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COLD TOLERANT FORAGE CROPS: PLANT PHYSIOLOGY, BREEDING, AND BIOTECHNOLOGY APPROACHES TO ENHANCE FORAGE YIELD - A REVIEW

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SUMMARY

Cold stress tolerance in forage crops refers to the ability of grasses and legumes to survive and maintain productivity under low-temperature conditions, including chilling (0-15°C) and freezing (<0°C). This trait is critical in temperate and high-altitude regions where frost events are frequent. Cold-tolerant forage species exhibit adaptive mechanisms such as osmotic adjustment, antioxidant defense, membrane stability, and cold acclimation, which reduce cellular damage and sustain growth. These adaptations ensure stable biomass production and continuous feed supply during colder seasons, thereby supporting livestock productivity and farm income. This review summarizes physiological mechanisms, breeding strategies, and biotechnological approaches to enhance cold tolerance and forage yield.

Key words: Alfalfa, cold tolerant, forage crops, freezing stress, physiology

Cold stress tolerance in forage crops is an essential trait that determines the survival, growth, and productivity of plants used for animal feed under low-temperature conditions. Forage crops, including grasses and legumes, form the backbone of livestock-based agricultural systems by providing a consistent and nutritious source of feed. However, their productivity is often challenged by environmental stresses, among which cold stress is one of the most significant, particularly in temperate, subtropical, and high-altitude regions Roychowdhury *et al.* (2025). Low temperatures, whether in the form of chilling (0-15°C) or freezing (<0°C), can severely affect plant physiological processes, leading to reduced growth, poor establishment, and in extreme cases, plant death. Therefore, understanding and improving cold stress tolerance in forage crops is vital for sustaining livestock production and ensuring agricultural stability. Cold stress affects plants at multiple levels, including cellular, physiological, biochemical, and molecular processes. Exposure to low temperatures can disrupt membrane integrity, reduce enzyme activity, and impair photosynthesis. Ice crystal formation during freezing conditions can physically damage plant cells, causing leakage of cellular contents and ultimately cell death. Even non-freezing chilling temperatures can lead to metabolic imbalances, resulting in reduced nutrient uptake, slower growth rates, and diminished biomass accumulation. These effects are particularly detrimental for forage crops, where biomass yield and quality are directly linked to livestock productivity. In regions that experience seasonal temperature fluctuations, forage crops must possess adaptive strategies to withstand cold conditions. One of the most important adaptive mechanisms is cold acclimation, a process by which plants gradually develop tolerance after exposure to mild low temperatures. During acclimation, plants undergo a series of physiological and biochemical changes, such as the accumulation of soluble sugars, amino acids like proline, and specific proteins that protect cellular structures. These compounds act as osmoprotectants, stabilizing cell membranes and maintaining cellular hydration under stress conditions. Additionally, changes in membrane lipid composition, particularly an increase in unsaturated fatty acids, help maintain membrane fluidity, which is critical for proper cellular function at low temperatures.

