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# WATERLOGGING TOLERANCE IN FORAGE CROPS: PHYSIOLOGICAL MECHANISMS AND BREEDING STRATEGIES – A REVIEW

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## SUMMARY

Waterlogging, characterized by prolonged soil saturation and oxygen ($O_2$) depletion in the root zone, severely constrains the growth, persistence, and productivity of forage legumes and grasses. Inhibition of aerobic respiration limits energy availability, root growth, and nutrient uptake, ultimately depressing shoot photosynthesis and biomass accumulation. Forage species exhibit diverse adaptive mechanisms-morphological, anatomical, physiological, and biochemical-that confer differential tolerance to waterlogging stress. Key tolerance traits include root aerenchyma formation, adventitious root development, barriers to radial oxygen loss, and the maintenance of nodulation and biological nitrogen ($N_2$) fixation under hypoxic conditions. While cereals such as rice possess well-characterized genetic pathways for flooding tolerance, mechanistic and genomic understanding in forage crops remains limited. This review synthesizes current knowledge on physiological responses and tolerance mechanisms in forage species and highlights research gaps and breeding priorities aimed at developing resilient forage systems under increasing waterlogging risk associated with climate change.

**Key words:** Adventitious roots. aerenchyma; forage grasses; forage legumes;waterlogging tolerance

Waterlogging-defined as prolonged saturation of the soil root zone-creates hypoxic or anoxic conditions that restrict oxygen diffusion to plant roots. The diffusion coefficient of oxygen in water is approximately 10,000 times lower than in air, rapidly limiting the supply required for aerobic respiration (Drew, 1997, Jackson and Armstrong, 1999). This oxygen deficiency induces an energy crisis that disrupts root metabolism, nutrient acquisition, and hormonal balance. In forage systems comprising perennial and annual grasses and legumes, waterlogging stress results in reduced dry-matter yield, impaired symbiotic nitrogen fixation, and poor stand persistence (Striker and Colmer, 2017).

Globally, more than 1.7 billion hectares of agricultural land are affected by flooding each year, a substantial proportion of which supports pasture and forage production. Climate change–driven increases in rainfall intensity, rising water tables, and inadequate drainage are expected to exacerbate the frequency and severity of waterlogging events (IPCC, 2022). Unlike annual cereal crops, forage species must maintain productivity across multiple seasons, often within mixed grass-legume swards. Consequently, both tolerance during flooding and rapid recovery after drainage are essential agronomic traits. In forage legumes, waterlogging is particularly detrimental because root nodules have high respiratory demand but are highly sensitive to oxygen deficiency. Grasses also suffer reductions in root growth and photosynthesis, although many species exhibit adaptive traits that enhance survival under saturated soil conditions. Understanding these physiological and morphological mechanisms is critical for breeding and management strategies suited to increasingly erratic rainfall regimes (Pan *et al.*, 2021).

## CLIMATE-RESILIENT FORAGE CROPS

Several forage crops have been identified as climate-resilient due to their capacity to tolerate abiotic stresses, including waterlogging. Among grasses, Guinea grass (*Megathyrsus maximus*), Bajra–Napier hybrids, tri-specific hybrids, and Dinanath grass (*Pennisetum pedicellatum*) have demonstrated adaptability under adverse moisture conditions (Singh *et al*., 2020, Dheeravathu *et al*., 2021a, 2021b, 2022a, 2022b; Antony *et al*., 2021). Among forage legumes, species such as cowpea (*Vigna unguiculata*), berseem (*Trifolium alexandrinum*), *Clitoria ternatea*, *Centrosema* spp., and *Siratro* (*Macroptilium atropurpureum*) have shown tolerance to multiple stresses, including excess soil moisture (Dheeravathu *et al.,* 2017a, 2017b, 2021a, 2021c, 2022c, 2023). Forage cereals and millets, including pearl millet, kodo millet, and sorghum, have also been reported to possess adaptive traits that confer resilience under variable climatic conditions (Singh *et al*., 2010; Malathi *et al*., 2022; Amrutha *et al*., 2023; Sravanthi *et al*., 2024, 2025).

