formed through lysigenous or schizogenous processes. In contrast, several dryland grain legumes exhibit inducible secondary aerenchyma associated with secondary growth in tissues such as the hypocotyl, taproot and adventitious roots [14–16]. These modifications can substantially improve internal aeration and enhance root survival under prolonged soil saturation.

Understanding the morphological and anatomical traits associated with waterlogging tolerance is important for identifying reliable phenotypic indicators for screening and breeding waterlogging-tolerant legume genotypes [17–19]. The expression of these structural traits is regulated by complex interactions among ethylene, abscisic acid, auxin and other hormonal and signalling pathways [20, 21]. Therefore, root adaptation to waterlogging represents an integrated response involving changes in root architecture, tissue anatomy, internal aeration and hormonal regulation.

This review synthesizes current knowledge on the morphological and anatomical adaptations of grain and forage legumes to waterlogging, with particular emphasis on oxygen deficiency, adventitious root formation, aerenchyma development and associated structural modifications. The review further discusses the significance of these traits as potential screening criteria for improving waterlogging tolerance and yield stability in legume production systems.

Oxygen Deficiency Under Waterlogging

Waterlogging occurs when excess rainfall, irrigation, flooding, poor drainage or low-permeability soil conditions result in prolonged soil saturation. As soil pores become filled with water, the continuity of air-filled pores is disrupted, substantially restricting the movement of oxygen from the atmosphere into the rhizosphere [3, 22]. In well-aerated soils, oxygen moves predominantly through interconnected gas-filled pores. However, when these pores become water-filled, oxygen diffusion is severely restricted because its diffusion through water is several orders of magnitude slower than through air [1, 23, 24].

The reduction in oxygen availability is further accelerated by the respiration of plant roots and soil microorganisms. Following soil saturation, microbial and root respiration rapidly consume the oxygen remaining within the soil pore system, resulting in a progressive decline in rhizospheric oxygen concentration [25, 26]. Depending on the intensity and duration of waterlogging, the root environment may consequently shift from normoxia to hypoxia and, under severe conditions, to near-anoxia or anoxia [2, 25, 26].

Oxygen deficiency has profound consequences for root metabolism. Under normoxic conditions, mitochondrial oxidative phosphorylation provides the principal source of ATP required for active ion transport, nutrient acquisition, root growth and maintenance of cellular homeostasis. Under hypoxic

or anoxic conditions, oxidative phosphorylation becomes severely constrained, resulting in a substantial decline in ATP production. Plants compensate, to some extent, by increasing glycolytic metabolism and fermentation; however, anaerobic ATP production is considerably less efficient than aerobic respiration [6, 7].

The resulting energy limitation affects several essential root functions. Active nutrient uptake is impaired, membrane integrity may decline, and root growth and development are restricted. In legumes, oxygen deficiency can additionally interfere with nodulation and biological nitrogen fixation because nitrogen-fixing nodules have high respiratory requirements and are particularly sensitive to oxygen limitation [3, 4]. Prolonged oxygen deprivation may therefore result in extensive root injury and loss of functional root biomass.

For dryland grain and forage legumes, which generally possess less constitutive internal aeration capacity than wetland-adapted species, waterlogging represents a particularly severe environmental challenge. These species must therefore induce structural and physiological adaptations to maintain oxygen supply to submerged tissues. The formation of adventitious roots, development of aerenchyma, modification of stem and root tissues, and changes in root architecture collectively contribute to improved internal aeration and maintenance of root function under waterlogged conditions [8, 12–16].

The severity of oxygen deficiency is influenced not only by the presence of excess water but also by soil texture, temperature, organic matter content, microbial activity, water depth and duration of saturation. Consequently, the physiological response of legumes to waterlogging varies considerably among species and genotypes. Genotypes capable of rapidly developing functional adventitious roots and efficient internal aeration systems generally exhibit greater survival and recovery following waterlogging [17–19].

These observations highlight oxygen deficiency as the primary environmental signal initiating a cascade of morphological, anatomical, physiological and molecular responses. Among these responses, adventitious root formation and aerenchyma development are particularly important because they directly modify the capacity of the plant to acquire resources and transport oxygen under saturated soil conditions.