Another key aspect of cold stress tolerance is the activation of antioxidant defense systems. Low temperatures often lead to the accumulation of reactive oxygen species (ROS), which can cause oxidative damage to proteins, lipids, and nucleic acids. To counteract this, plants produce antioxidant enzymes such as superoxide dismutase, catalase, and peroxidase. These enzymes play a crucial role in detoxifying ROS and protecting plant cells from oxidative stress. The efficiency of this defense system is often associated with the degree of cold tolerance in forage species. Forage crops exhibit considerable variation in their ability to tolerate cold stress. Temperate grasses such as ryegrass, fescue, and timothy are generally more cold-tolerant compared to tropical species. Similarly, leguminous forage crops like alfalfa and clover have developed mechanisms to survive harsh winter conditions, including dormancy and regrowth capacity. These species are widely cultivated in regions with cold climates due to their ability to maintain productivity and recover quickly after stress. On the other hand, many tropical forage species are highly sensitive to low temperatures and may suffer significant yield losses when exposed to cold stress. The importance of cold stress tolerance in forage crops extends beyond plant survival to broader agricultural and economic implications. Livestock production systems rely heavily on the availability of quality forage throughout the year. In cold regions, winter feed shortages are a common challenge, often leading to increased dependence on stored feed or expensive supplements. Cold-tolerant forage crops can help mitigate this problem by ensuring consistent biomass production and extending the grazing season. This not only reduces feed costs but also improves livestock health and productivity, ultimately contributing to the profitability and sustainability of farming systems. Agronomic practices also play a significant role in enhancing cold stress tolerance in forage crops (Ali *et al.*, 2023). Proper selection of species and varieties suited to local climatic conditions is a fundamental step. Timely sowing ensures that plants are well established before the onset of cold weather, improving their chances of survival. Nutrient management, particularly adequate potassium supply, has been shown to enhance stress tolerance by improving water regulation and enzyme activity. Additionally, practices such as irrigation before frost events, mulching, and controlled grazing can help reduce the impact of cold stress on forage crops. Advancements in plant breeding and biotechnology have opened new avenues for improving cold stress tolerance. Traditional breeding approaches focus on selecting and crossing cold-tolerant genotypes to develop improved varieties with enhanced resilience. Marker-assisted selection has further accelerated this process by enabling the identification of genetic traits associated with cold tolerance Ali *et al.* (2023). At the molecular level, research has identified specific genes and regulatory pathways involved in cold stress response, providing opportunities for genetic engineering and gene editing. These approaches aim to develop forage crops that can better withstand low-temperature stress while maintaining high yield and nutritional quality. Climate change adds another layer of complexity to the issue of cold stress in forage crops. While global temperatures are generally rising, climate variability has led to an increase in extreme weather events, including unexpected frost and cold waves. Such fluctuations can be particularly damaging to forage crops that are not adequately adapted to sudden temperature changes. Therefore, developing forage systems that are resilient to both cold stress and other environmental challenges is becoming increasingly important Verma (2019).

Physiological Mechanisms of Cold Tolerance

Cold Acclimation

Cold acclimation is a crucial adaptive process in which forage crops develop increased tolerance to freezing after exposure to low but non-freezing temperatures. This process involves a series of physiological and biochemical changes that prepare the plant for harsher conditions. During acclimation: Plants accumulate soluble sugars (such as sucrose and raffinose) that act as cryoprotectants. These sugars stabilize cellular structures and lower the freezing point of cell sap. Protective proteins are synthesized, including dehydrins, which prevent damage to cellular components. There is improvement in membrane stability, reducing the risk of leakage and damage caused by ice crystal formation. Metabolic adjustments occur, allowing plants to maintain basic functions even at low temperatures. This mechanism is well developed in temperate forage crops like alfalfa and ryegrass, enabling them to survive winter conditions (Ali *et al.*, 2023).

Osmotic Adjustment

Osmotic adjustment helps plants maintain water balance and cell turgor during cold stress, especially when freezing reduces water availability. Accumulation of compatible solutes such as proline, glycine betaine, soluble sugars, and amino acids. These solutes lower the osmotic potential of cells, allowing them to retain water and prevent dehydration. They also act as osmoprotectants, stabilizing proteins, membranes, and enzymes. Proline, in particular, plays multiple roles including ROS scavenging and maintaining cellular integrity. This mechanism ensures that cells remain functional even when external conditions limit water uptake.

Antioxidant Defense System

Cold stress often leads to the overproduction of reactive oxygen species (ROS) such as superoxide radicals, hydrogen peroxide, and hydroxyl radicals. These molecules can cause oxidative damage to lipids, proteins, and DNA. To counteract this, forage crops activate an antioxidant defense system:Superoxide dismutase (SOD) converts superoxide radicals into hydrogen peroxide. Catalase (CAT) and peroxidase (POD) further break down hydrogen peroxide into water and oxygen. Non-enzymatic antioxidants such as ascorbate (vitamin C), glutathione, and carotenoids also help neutralize ROS. A strong antioxidant system is directly associated with higher cold tolerance, as it protects cells from oxidative injury.