## PHYSIOLOGICAL AND GROWTH EFFECTS OF WATERLOGGING STRESS

### Root-zone hypoxia and respiration

Oxygen deprivation under waterlogged conditions forces plants to shift from efficient aerobic respiration to less efficient anaerobic pathways, leading to reduced ATP production and metabolic imbalance. In *Medicago sativa*, continued glycolysis coupled with restricted respiration results in carbohydrate accumulation but insufficient energy for sustained root growth (Drew, 1997, Pang *et al.,* 2004). Root elongation and lateral root development are severely inhibited, altering root architecture and reducing nutrient uptake capacity. Comparable responses are observed in forage grasses; for example, in *Dactylis glomerata*, 15 days of waterlogging nearly halted root relative growth rate, and recovery after re-aeration was incomplete (Di Bella *et al.,* 2022). Thus, energy limitation in roots represents the primary physiological constraint under waterlogging, cascading into nutrient deficiency, hormonal imbalance, and suppressed shoot growth (Colmer and Voesenek, 2009).

### Shoot responses: photosynthesis and nutrient status

Root dysfunction rapidly influences aboveground processes. Photosynthetic rate (Pn) in waterlogging-sensitive legumes may decline to 15–20% of control levels within two weeks, as observed in *M. sativa* (Loreti *et al.*, 2016). Impaired nutrient uptake leads to deficiencies of nitrogen, phosphorus, and potassium, accelerating chlorophyll degradation and leaf senescence (Pan *et al.,* 2021). In contrast, tolerant species such as *Lotus tenuis* and *L. corniculatus* maintain photosynthetic activity for longer periods, preserve leaf chlorophyll, and sustain nutrient concentrations closer to control levels (Striker and Colmer, 2017). Maintenance of photosynthesis is therefore strongly correlated with overall tolerance and post-stress recovery capacity.

### Biomass production and persistence

Significant interspecific variation exists in biomass response to waterlogging. Sensitive legumes such as *M. sativa* and *Trifolium pratense* may lose more than 50% of biomass under prolonged flooding, whereas tolerant species including *L. tenuis*, *L. corniculatus*, and *T. fragiferum* retain 75% or more of control dry matter (Reinoso *et al.,* 2004; Striker *et al.,* 2005). Among perennial grasses, biomass retention after 18-21 days of flooding ranges from approximately 45% in susceptible *Urochloa brizantha* to nearly 100% in tolerant *U. humidicola* (Di Bella *et al.,* 2022). Recovery following de-flooding also varies widely among species, emphasizing that waterlogging tolerance encompasses both survival during stress and effective regrowth thereafter.

### Secondary and compound stresses

In addition to oxygen deficiency, waterlogged soils often accumulate reduced ions such as $Fe^{2+}$, $Mn^{2+}$, and hydrogen sulfide ($H_2S$), and may undergo pH changes that exacerbate phytotoxicity (Pang et al., 2004). Anaerobic conditions also favor the proliferation of soil-borne pathogens. Consequently, plant responses to waterlogging reflect the combined effects of hypoxia and associated chemical and biological stresses (Setter and Waters, 2003).

## TOLERANCE MECHANISMS IN FORAGE CROPS

Waterlogging tolerance arises from integrated responses at morphological, anatomical, physiological, and biochemical levels (Colmer and Voesenek, 2009; Pan *et al.,* 2021).

### Root aerenchyma formation and internal oxygen diffusion

Aerenchyma-gas-filled intercellular spaces in the root cortex-facilitates internal oxygen transport from shoots to root tips and nodules. Root porosity varies widely among forage legumes, ranging from approximately 2% in *M. sativa* to 14% in *L. tenuis* and 18% in *Melilotus siculus* (Striker and Colmer, 2017). A strong positive correlation exists between root porosity and relative dry-matter production under waterlogging (Reinoso et al., 2004). Ethylene-induced aerenchyma formation enhances internal aeration and sustains aerobic respiration in submerged roots (Jackson and Armstrong, 1999).

### Nodule adaptations and maintenance of N, fixation

Symbiotic nitrogen fixation is highly sensitive to oxygen availability. Tolerant legumes employ structural and functional modifications to sustain N, fixation under hypoxia. For example, *M. siculus* develops a phellem-type secondary aerenchyma that regulates oxygen diffusion to the bacteroid zone, protecting nitrogenase activity (Striker and Colmer, 2017). In some species, nodules form on adventitious or stem roots closer to the soil surface, where oxygen availability is higher (Reinoso *et al.,* 2004). These adaptations are critical for maintaining nitrogen supply and shoot growth during flooding.