Morphological Adaptations

Waterlogging induces substantial changes in root system architecture as plants attempt to maintain water and nutrient acquisition under oxygen-deficient conditions. In legumes, these responses include the formation of adventitious roots, modification of lateral root development, changes in root hair characteristics and redistribution of biomass between roots and shoots. The extent and effectiveness of these responses vary considerably among species and genotypes and are important determinants of waterlogging tolerance.

Adventitious Root Formation

Adventitious root (AR) formation is one of the most important morphological adaptations associated with waterlogging tolerance in many crop species. When the primary root system is exposed to prolonged oxygen deficiency, root respiration, growth and nutrient uptake are progressively impaired. Under these conditions, new roots may emerge from basal stem nodes, hypocotyls or lower stem tissues, thereby providing an alternative functional root system [7, 10, 11, 19].

The relatively shallow position of adventitious roots enables them to develop close to the soil surface, where oxygen

availability is generally greater than in deeper waterlogged soil layers. Consequently, these roots can contribute to continued water and nutrient acquisition while reducing dependence on severely hypoxic portions of the original root system^[6, 33]. Their effectiveness is further enhanced when they develop a high degree of root porosity and aerenchymatous tissues, which facilitate internal oxygen movement from the shoot towards submerged root tissues^[8, 29, 36].

The initiation and development of adventitious roots are regulated by complex hormonal interactions. Ethylene accumulation is an important response to tissue submergence because restricted gas diffusion promotes its accumulation in submerged tissues. Ethylene interacts with auxin and other hormonal pathways to regulate cell division, root primordium initiation and subsequent root emergence^[20, 21, 27, 28]. Cytokinins and other hormonal signals may additionally influence the balance between root initiation and shoot growth during stress.

Considerable genotypic variation exists in adventitious root formation among legumes. In soybean (*Glycine max* L.), waterlogging-tolerant genotypes have been reported to produce adventitious roots from the hypocotyl and lower stem regions more rapidly and extensively than susceptible genotypes^[19, 20, 37]. Such differences are associated with improved root aeration and maintenance of root function under flooded conditions. In addition to increasing root number, tolerant genotypes may modify root system distribution by favouring shallower root development and greater proliferation within relatively oxygenated surface soil layers^[33].

Recent evidence from cowpea also indicates that adventitious root formation can contribute substantially to waterlogging tolerance. Genotypes capable of producing adventitious roots rapidly under waterlogged conditions can maintain greater root functionality and exhibit improved recovery following stress^[19]. Therefore, adventitious root number, emergence rate, length and associated root porosity have considerable potential as phenotypic traits for screening legume genotypes for waterlogging tolerance.

Root System Architecture

Waterlogging can alter the spatial distribution and growth pattern of roots, resulting in a shift from deep root exploration towards shallower proliferation in relatively oxygenated soil layers. This modification represents an important form of root architectural plasticity because deeper soil layers generally experience more severe oxygen depletion during prolonged saturation^[33].

Root angle, rooting depth, root length and the distribution of lateral roots can therefore influence the ability of a genotype to maintain functional root tissue under waterlogged conditions. Tolerant genotypes may exhibit greater plasticity in root orientation and distribution, allowing roots to exploit the upper soil profile while reducing investment in severely oxygen-deficient zones^[19, 33]. However, the adaptive value of a particular root architecture is strongly dependent on soil depth, water-table position, duration of waterlogging and the capacity of the genotype to develop internal aeration pathways.

Thus, waterlogging tolerance should not be associated with a single optimal root architecture. Rather, the ability to dynamically modify root distribution in response to changing oxygen availability may be more important than constitutive root traits.

Lateral Root Development

Lateral roots constitute a major proportion of total root length

and surface area in many dicotyledonous crops and consequently contribute substantially to water and nutrient acquisition^[32, 33]. Their development is strongly influenced by oxygen availability and changes markedly during and after waterlogging.