Membrane Lipid Composition

Cell membranes are highly sensitive to temperature changes. At low temperatures, membranes can become rigid and lose functionality. Plants adapt by modifying their membrane lipid composition: There is an increase in unsaturated fatty acids (e.g., linoleic and linolenic acids). Unsaturated lipids maintain membrane fluidity, ensuring proper functioning of membrane-bound proteins and transport systems. This prevents membrane leakage and cellular damage during freezing conditions. Maintaining membrane integrity is essential for sustaining cellular processes under cold stress.

Protective Proteins

Cold stress induces the production of specific proteins that help plants survive adverse conditions. Cold-regulated (COR) proteins: These stabilize cellular structures and protect enzymes from denaturation. Dehydrins: A group of proteins that protect membranes and proteins from dehydration caused by freezing. Antifreeze proteins (AFPs): These inhibit the growth and recrystallization of ice crystals within plant tissues, reducing physical damage. Heat shock proteins (HSPs) (also involved in cold stress): Assist in protein folding and prevent aggregation of damaged proteins. These proteins play a vital role in maintaining cellular integrity and metabolic activity during cold exposure.

Management Practices to Improve Cold Tolerance

Management practices play a crucial role in improving cold stress tolerance in forage crops and ensuring stable productivity under low-temperature conditions. One of the most important practices is the selection of suitable crop species and varieties. Farmers should choose cold-tolerant and region-specific forage crops such as hardy grasses and legumes that are well adapted to local climatic conditions. Using certified and high-quality seeds also enhances germination and early plant vigor, which are essential for withstanding cold stress. Timely sowing is another key factor. Early planting allows crops to establish a strong root system and sufficient biomass before the onset of cold weather. Well-established plants are more capable of surviving frost and freezing conditions compared to young seedlings (Natalja *et al.*, 2025). In addition, maintaining proper plant density ensures efficient use of resources like light, nutrients, and moisture, which supports better growth and stress resistance. Nutrient management significantly influences cold tolerance. Adequate application of essential nutrients, particularly potassium and phosphorus, improves plant strength, root development, and resistance to stress. Potassium plays a vital role in regulating water balance and enhancing membrane stability, while phosphorus supports energy transfer and root growth. Avoiding

TABLE 1
Mechanisms of cold tolerant forage grasses, legumes, cereal and mechanisms

Crop Name	Type	Level of Cold Tolerance	Key Features
Forage Grasses			
Ryegrass	Grass	High	Rapid establishment, good regrowth
Tall fescue	Grass	Very High	Deep roots, drought and cold hardy
Timothy	Grass	High	Suitable for cool climates, good hay quality
Orchardgrass	Grass	Moderate to High	Early growth in spring
Kentucky bluegrass	Grass	High	Excellent winter hardiness
Smooth bromegrass	Grass	High	Strong rhizome system, persistent
Reed canary grass	Grass	High	Tolerates waterlogging and cold
Forage Legumes			
Crop Name	Type	Level of Cold Tolerance	Key Features
Alfalfa	Legume	Very High	Deep roots, good regrowth after winter
Red clover	Legume	High	Good biomass, short-lived perennial
White clover	Legume	Moderate	Spreading growth, tolerant to grazing
Berseem clover	Legume	Low to Moderate	Sensitive to frost
Subterranean clover	Legume	Moderate	Self-seeding ability
Birdsfoot trefoil	Legume	High	Tolerates poor soils and cold
Forage Cereals			
Crop Name	Type	Level of Cold Tolerance	Key Features
Oats	Cereal	Moderate	Fast growth, used as green fodder
Barley	Cereal	Moderate to High	Early maturity
Rye	Cereal	Very High	Excellent winter hardiness
Wheat (for forage)	Cereal	Moderate to High	Multi-purpose (grain + fodder)
Triticale	Cereal	High	Hybrid vigor, stress tolerant
Mechanisms of cold tolerance in forage crops with examples			
Mechanism	Example Crops Showing Strong Responses		
Cold acclimation	Alfalfa, ryegrass, fescue		
Osmotic adjustment	Oats, barley, clover		
Antioxidant defense	Ryegrass, alfalfa, timothy		
Membrane modification	Tall fescue, bromegrass		
Protective proteins	Rye, alfalfa		