### Adventitious roots and barriers to radial oxygen loss

Flooding often induces the formation of adventitious roots from basal nodes or crowns. These roots exploit better-aerated surface soil layers, restoring water and nutrient uptake. In *Lotus* species, abundant surface roots develop within 7-10 days of inundation, markedly enhancing survival (Striker *et al.,* 2005). Certain tolerant grasses also develop barriers to radial oxygen loss, conserving internally transported oxygen for root tips rather than allowing diffusion into anoxic soil. This trait is strongly associated with post-flood recovery capacity (Colmer and Voesenek, 2009, Di Bella et al., 2022).

### Shoot physiology and carbohydrate management

Waterlogging tolerance extends beyond the root system to include critical shoot-level adjustments. Maintenance of photosynthetic activity during stress and efficient mobilization of carbohydrates during recovery are decisive determinants of tolerance (Pan *et al.,* 2021). In tolerant forage legumes, soluble sugar accumulation remains moderate, reflecting balanced source–sink relationships, whereas sensitive species often accumulate excess soluble sugars due to severe growth inhibition and impaired sink activity (Pang *et al.,* 2004). Following de-flooding, tolerant species rapidly remobilize stored carbohydrates to support regeneration of roots and shoots. Greater resilience of the photosynthetic apparatus and sustained chlorophyll retention in tolerant forages such as *Lotus tenuis* and *L. corniculatus* delay leaf senescence and significantly enhance post-flood recovery (Striker and Colmer, 2017).

### Biochemical and hormonal responses

Under hypoxic conditions, plants activate anaerobic fermentation pathways, including lactate and ethanol production, along with complex hormonal signaling involving ethylene, abscisic acid (ABA), and gibberellins (GA) (Bailey-Serres *et al.,* 2012, Loreti *et al.,* 2016). Ethylene plays a central role in inducing aerenchyma formation and adventitious root development, while ABA contributes to stomatal regulation and maintenance of plant water status. Tolerant species effectively maintain cellular redox homeostasis through enhanced antioxidant defense systems that scavenge reactive oxygen species (ROS) generated during re-aeration (Narsai *et al.,* 2011; Pan *et al.,* 2021). These coordinated metabolic and hormonal adjustments enable plants to transition efficiently from anaerobic survival during flooding to aerobic growth during recovery.

### Interspecific variation and trait correlations

Comparative studies demonstrate clear interspecific differences in waterlogging tolerance. Among forage legumes, *L. corniculatus*, *L. tenuis*, and *Trifolium fragiferum* retain approximately 75–80% of biomass under flooding, whereas *Medicago sativa* and *T. pratense* often retain less than 40% (Reinoso *et al.,* 2004; Striker *et al.,* 2005). Among grasses, *Urochloa humidicola*, *Paspalum dilatatum*, *Festuca arundinacea*, and *Lolium perenne* exhibit near-normal growth under moderate waterlogging, while *U. brizantha* and Brachiaria hybrids are comparatively susceptible (Di Bella *et al.,* 2022).

Tolerance-related traits exhibit consistent functional associations, including:

High root porosity and well-developed aerenchyma → enhanced internal oxygen diffusion → sustained root respiration, Adventitious root formation and barriers to radial oxygen loss (ROL) → maintenance of root function in aerated soil layers, Functional nodulation under hypoxia → continued biological N, fixation and shoot growth, Maintenance of photosynthesis → higher shoot biomass and improved recovery, Rapid regrowth following de-flooding → long-term persistence of perennial forage stands (Striker and Colmer, 2017, Pan *et al.,* 2021).

## Breeding strategies for waterlogging tolerance

### Genetic variation and heritability

Waterlogging tolerance exhibits substantial genetic variation both within and among forage species. Heritability estimates for key traits such as root porosity, adventitious root formation, and post-flood recovery range from moderate to high (Striker and Colmer, 2017). Selection within tolerant germplasm-particularly *Lotus tenuis*, *L. corniculatus*, and *Trifolium fragiferum* among legumes, and *Urochloa humidicola*, *Festuca arundinacea*, and *Paspalum dilatatum* among grasses-has resulted in genotypes with improved persistence in poorly drained soils (Di Bella et al., 2022). Natural selection under recurrent flooding has also driven ecotypic differentiation; for example, *L. tenuis* populations from low-lying, periodically flooded pampas exhibit greater aerenchyma development and nodulation efficiency than upland ecotypes (Reinoso *et al.,* 2004). Such diversity provides a valuable resource for breeding and molecular dissection of tolerance mechanisms.