During the initial stages of waterlogging, oxygen deficiency and the associated decline in cellular energy status can inhibit lateral root initiation and elongation^[7, 31]. Restricted root respiration, altered carbohydrate availability and changes in hormonal signalling may collectively suppress the development of lateral roots in severely oxygen-deficient tissues. This reduction in lateral root activity limits the capacity of the primary root system to explore the surrounding soil.

As adventitious roots and other functional root tissues develop in relatively oxygenated regions, lateral root production may resume and contribute to restoration of the absorbing root surface^[6, 33]. The ability to rapidly establish new lateral roots following waterlogging or after drainage may therefore be an important component of root-system recovery. Genotypes that maintain greater root metabolic activity and carbohydrate availability during stress may possess a greater capacity for post-waterlogging root regeneration^[30].

Consequently, both the degree of lateral-root inhibition during waterlogging and the rate of lateral-root recovery after stress termination may provide useful indicators of genotype-specific resilience. Further research is required to establish whether these traits can be reliably incorporated into routine screening programmes for legume waterlogging tolerance.

Root Hair Responses

Root hairs substantially increase the effective absorptive surface of roots and facilitate the acquisition of water and mineral nutrients. Their development is therefore potentially important for maintaining nutrient acquisition when waterlogging alters soil nutrient availability and root activity.

However, the response of root hairs to waterlogging is highly dependent on species, genotype, stress duration and the developmental stage at which stress occurs. Severe oxygen deficiency can restrict root growth and cellular differentiation, potentially reducing the development and functional activity of root hairs. Conversely, newly formed roots in relatively oxygenated surface layers may develop root hairs that contribute to the restoration of absorptive capacity.

Compared with adventitious root formation, aerenchyma development and root porosity, root hair responses remain comparatively less characterized as screening traits for waterlogging tolerance in grain legumes. Therefore, further comparative studies are required to determine whether root hair density, length and persistence provide consistent indicators of adaptive capacity under waterlogged conditions.

Root Biomass Allocation

Waterlogging modifies whole-plant carbon allocation and consequently influences the balance between root and shoot biomass. Under prolonged waterlogging, reductions in photosynthesis, carbohydrate production and phloem transport can restrict carbon availability for root growth and maintenance^[34, 35]. As a result, total root biomass may decline, particularly when the primary root system undergoes severe injury.

Waterlogging-tolerant genotypes may nevertheless exhibit a degree of plasticity in carbon allocation that favours the maintenance or formation of functional root tissues in relatively oxygenated zones. In soybean and other legumes, this may involve greater investment in adventitious roots, stem-derived roots and associated anatomical modifications rather than

continued development of deep primary roots under severely hypoxic conditions [19, 33, 38].

The root-to-shoot ratio, however, should be interpreted cautiously as an indicator of waterlogging tolerance. A lower or higher ratio does not necessarily indicate superior tolerance because changes in the ratio may arise from differential effects of stress on root and shoot growth rather than from an adaptive allocation response. Consequently, biomass partitioning should preferably be evaluated together with root survival, adventitious root formation, root porosity, shoot recovery and yield-related traits.

Overall, morphological adaptation to waterlogging involves coordinated modification of root architecture and biomass allocation rather than a single structural response. Rapid adventitious root formation, appropriate redistribution of lateral roots, maintenance or recovery of absorptive root tissues and flexible carbon allocation can collectively improve plant performance under oxygen-deficient conditions. The magnitude and timing of these responses differ among legume species and genotypes, highlighting the importance of integrating multiple root traits when evaluating waterlogging tolerance.

Anatomical Adaptations

Morphological changes in the root system are accompanied by substantial anatomical modifications that improve internal aeration and maintain root functionality under waterlogged conditions. The major anatomical responses include aerenchyma formation, development of secondary aerenchyma, modification of radial oxygen loss (ROL), cortical senescence and reinforcement of apoplastic barriers through suberin and lignin deposition. The relative importance of these adaptations differs among plant species and depends on genotype, developmental stage, duration of waterlogging and the severity of oxygen deficiency [12–16].

