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REVIEW ARTICLE

Reproductive physiology of small millets - An overview

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Abstract

Small millets are climate-resilient cereals cultivated primarily in rainfed and marginal ecosystems of Asia and Africa. These crops exhibit superior adaptability to abiotic stress due to features such as C_4 photosynthesis, efficient water use and robust root systems. Among the various growth stages, the reproductive phase is highly sensitive to drought and other environmental stresses, often resulting in reduced pollen viability, poor seed set and diminished grain yield. However, small millets possess unique adaptive mechanisms, including early flowering, condensed reproductive duration, high reproductive efficiency and synchronized panicle emergence, which collectively enhance their performance under water-limited conditions. Hormonal regulation involving abscisic acid and cytokinins, coupled with increased antioxidant enzyme activity, contributes to the protection of reproductive tissues and ensures successful grain formation. Despite these advantages, detailed physiological and biochemical studies on their reproductive resilience remain limited. This review consolidates existing knowledge on the reproductive physiology of small millets under rainfed conditions, emphasizing mechanisms that sustain productivity and offering insights for future crop improvement strategies.

Keywords: biochemical; nutrients; physiology; small millets

Introduction

Small millets are of climate-resilient crops that significantly contribute to food and nutritional security, especially in rainfed and resource-limited environments. Cultivated predominantly in arid and semi-arid zones, they thrive in marginal soils and require minimal irrigation, displaying strong tolerance to abiotic stresses such as drought and heat (1). These crops are nutritionally rich, offering high levels of dietary fibre, calcium, iron and essential amino acids making them instrumental in mitigating malnutrition and micronutrient deficiencies (2).

Enhanced environmental resilience in small millets derives from their efficient C_4 photosynthetic system, deep root architecture and rapid phenological progression under stress (3). Although these traits support consistent growth under fluctuating conditions, the reproductive stage remains particularly vulnerable. Drought and heat stress during flowering, pollination and grain filling can lead to substantial reductions in reproductive effectiveness, resulting in low seed set and reduced yield potential (4).

Among physiological adaptations during the reproductive stage are early panicle initiation, high pollen viability, synchronized flowering and condensed grain filling traits that collectively improve drought tolerance in adverse conditions. These features are tightly regulated by hormonal balance, notably between abscisic acid and cytokinins and supported by robust antioxidant enzyme activity that protects reproductive tissues from oxidative stress (5,6). Although these mechanisms confer clear advantages, in-depth molecular and physiological studies on reproductive resilience in small millets are still limited, especially when compared to more widely researched crops (7). Bridging this knowledge gap is essential for realizing the full potential of small millets in sustainable agriculture under changing climatic regimes.

Physiological characterization of small millet varieties under rainfed conditions

Plant height

Plant height is essentially a hereditary trait; it is influenced by natural conditions and management practices. It is a significant component that helps in the determination of growth. Additionally, plant height is an important trait in the selection of genotypes for dry zones (8). Plant height plays a role in the yield determination of foxtail millet and there is a positive correlation between plant height and yield. The high-yielding genotypes had relatively lower plant height at maturity in proso millet. Plant height was consistent during the growth cycle; however, differences in height at harvest were due to head length. Plant height showed a significant positive correlation with leaf area and yield components in foxtail millet (9).

Plant height is perhaps the most important growth parameter; an increase to an optimal height is desirable for every cereal to enhance its grain and fodder value. Plant height and ear length are highly correlated in corn (10).

In pearl millet, plant height showed a significant level of importance for grain yield as well as ear length. The height parameter in cotton presented an interesting pattern. For example, the height of cotton at the time of flowering was distinctive. In contrast, growth in terms of weight followed a distinct curve from germination until flowering. The nodes of sorghum were also studied by various researchers. The time needed to develop extra nodes was reflected in the corresponding delay in heading and growth in sorghum (11).

The time pattern of growth in certain ragi cultivars was examined, showing a continuous increase in plant height in cultivars PR 202, VZM 1 and Annapoorna up to 80 days after planting, after which height increase was insignificant. In another cultivar, Aruna, the maximum height was reached by 50 days after planting, with no significant increase thereafter. Thus, cultivar differences were distinctly expressed (12).

Root length

Root traits had positive relationships with yield and yield components under drought stress in rice. Fundamentally, these traits are genetically controlled but are also influenced by soil conditions and crop management. A deep root system has been correlated with tall plant height and a tendency for low tillering, with the latter being more closely associated with deep rooting. Drought-tolerant cultivars were characterized by longer and more extensive roots and drought tolerance increased with greater planting depth. Root penetration through compacted soil layers was also observed (13). Increased root length (18.6-37.0 cm), higher root volume (20.8-35.5 cc) and greater root dry weight (20.5-34.8 g) were recorded in drought-tolerant rice genotypes such as B35, MS73, CO21, CO22, Tenkasi1, AS2059, AS5078, AS2752, AS5057, AS4289 and MS7819, which improve water acquisition under stress conditions (14). These cultivars also exhibited heavier root biomass and larger root volume compared to drought-susceptible lines (15). Studies in Gramineae demonstrated that substantial interspecies variation in root production, with rapid development during the vegetative phase that slowed during reproduction, often resulting in reduced root weight at maturity (16). In ragi, thiamine application significantly influenced root development, with the highest root length observed at 1 ppm concentration. In sorghum, genotypic variation in root traits including length, weight and root/shoot ratio served as reliable indicators of drought tolerance (17).