excessive nitrogen application before winter is also important, as it may promote tender growth that is more susceptible to cold injury.Irrigation management can help reduce the effects of cold stress. Providing light irrigation before an expected frost can help maintain soil moisture and reduce temperature fluctuations around the root zone. Moist soil retains more heat than dry soil, offering some protection to plant roots. Additionally, proper drainage should be ensured to prevent water-logging, which can worsen cold damage. Mulching and residue management are effective in protecting forage crops from extreme temperature variations. Applying organic mulches such as straw or crop residues helps insulate the soil, conserve moisture, and maintain a more stable soil temperature. This reduces the risk of root damage during freezing conditions. Grazing management is also critical. Overgrazing before the onset of winter weakens plants and reduces their ability to store energy reserves needed for survival and regrowth. Controlled or rotational grazing should be practiced to maintain adequate plant cover and vigor. Finally, adopting improved agronomic practices and stress management techniques, including the use of growth regulators or protective sprays, can further enhance plant resilience. Overall, integrating these management strategies helps forage crops better withstand cold stress, ensuring sustained biomass production and reliable feed supply for livestock.

RESILIENT FORAGE CROPS

Several forage crops have been identified as climate-resilient due to their capacity to tolerate abiotic stresses, including 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). 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, Singh *et al.* (2021), Dheeravathu *et al*., 2021a, 2021b, 2022a, 2022b). 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; Dheeravathu *et al.* (2024a and b), Sravanthi *et al*., 2024, 2025).

Approaches to Enhance Forage Yield

Forage crops are a critical component of livestock production systems, providing the primary source of nutrients and biomass required for animal growth, milk production, and meat quality. Enhancing forage yield is therefore a priority for sustainable agriculture, particularly in regions where climatic variability and soil constraints limit plant growth. Improvements in forage productivity are achieved through a combination of understanding plant physiological responses, employing traditional and modern breeding techniques, and leveraging biotechnological interventions.

Plant Physiological Approaches

Plant physiology plays a central role in determining forage productivity. Key physiological traits include photosynthetic efficiency, nutrient uptake, root system development, water use efficiency, and stress tolerance. Among these, photosynthesis is the fundamental driver of biomass accumulation. The ability of a plant to capture light energy, fix carbon dioxide efficiently, and convert it into carbohydrates determines both the quantity and quality of forage. Factors such as chlorophyll content, leaf area index, stomatal conductance, and enzymatic activity of the Calvin cycle influence photosynthetic efficiency. Genotypes with higher photosynthetic rates often exhibit faster growth and increased biomass production (Shuangyan, 2024, Soualihou *et al.*, 2022). Root system architecture is another critical physiological trait affecting forage yield. Deep and extensive root systems enhance water and nutrient acquisition, particularly under suboptimal soil conditions. Forage crops such as alfalfa and tall fescue exhibit well-developed root systems that contribute to drought tolerance and consistent biomass production. Similarly, water-use efficiency, the plant’s ability to maintain growth under limited water availability, directly impacts yield, especially in arid and semi-arid regions. Stress tolerance, particularly to abiotic factors like cold, drought, and salinity, are closely linked to forage productivity. Physiological adaptations such as osmotic adjustment, antioxidant defense systems, and membrane stability enable plants to maintain metabolic activity under stress, minimizing yield losses. For example, forage species that accumulate compatible solutes like proline or soluble sugars can maintain cell turgor and sustain growth during cold or drought episodes.