Lysigenous Aerenchyma

Lysigenous aerenchyma is an important anatomical adaptation that enhances internal oxygen transport to roots exposed to oxygen-deficient conditions [12–14]. It is characterized by the formation of longitudinal, gas-filled spaces within the root cortex through selective death and lysis of cortical cells [13, 42]. The resulting interconnected air spaces increase root porosity and provide a relatively low-resistance pathway for oxygen movement from aerial tissues towards submerged root tissues.

Lysigenous aerenchyma formation is commonly associated with ethylene signalling under waterlogged conditions. Accumulation of ethylene in submerged tissues can interact with reactive oxygen species (ROS), calcium-dependent signalling and other regulatory pathways to promote selective cell death in specific cortical cell files [39, 40]. Cell-wall-modifying enzymes, including cellulases, pectin-degrading enzymes and other hydrolytic enzymes, contribute to the breakdown of cellular components and expansion of intercellular air spaces during aerenchyma development [37, 41].

The development of aerenchyma has two major functional consequences. First, the resulting gas-filled channels facilitate internal diffusion of oxygen from aerial tissues towards oxygen-deprived root regions [12, 43]. Second, selective loss of metabolically active cortical cells can reduce the respiratory demand of the root, thereby conserving limited carbohydrate and energy resources under oxygen-deficient conditions [13, 33]. However, the extent to which this respiratory saving contributes to overall waterlogging tolerance depends on the timing and degree of cortical cell death and the maintenance of functional

vascular and absorptive tissues.

Schizogenous Aerenchyma

Schizogenous aerenchyma differs from lysigenous aerenchyma in its developmental origin. Instead of being generated primarily through programmed cell death and subsequent cortical cell lysis, schizogenous air spaces arise through separation of adjacent living cells during tissue development [12, 42]. Modification of cell adhesion and localized changes in the middle lamella permit neighbouring cells to separate and generate intercellular air spaces while maintaining the integrity of the surrounding cells.

Schizogenous aerenchyma can occur as part of normal root development and may also contribute to enhanced internal aeration under waterlogged conditions [12, 42]. Because the surrounding cells remain viable, this type of aerenchyma differs structurally and developmentally from the larger lacunae generated through lysigenous processes. The distinction is particularly important when comparing wetland-adapted species with dryland crops because the developmental pathway and inducibility of aerenchyma vary considerably among plant groups.

In legumes, the contribution of primary schizogenous aerenchyma to waterlogging tolerance appears to be less prominent than the formation of secondary aerenchyma in several species. Therefore, comparisons between species should consider both the developmental origin of the air spaces and their functional contribution to internal oxygen transport.

Secondary Aerenchyma

Secondary aerenchyma is particularly important in several dicotyledonous crops and grain legumes that lack the extensive constitutive primary aerenchyma characteristic of many wetland-adapted species [14, 15, 42]. Unlike primary aerenchyma, which develops within primary tissues, secondary aerenchyma is associated with secondary growth and can arise from secondary meristematic tissues such as the phellogen and, depending on the organ and species, other tissues associated with secondary growth [42].

In waterlogged legumes, secondary aerenchyma may develop in hypocotyls, stems, taproots and adventitious roots. The formation of these porous tissues can substantially increase the capacity for internal gas movement between aerial organs and submerged roots [15, 37]. This adaptation is particularly important in species in which the original primary root system has limited capacity for internal aeration.

Soybean provides one of the best-characterized examples of secondary aerenchyma formation among grain legumes. Under flooding, soybean can develop secondary aerenchyma in the hypocotyl and root tissues, together with hypertrophic lenticels on submerged stem and root surfaces [15, 37, 48]. These structures collectively enhance gas exchange between the atmosphere and the internal root aeration system. Genotypic differences in the capacity and rate of secondary aerenchyma formation are associated with differences in waterlogging response [15, 17, 37].

The formation of secondary aerenchyma is closely associated with hormonal regulation, particularly ethylene and auxin signalling, while interactions with abscisic acid and other hormonal pathways may influence the developmental response [20, 37, 48]. Nevertheless, the regulatory mechanisms differ among species and should not be generalized from soybean to all grain legumes.