### Trait-based phenotyping

Phenotyping for waterlogging tolerance requires an integrated assessment of morphological, physiological, and biochemical traits. Key selection criteria include: Root porosity and aerenchyma formation: quantified using image analysis or gas displacement techniques (Striker, 2012). Adventitious rooting and root distribution: assessed through visual scoring or root scanning methods (Colmer and Voesenek, 2009), Photosynthetic rate (P™ ), SPAD chlorophyll index, and leaf senescence: indicators of shoot-level tolerance (Pang et al., 2004).Post-flood regrowth and biomass recovery: critical for forage persistence and yield stability (Di Bella *et al.,* 2022). Recent advances in non-destructive phenotyping, including chlorophyll fluorescence (Fv/Fm) and hyperspectral indices, allow early detection of flooding stress and enhance screening efficiency under controlled conditions (Pan *et al.,* 2021).

### Molecular and genomic insights

Compared with cereals such as rice and maize, genomic resources for forage crops remain limited but are rapidly expanding. Transcriptomic analyses in *Lotus japonicus*, *Medicago truncatula*, and *Trifolium pratense* have identified key waterlogging-responsive genes involved in ethylene signaling, cell wall modification, and anaerobic metabolism (Yong et al., 2017). In *L. tenuis*, hypoxia-induced upregulation of ethylene-responsive factors (ERFs), sucrose synthase, and alcohol dehydrogenase (ADH) parallels mechanisms reported in rice SUB1A-mediated flooding tolerance (Pan et al., 2021). Quantitative trait loci (QTLs) associated with root porosity and regrowth have been identified in *L. japonicus* and *M. truncatula*, offering opportunities for marker-assisted selection (Striker and Colmer, 2017).

### Breeding approaches and progress

Conventional breeding remains central to improving waterlogging tolerance, particularly through recurrent selection and interspecific hybridization. Crosses between *L. tenuis* (highly tolerant) and *L. corniculatus* (high yielding but less tolerant) have produced hybrid lines combining superior persistence with enhanced biomass production (Striker et al., 2005). In tropical forage grasses, breeding programs in *Urochloa* and *Paspalum* have successfully identified cultivars adapted to flood-prone environments (Di Bella et al., 2022). Increasingly, breeding pipelines integrate physiological screening with molecular tools to accelerate genetic gains (Pan *et al.,* 2021).

### Biotechnological and omics approaches

Advances in genomics, transcriptomics, proteomics, and metabolomics have enabled detailed dissection of complex flooding stress responses. RNA-seq studies reveal coordinated regulation of genes involved in ethylene biosynthesis, cell wall loosening, and carbohydrate metabolism under hypoxia (Yong *et al.,* 2017). Proteomic analyses have identified stress-responsive proteins associated with antioxidant defense and anaerobic metabolism (Narsai *et al.,* 2011). Although genome-editing technologies such as CRISPR/Cas9 are not yet widely applied in forage crops, they hold considerable potential for targeted manipulation of regulatory genes conferring submergence or hypoxia tolerance (Pan et al., 2021). These approaches can effectively complement conventional breeding and facilitate rapid introgression of tolerance traits.

## AGRONOMIC AND MANAGEMENT STRATEGIES

### Drainage and soil management

Although genetic improvement enhances inherent tolerance, agronomic interventions remain essential for mitigating waterlogging damage in forage systems. Adequate drainage-achieved through raised beds, land contouring, surface drains, or sub-surface tile drainage-reduces the frequency and duration of soil saturation and improves root-zone aeration (Setter and Waters, 2003). In pasture systems where drainage infrastructure is limited, rotational grazing and avoidance of machinery or livestock traffic under wet conditions help prevent soil compaction and preserve soil porosity (Striker, 2012). Soil amelioration with organic amendments or gypsum improves aggregate stability, infiltration, and drainage. Additionally, the inclusion of deep-rooted cover or companion species, such as chicory (*Cichorium intybus*) and *Plantago lanceolata*, can enhance soil structure, water movement, and aeration in mixed swards (Pang et al., 2004).