Shoot length

Shoot length had pivotal role in the reproductive development of small millets, directly influencing panicle emergence and grain yield. Drought stress during the reproductive phase significantly reduces shoot length in finger millet (*Eleusine coracana*), which adversely affects panicle exertion and seed set. In pearl millet (*Pennisetum americanum*), the duration of the vegetative phase impacts shoot growth and development, ultimately affecting yield components. In proso millet (*Panicum miliaceum*), panicle length increases up to 35 days after anthesis, correlating with enhanced seed maturation and weight (18). Similar responses have been observed in other small millet species, where shoot elongation was positively associated with reproductive success under limited water conditions. Additionally, genetic variability in shoot growth dynamics across millet genotypes highlights its potential as a selection trait in drought-resilient breeding programs. These findings underscore the importance of optimizing shoot growth during critical reproductive stages to ensure successful panicle development and maximize grain yield in small millets (19).

Number of leaves

The leaf is considered a significant functional unit of the plant, contributing to yield. The number of leaves is an important factor influencing crop yield. A positive relationship between yield and number of leaves was observed in mung bean. The development phase of cereals is controlled by the number of leaves produced, including the period from planting to seedling development (average 4 days), days from germination to panicle initiation (average 42 days), days from first panicle initiation to flowering (average 6 days), days from flowering to maturity (average 31 days) and days from maturity to harvest (average 5 days) (20). From planting to panicle initiation, each test plant produced an average of eight fully developed leaves while maintaining an average number of tillers. In rice vegetative development, there is a close association between the presence of each tiller and the emergence of leaves on the main culm. Each individual leaf, on both the main culm and tillers, develops in coordination with the development of the leaves of the main culm. Additionally, the number of headed tillers is an important yield component in cereal grain production. The system for measuring grain, leaf and tiller development is comprehensive, as each leaf and tiller on the plant is assigned a unique identifier (21).

Leaf area

Leaf Area (LA) is the total surface area of all leaves on a plant and serves as a vital physiological trait influencing photosynthetic activity, light interception and ultimately reproductive success through improved assimilate supply to developing grains. In crops such as *Vigna radiata* (green gram), *Eleusine coracana* (finger millet) and *Pennisetum americanum* (pearl millet), LA has shown a strong positive correlation with reproductive efficiency and seed yield (20). Maintenance of higher LA appears to be an important factor for high yield. The largest LA was observed in rainfed *Pennisetum americanum* planted at a wider spacing of 90 cm compared to 50 cm. Increased LA has also been associated with higher photosynthetic rates in *Eleusine coracana* (21,22). Typically, high-yielding cultivars produce approximately 10 % more LA than low-yielding ones. Leaf Area Index (LAI) is the ratio of LA to ground area is a key determinant of dry matter accumulation and yield potential. Enhanced LAI can be achieved through increased plant population and improved nutrient supply, particularly potassium (23). In sorghum, the relationship between LA and grain yield showed that early-maturing cultivars with smaller LA were highly efficient in producing grain per unit of LA, with peak LA occurring under adequate soil moisture conditions (24). LA typically peaks during the phase of maximum tiller development and shoot elongation. In maize (*Zea mays*), the LA attained before grain development is closely linked to final grain yield, emphasizing the importance of sustaining LA during early growth phases (25). Furthermore, high-yielding genotypes of *Panicum miliaceum* (proso millet) maintain greater LAI throughout development, likely due to their higher number of green leaves and tillers per plant (26). These findings highlight the reproductive significance of LA and LAI across small millet species and related cereals, underscoring their potential as selection traits in breeding programs for yield enhancement under stress conditions.

Leaf area duration

Leaf Area Duration (LAD) represents the persistence of LA on plants and is a critical growth parameter reflecting the efficiency of the photosynthetic system. It shows a strong correlation with dry matter accumulation and crop productivity (27). Maintaining higher LAD during the grain-filling period is especially important, as most photosynthates at this stage are directed toward developing grains. Yield potential is closely associated with the plant's ability to sustain adequate LA over time, thereby maximizing its capacity for carbon assimilation per unit land area (28). However, a negative correlation between LAD and yield has also been reported in *Glycine max* (soybean), possibly due to excessive vegetative growth limiting partitioning to grains (27,28).

Despite this, the positive association between LAD and total dry matter indicates that biomass accumulation is largely dependent on radiation interception throughout the crop lifecycle (29). In *Echinochloa frumentacea* (barnyard millet), LAD increased from 15-30 Days After Sowing (DAS) to 30-45 DAS, then declined thereafter. Similarly, in *Setaria italica* (foxtail millet), LAD increased with crop age, peaking at 80 DAS before gradually decreasing (29). Higher LAD, particularly during the post-anthesis phase, plays a crucial role in assimilate accumulation in grains. This prolonged photosynthetic activity during grain development supports better yield outcomes in *S. italica* (30).