The development of secondary aerenchyma therefore represents an important structural strategy by which dryland legumes can

improve internal aeration under prolonged waterlogging. However, its effectiveness depends on the continuity of the internal air spaces, the efficiency of oxygen transport and the presence of complementary structures such as hypertrophic lenticels and ROL barriers.

Hypertrophic Lenticels and Surface Aeration

Hypertrophic lenticels are another important anatomical response observed in several waterlogging-tolerant species, particularly soybean. Under prolonged soil saturation, lenticels on submerged stems and hypocotyls may enlarge substantially, increasing the surface area available for gas exchange [15].

The enlargement of these structures can facilitate atmospheric oxygen entry into internal aerenchymatous tissues. When connected with secondary aerenchyma, hypertrophic lenticels can therefore form an important component of the internal aeration pathway between aerial tissues and submerged roots [15, 48].

The formation and enlargement of hypertrophic lenticels vary among species and genotypes. Their occurrence should consequently be interpreted together with secondary aerenchyma development and root porosity rather than as an independent indicator of waterlogging tolerance.

Radial Oxygen Loss Barrier

Once oxygen enters the plant and is transported through aerenchymatous tissues towards the root apex, a proportion may diffuse radially from the root into the surrounding soil. This process is referred to as radial oxygen loss (ROL) [43]. Although ROL can oxygenate the immediate rhizosphere and influence microbial processes around the root, excessive oxygen loss from the basal and mature portions of the root can reduce the amount of oxygen available for transport towards distal root regions.

Several wetland-adapted plants therefore develop barriers to radial oxygen loss in the outer root tissues. These barriers reduce radial diffusion of oxygen and promote longitudinal movement through the internal aerenchyma towards the root apex [43, 44]. The effectiveness of the ROL barrier depends largely on the anatomical and chemical properties of the outer root layers.

Suberin and lignin deposition in the exodermis or hypodermis is an important component of ROL barrier formation [45, 46]. The development of these hydrophobic barriers decreases radial permeability and helps maintain oxygen within the internal root aeration system. The barrier can consequently improve oxygen delivery to distal root tissues under waterlogged conditions [43–46].

The strength and spatial distribution of ROL barriers vary substantially among species and root developmental zones. Therefore, a strong ROL barrier should not be considered universally beneficial; rather, its effectiveness depends on the balance between longitudinal oxygen transport, radial oxygen loss and the requirement for localized rhizosphere oxygenation.

Root Cortical Senescence

Root cortical senescence represents another structural response that can influence root function under prolonged stress. During severe waterlogging, cortical tissues may undergo senescence and degeneration, contributing to increased root porosity and modification of the internal root structure [13, 33].

Loss of metabolically active cortical tissue can potentially reduce respiratory demand and thereby conserve limited energy resources under oxygen deficiency. When cortical cell death is spatially controlled, the resulting air spaces may additionally contribute to internal gas diffusion [12, 13]. However, excessive or

premature cortical degradation can compromise root structural integrity and reduce the capacity for water and nutrient uptake.

Thus, cortical senescence represents a trade-off between metabolic economy and root functionality. Its contribution to waterlogging tolerance depends on the extent and timing of tissue degradation and on the plant's ability to maintain functional vascular tissues and develop replacement roots. This response should therefore be distinguished from regulated aerenchyma formation, although both processes can involve cortical cell death and increased root porosity.

Suberin and Lignin Deposition

Modification of apoplastic barriers through suberin and lignin deposition represents an important component of root adaptation to oxygen-deficient conditions. These barriers are particularly associated with the exodermis or hypodermis and endodermis, where deposition of hydrophobic compounds can regulate radial movement of gases, water and solutes [45, 46].

Under waterlogging, changes in the deposition of suberin and lignin can alter the permeability of root tissues. Suberin lamellae and lignified cell-wall domains reduce apoplastic transport and can contribute to the development of barriers to radial oxygen loss [45, 46]. This promotes retention of oxygen within internal aerenchymatous channels and supports longitudinal oxygen transport towards distal root tissues.