### Species and cultivar selection

Species and cultivar selection represents a primary management decision in flood-prone environments. For such areas, the following forage species have consistently demonstrated superior tolerance to waterlogging:

**Legumes:** *Lotus tenuis*, *L. corniculatus*, *Trifolium fragiferum*, *Melilotus siculus*

**Grasses:** *Urochloa humidicola*, *Paspalum dilatatum*, *Festuca arundinacea*, *Lolium multiflorum.*

Waterlogging-tolerant cultivars maintain higher productivity and stand persistence over multiple seasons, thereby reducing re-establishment costs and management inputs (Di Bella *et al.*, 2022). In mixed swards, combining tolerant grasses with compatible legumes enhances system-level resilience, improves forage quality, and stabilizes nitrogen supply under fluctuating soil moisture conditions (Striker and Colmer, 2017).

### Nutrient and water management

Waterlogging substantially alters soil nutrient dynamics, often increasing the availability of reduced ions such as $Fe^{2}$z and $Mn^{2}$z while restricting the uptake of nitrogen and phosphorus (Setter and Waters, 2003). Split fertilizer applications-particularly of nitrogen-and the use of slow-release or stabilized formulations reduce nutrient losses during and after flooding events. In legume-based systems, inoculation with waterlogging-tolerant *Rhizobium* strains enhances nodulation efficiency and sustains biological N, fixation under hypoxic conditions (Pang *et al.*, 2004). Efficient irrigation scheduling is equally important to avoid unnecessary soil saturation. In regions prone to both drought and flooding, flexible irrigation-drainage systems provide adaptive capacity and improve overall water-use efficiency (Pan *et al.*, 2021).

### Integrated systems and grazing management

Waterlogging tolerance should be viewed not only as a plant trait but also as an emergent property of the agroecosystem. Integrating tolerant forage species into silvopastoral systems or well-managed rotational grazing regimes distributes stress exposure spatially and temporally, while enhancing soil structure through positive root–soil–microbe interactions (Striker, 2012). Periodic soil aeration through light tillage, grazing rest, or strategic pasture renovation supports microbial recovery and nutrient cycling following flooding events. Forage mixtures containing tolerant legumes such as *L. tenuis* improve pasture nitrogen balance and forage quality, even when grass components experience temporary growth suppression (Reinoso *et al.*, 2004).