Breeding Approaches

Traditional breeding has long been the cornerstone of forage improvement. Conventional selection involves identifying high-yielding genotypes based on traits such as biomass accumulation, regrowth capacity, nutritional quality, and stress tolerance. Crossbreeding and recurrent selection are used to combine desirable traits from multiple parental lines, producing progenies with superior performance. Over successive generations, breeders select individuals with enhanced yield, persistence, and adaptability to specific environmental conditions. One limitation of conventional breeding is the time required to evaluate multiple generations under field conditions. To accelerate progress, marker-assisted selection (MAS) has been widely adopted. MAS utilizes molecular markers linked to quantitative trait loci (QTLs) associated with forage yield and related traits, such as drought tolerance, disease resistance, or nutrient use efficiency. By identifying these markers early in plant development, breeders can select superior genotypes without waiting for full phenotypic expression, significantly reducing breeding cycles and increasing precision. Polyploidy and hybridization are other breeding strategies that have been effective in improving forage yield. Many forage grasses, such as ryegrass and fescue, are polyploid, which enhances genetic variability, heterosis, and biomass production. Hybrid varieties, developed by crossing elite parental lines, often show increased vigor, faster growth, and higher stress resilience compared to inbred lines.

Biotechnology Approaches

Advances in biotechnology have expanded the toolbox for improving forage yield beyond traditional methods. Genetic engineering enables the introduction or modification of genes that directly influence growth, stress tolerance, or nutrient efficiency. For example, genes regulating photosynthetic enzymes, cell wall biosynthesis, or osmoprotectant production can be inserted into forage crops to improve biomass accumulation and resilience under adverse conditions. Transgenic approaches have been successfully applied in species such as alfalfa, tall fescue, and timothy grass to enhance traits like drought tolerance, nitrogen fixation, and cold resilience, which indirectly boost forage yield. Gene editing technologies, particularly CRISPR-Cas9, offer precise modification of target genes involved in growth regulation, flowering time, or stress response. By selectively knocking out negative regulators or enhancing positive regulators of biomass production, gene editing can produce forage varieties with optimized growth under diverse environmental conditions. Molecular breeding is another promising approach, integrating genomics, transcriptomics, and proteomics to identify candidate genes controlling yield-related traits. For instance, studies on forage legumes have identified genes controlling nodulation, nitrogen assimilation, and root development, which are crucial for enhancing growth and protein content. Marker-assisted pyramiding of these genes can lead to varieties with superior nutrient-use efficiency and higher biomass production.

Agronomic Integration

While plant physiology, breeding, and biotechnology provide the genetic potential for high yields, agronomic management is essential to realize this potential. Optimal sowing time, plant density, nutrient management, irrigation, and grazing practices significantly influence forage yield. For example, adequate potassium and phosphorus nutrition enhances root development and enzyme activity, while controlled grazing prevents overharvesting and ensures regrowth. Integrating physiological insights with improved genotypes allows farmers to maximize forage productivity under field conditions.

CONCLUSION

Enhancing forage yield requires a multi-faceted approach that combines understanding plant physiological processes, applying traditional and modern breeding techniques, and utilizing biotechnological interventions. Physiological traits such as photosynthesis, root development, water-use efficiency, and stress tolerance form the foundation for high biomass production. Conventional breeding, marker-assisted selection, hybridization, and polyploidy exploit genetic variability to develop superior forage varieties. Biotechnology, including genetic engineering and gene editing, provides precise tools to introduce or optimize traits critical for yield enhancement. By integrating these strategies with sound agronomic management, it is possible to produce forage crops that are resilient, high-yielding, and nutritionally efficient, supporting sustainable livestock production and agricultural stability in diverse environments.

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