The endodermis also represents an important selective barrier between the cortex and vascular tissues. Modification of Casparian strips and suberin lamellae can regulate radial movement of water and dissolved solutes towards the stele. However, the relationship between enhanced apoplastic barrier formation and waterlogging tolerance is complex because excessive barrier development may also restrict radial water and nutrient movement.

In addition to their role in oxygen conservation, apoplastic barriers can influence the movement of potentially toxic reduced compounds that accumulate in waterlogged soils. Therefore, changes in suberin and lignin deposition may provide a dual protective function by modifying both gas movement and solute transport [45–47].

Overall, anatomical adaptation to waterlogging involves the coordinated development of internal air spaces, modification of surface gas-exchange structures and regulation of radial transport. Aerenchyma and secondary aerenchyma facilitate longitudinal oxygen movement, hypertrophic lenticels enhance atmospheric gas exchange, while ROL barriers and apoplastic modifications regulate the distribution and retention of oxygen within the root system. The relative contribution of each mechanism varies among legume species and genotypes, emphasizing the importance of integrating multiple anatomical traits when assessing waterlogging tolerance.

References

1. Armstrong W. Aeration in higher plants. *Adv Bot Res.* 1980;7:225-332.
2. Bailey-Serres J, Voesenek LACJ. Flooding stress: acclimations and genetic diversity. *Annu Rev Plant Biol.* 2008;59:313-339.
3. Alam I, Lee DG, Kim KH, Park CH, Sharmin SA, Lee H, *et al.* Proteome analysis of soybean roots under waterlogging stress at an early vegetative stage. *J Biosci.* 2010;35:49-62.
4. Kokubun M. Genetic and cultural improvement of soybean for waterlogged conditions in Asia. *Field Crops Res.* 2013;152:3-7.
5. Senthamil E, Angadi SS, Halli HM, Salakinkop SR,