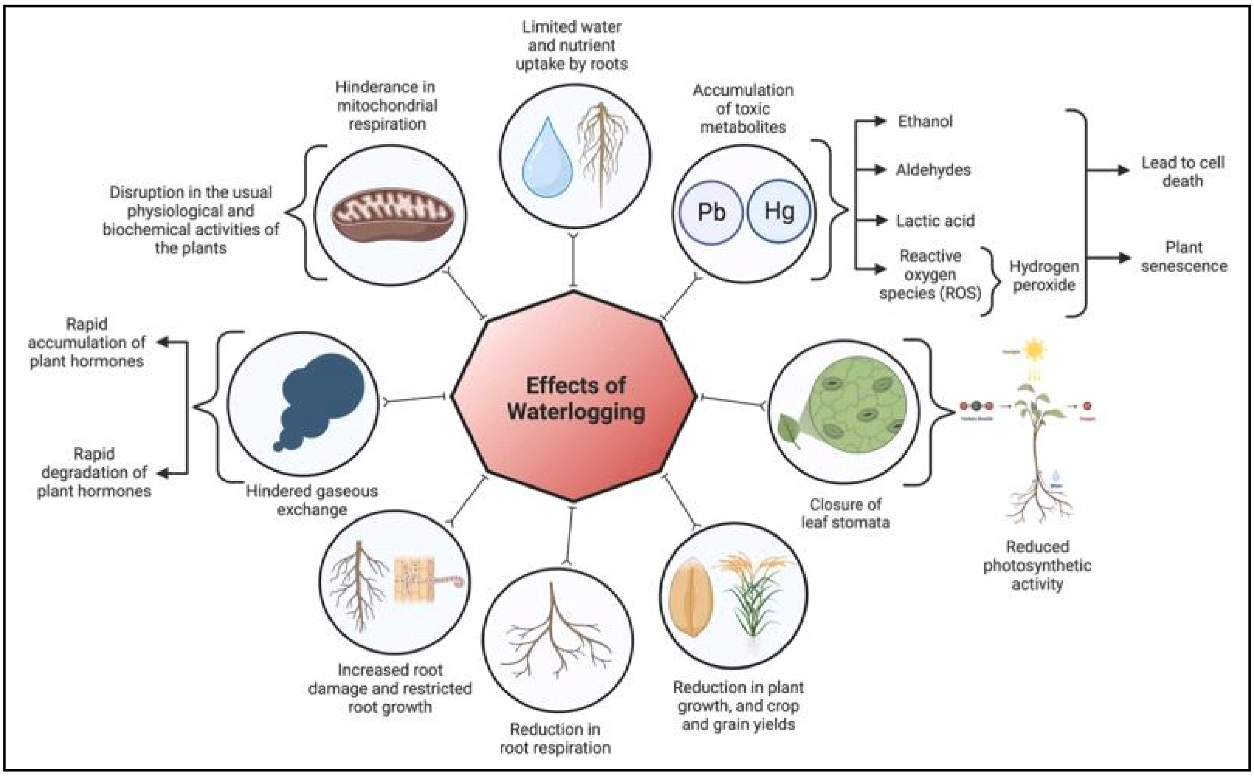


Fig. 1. Effects of waterlogging on crops (source Hakim *et al.*, 2025)

## FUTURE PERSPECTIVES

### Climate change and increasing flooding risk

Projected increases in rainfall variability and the frequency of extreme precipitation events under climate change scenarios are expected to expand the global area affected by waterlogging. Climate models predict a 10-20% increase in flood frequency across temperate and subtropical regions by 2050 (IPCC, 2022). Consequently, the development of forage species and systems capable of tolerating both drought and waterlogging-termed "dual resilience"-has emerged as a major research priority (Pan *et al.*, 2021).

### Integrating multi-omics and systems biology

Future advances in waterlogging tolerance will depend on integrating multi-omics approaches, including transcriptomics, proteomics, and metabolomics, with detailed physiological phenotyping to identify key regulatory networks governing stress responses (Narsai *et al.*, 2011, Yong *et al.*, 2017). Functional genomics studies in model legumes such as *Lotus japonicus* and *Medicago truncatula* will continue to guide candidate gene discovery for forage improvement. In parallel, machine learning tools and high-throughput imaging platforms offer promising opportunities to predict tolerance based on integrated trait profiles and accelerate selection efficiency in breeding programs (Pan *et al.*, 2021).

### Breeding for resilience and ecosystem services

Beyond maintaining forage yield, waterlogging tolerance contributes to broader ecosystem services, including soil protection, erosion control, nutrient retention, and mitigation of greenhouse gas emissions. Tolerant forage species maintain vegetative cover during wet periods, thereby reducing nutrient leaching and soil degradation (Striker and Colmer, 2017). Incorporating waterlogging tolerance into breeding objectives thus supports both productivity and environmental sustainability. Collaborative research efforts linking breeders, physiologists, soil scientists, and climate modelers will be essential to develop cultivars and systems adapted to variable climates and low-input production environments (Di Bella *et al.*, 2022).

## CONCLUSIONS

Waterlogging imposes severe constraints on forage production worldwide; however, substantial interspecific and intraspecific variation in tolerance exists among forage crops. Tolerant species such as *Lotus tenuis*, *L. corniculatus*, *Trifolium fragiferum*, *Urochloa humidicola*, and *Festuca arundinacea* sustain productivity through coordinated morphological (aerenchyma formation, adventitious rooting), physiological (maintenance of photosynthesis), and biochemical (regulated ethylene signaling and antioxidant defense) adaptations. Advances in phenotyping and genomics are increasingly elucidating the molecular basis of these traits, enabling targeted breeding strategies. When combined with improved drainage, optimized nutrient management, and adaptive grazing practices, these innovations offer a robust pathway to enhancing pasture resilience under increasingly variable hydrological regimes. Developing forage systems with dual tolerance to both drought and flooding will be critical for sustaining livestock production under future climate uncertainty.

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