- Doddamani MB, Gundlur SS. Effect of transient waterlogging stress on growth, physiology and yield of cowpea (*Vigna unguiculata* L.) in semi-arid region. *Int J Plant Soil Sci.* 2024;36(8):45-56.
6. Sairam RK, Kumutha D, Ezhilmathi K, Deshmukh PS, Srivastava GC. Physiology and biochemistry of waterlogging tolerance in plants. *Biol Plant.* 2008;52:401-412.
 7. Colmer TD, Voesenek LACJ. Flooding tolerance: suites of plant traits in variable environments. *Funct Plant Biol.* 2009;36:665-681.
 8. Steffens B, Rasmussen A. The physiology of adventitious roots. *Plant Physiol.* 2016;170:603-617.
 9. Hattori Y, Nagai K, Furukawa S, Song XJ, Kawano R, Sakakibara H, *et al.* The ethylene response factors SNORKEL1 and SNORKEL2 allow rice to adapt to deep water. *Nature.* 2009;460:1026-1030.
 10. Xu X, Ji J, Ma X, Xu Q, Qi X, Chen X. Comparative proteomic analysis provides insight into the key proteins involved in cucumber (*Cucumis sativus* L.) adventitious root emergence under waterlogging stress. *Front Plant Sci.* 2016;7:1515.
 11. Eysholdt-Derzso E, Sauter M. Hypoxia and the group VII ethylene response transcription factor HRE2 promote adventitious root elongation in Arabidopsis. *Plant Biol.* 2019;21:103-108.
 12. Evans DE. Aerenchyma formation. *New Phytol.* 2004;161:35-49.
 13. Drew MC, He C-J, Morgan PW. Programmed cell death and aerenchyma formation in roots. *Trends Plant Sci.* 2000;5:123-127.
 14. Yamauchi T, Shimamura S, Nakazono M, Mochizuki T. Aerenchyma formation in crop species: a review. *Field Crops Res.* 2013;152:8-16.
 15. Shimamura S, Yamamoto R, Nakamura T, Shimada S, Komatsu S. Stem hypertrophic lenticels and secondary aerenchyma enable oxygen transport to roots of soybean in flooded soil. *Ann Bot.* 2010;106:277-284.
 16. Teakle NL, Armstrong J, Barrett-Lennard EG, Colmer TD. *Aerenchymatous phellem* in hypocotyl and roots enables O₂ transport in *Melilotus siculus*. *New Phytol.* 2011;190:340-350.
 17. Bacanamwo M, Purcell LC. Soybean root morphological and anatomical traits associated with acclimation to flooding. *Crop Sci.* 1999;39:143-149.
 18. Koo SC, Kim HT, Kang BK, Lee YH, Oh KW, Kim HY, *et al.* Screening of flooding tolerance in soybean germplasm collection. *Korean J Breed Sci.* 2014;46:129-135.
 19. Basavaraj PS, Jangid KK, Babar R, Gangana Gowdra VM, Gangurde A, Shinde S, *et al.* Adventitious root formation confers waterlogging tolerance in cowpea (*Vigna unguiculata* (L.) Walp.). *Front Sustain Food Syst.* 2024;8:1373183.
 20. Kim YH, Hwang SJ, Waqas M, Khan AL, Lee JH, Lee JD, *et al.* Comparative analysis of endogenous hormones level in two soybean (*Glycine max* L.) lines differing in waterlogging tolerance. *Front Plant Sci.* 2015;6:714.
 21. Vidoz ML, Loreti E, Mensuali A, Alpi A, Perata P. Hormonal interplay during adventitious root formation in flooded tomato plants. *Plant J.* 2010;63:551-562.
 22. Sasidharan R, Voesenek LACJ. Ethylene-mediated acclimations to flooding stress. *Plant Physiol.* 2015;169:3-12.
 23. Armstrong W, Drew MC. Root growth and metabolism under oxygen deficiency. In: Waisel Y, Eshel A, Beeckman T, Kafkafi U, editors. *Plant roots: the hidden half.* 3rd ed. Boca Raton: CRC Press; 2002. p. 729-761.
 24. Colmer TD, Flowers TJ. Flooding tolerance in halophytes. *New Phytol.* 2008;179:964-974.
 25. Kennedy RA, Rumpho ME, Fox TC. Anaerobic metabolism in plants. *Plant Physiol.* 1992;100:1-6.
 26. Dennis ES, Dolferus R, Ellis M, Rahman M, Wu Y, Hoeren FU, *et al.* Molecular strategies for improving waterlogging tolerance in plants. *J Exp Bot.* 2000;51:89-97.
 27. Visser E, Cohen JD, Barendse G, Blom C, Voesenek L. An ethylene-mediated increase in sensitivity to auxin induces adventitious root formation in flooded *Rumex palustris* Sm. *Plant Physiol.* 1996;112:1687-1692.
 28. Qi X, Li Q, Ma X, Qian C, Wang H, Ren N, *et al.* Waterlogging-induced adventitious root formation in cucumber is regulated by ethylene and auxin through reactive oxygen species signalling. *Plant Cell Environ.* 2019;42:1458-1470.
 29. Visser EJW, Voesenek LACJ. Acclimation to soil flooding: sensing and signal transduction. *Plant Soil.* 2005;274:197-214.
 30. Thomas AL, Guerreiro SMC, Sodek L. Aerenchyma formation and recovery from hypoxia of the flooded root system of nodulated soybean. *Ann Bot.* 2005;96:1191-1198.
 31. Ren B, Zhang J, Dong S, Liu P, Zhao B. Root and shoot responses of summer maize to waterlogging at different stages. *Agron J.* 2016;108:1060-1069.
 32. Visser EJW, Nabben RHM, Blom CWPM, Voesenek LACJ. Elongation by primary lateral roots and adventitious roots during conditions of hypoxia and high ethylene concentrations. *Plant Cell Environ.* 1997;20:647-653.
 33. Liu M, Hulting A, Mallory-Smith C. Comparison of growth and physiological characteristics between roughstalk bluegrass and tall fescue in response to simulated waterlogging. *PLoS One.* 2017;12(7):e0182035.
 34. Olorunwa OJ, Adhikari B, Shi A, Barickman TC. Screening of cowpea (*Vigna unguiculata* (L.) Walp.) genotypes for waterlogging tolerance using morpho-physiological traits at early growth stage. *Plant Sci.* 2022;315:111136.
 35. Olorunwa OJ, Adhikari B, Brazel S, Shi A, Popescu SC, Popescu GV, *et al.* Growth and photosynthetic responses of cowpea genotypes under waterlogging at the reproductive stage. *Plants.* 2022;11:2315.
 36. Zhang X, Shabala S, Koutoulis A, Shabala L, Johnson P, Hayes D, *et al.* Waterlogging tolerance in barley is associated with faster aerenchyma formation in adventitious roots. *Plant Soil.* 2015;394:355-372.
 37. Shimamura S, Yoshioka T, Yamamoto R, Hiraga S, Nakamura T, Shimada S, *et al.* Role of abscisic acid in flood-induced secondary aerenchyma formation in soybean (*Glycine max*) hypocotyls. *Plant Prod Sci.* 2014;17:131-137.
 38. Islam MR, Hasan M, Akter N, Akhtar S. Cytokinin and gibberellic acid alleviate the effect of waterlogging in mungbean (*Vigna radiata* L. Wilczek). *J CleanWAS.* 2021;5(1):21-26.
 39. Yamauchi T, Yoshioka M, Fukazawa A, Mori H, Nishizawa NK, Tsutsumi N, *et al.* An NADPH oxidase RBOH functions in rice roots during lysigenous aerenchyma formation under oxygen-deficient conditions. *Plant Cell.* 2017;29:775-790.
 40. Steffens B, Geske T, Sauter M. Aerenchyma formation in the rice stem and its promotion by H₂O₂. *New Phytol.* 2011;190:369-378.

41. Bragina TV, Rodionova NA, Grinieva GM. Ethylene production and activation of hydrolytic enzymes during acclimation of maize seedlings to partial flooding. *Russ J Plant Physiol.* 2003;50:794-798.
42. Jackson MB, Armstrong W. Formation of aerenchyma and the processes of plant ventilation in relation to soil flooding and submergence. *Plant Biol.* 1999;1:274-287.
43. Yamauchi T, Colmer TD, Pedersen O, Nakazono M. Regulation of root traits for internal aeration and tolerance to soil waterlogging-flooding stress. *Plant Physiol.* 2018;176:1118-1130.
44. McDonald MP, Galwey NW, Colmer TD. Waterlogging tolerance in the tribe Triticeae: the adventitious roots of *Critasion maritimum* have a relatively high porosity and a barrier to radial oxygen loss. *Plant Cell Environ.* 2001;24:585-596.
45. Jiménez J de la C, Cardoso JA, Kotula L, Veneklaas EJ, Pedersen O, Colmer TD. Root length is proxy for high-throughput screening of waterlogging tolerance in *Urochloa* spp. grasses. *Funct Plant Biol.* 2020.
46. Guhr T, Song Z, Krogh Andersen AM, Jiménez J de la C, Pedersen O. Root morphology and anatomy respond similarly to drought and flooding in two wheat cultivars. *Ann Bot.* 2025.
47. Armstrong J, Armstrong W. *Phragmites australis*: a preliminary study of soil-oxidizing sites and internal gas transport pathways. *New Phytol.* 1988;108:373-382.
48. Shimamura S, Nishimura T, Koshiba T, Yamamoto R, Hiraga S, Nakamura T, *et al.* Effects of anti-auxins on secondary aerenchyma formation in flooded soybean hypocotyls. *Plant Prod Sci.* 2016;19:154-160.
49. Zeng R, Chen L, Wang X, Cao J, Li X, Xu X, *et al.* Effect of waterlogging stress on dry matter accumulation, photosynthesis characteristics, yield, and yield components in three different ecotypes of peanut (*Arachis hypogaea* L.). *Agronomy.* 2020;10:1244.