Specific leaf weight

Specific Leaf Weight (SLW) refers to photosynthetic efficiency and consequently, greater total dry matter accumulation. It is defined as the leaf dry weight per unit LA. A positive correlation between seed leaf weight, dry matter production and seed yield in *Glycine max* (soybean) has been established (31). SLW is an indicator of leaf thickness, with thicker leaves generally possessing higher chlorophyll content and greater concentrations of photosynthetic proteins per unit area. SLW has demonstrated a strong positive relationship with photosynthetic rate in several crops, including *Oryza sativa* (rice), *Zea mays* (maize), *Medicago sativa* (alfalfa), *Glycine max* (soybean), *Triticum aestivum* (wheat) and *Eleusine coracana* (finger millet) (31,32). In *Medicago sativa*, SLW of young leaves measured approximately 5 mg cm^{-2} under field conditions and 3 mg cm^{-2} in controlled growth chambers. Interestingly, SLW increased with leaf age in growth chamber environments but declined in unthinned field plots. These patterns suggest that environmental light conditions and canopy dynamics influence SLW and photosynthetic performance (32). A significant positive correlation between photosynthesis and SLW was also observed in *M. sativa*, where photosynthetic rates increased from 27 to 58 mg CO_2 dm^{-2} h^{-1} as SLW rose from 1.9 to 5.3 mg cm^{-2} (33).

Days to 50 % flowering

Most small millet species in the *Gramineae* family are cleistogamous, meaning fertilization occurs before the flower opens. Each spike contains approximately 50-70 spikelets arranged alternately on one side of the rachis. Within a spike, spikelets open from top to bottom, while within each spikelet, florets open from the base upward, typically with one floret opening each day (34).

In *Setaria italica* (foxtail millet), flowering beneath the tip of the panicle begins when about three-fourths of the head has emerged from the sheath, progressing from top to bottom in the main spike. The inflorescence consists of a central axis with short lateral branches and spikelets are borne in two rows on long and short pedicels. The highest number of florets tends to open on the sixth day after panicle emergence. In *Panicum sumatrense* (little millet), spikelet initiation begins on the second or third day after panicle emergence, with flowering advancing from the apex to the base.

In *Paspalum scrobiculatum* (kodo millet), peak flowering occurs on the sixth or seventh day, with spikelets in the centre of the raceme opening first and then gradually spreading to both ends (35). The panicle in *S. italica* typically requires 10-14 days to fully emerge and the maximum floret opening occurs 6-8 days after the start of flowering. Grains of small millets are round to oval in shape, with a 1000-seed weight ranging from 1.9 to 5.5 g and a volume of 1.3 to 3.8 mL. The seed coat and husk of *S. italica*, *P. sumatrense* and *Panicum miliaceum* (proso millet) are mostly single layered with a glossy appearance, while *P. scrobiculatum* and *Echinochloa frumentacea* (barnyard millet) possess multi-layered seed coats. The seed coat of *P. scrobiculatum* typically exhibits multiple brown shades, *S. italica* is yellowish and other species tend to display greyish coloration (36).

These reproductive phenological traits including spikelet emergence patterns, duration of flowering and seed coat characteristics are not only species-specific but also play a pivotal role in stress adaptation and yield stability under adverse climatic conditions. Days to 50 % flowering, pollen viability and flowering synchronization significantly influence reproductive success in varying drought scenarios. Table 1 summarizes key reproductive traits in different small millet species, highlighting their observed impacts on yield under specific stress conditions, along with supporting study contexts.

Table 1. Reproductive traits and yield impact in small millets under stress conditions

Species	Reproductive trait	Observed impact on yield	Stress condition type	Reference source / study context
Finger millet	Days to 50 % flowering	Early flowering improves drought escape and yield stability	Terminal drought	37,38
Foxtail millet	Pollen viability	Higher viability linked to better grain set and yield retention	Moderate drought	39,40
Little millet	Panicle exertion percentage	Greater exertion improves pollination success	High temperature + drought	41,42
Kodo millet	Flowering synchronization	Better synchronization enhances cross-pollination efficiency	Intermittent drought	43
Barnyard millet	Stigma receptivity duration	Extended receptivity correlates with higher seed set	Pre-anthesis drought	44

Crop growth rate

Crop Growth Rate (CGR) is a crucial physiological parameter that reflects the increase in dry matter per unit area over time, significantly influencing the reproductive efficiency and yield potential of small millets. In *Eleusine coracana* (finger millet), higher CGR during the booting to grain-filling stage strongly correlates with enhanced panicle development and grain yield under both irrigated and drought conditions (45). Similarly, in *Setaria italica* (foxtail millet), CGR peaks during the early reproductive stage, indicating that timely availability of nutrients and water during this period optimizes biomass accumulation and reproductive output. Research in *Pennisetum glaucum* (pearl millet) further reveals that drought-tolerant genotypes sustain higher CGR under stress, promoting improved biomass partitioning and effective grain setting (46). These insights emphasize the importance of CGR as a selection criterion in breeding programs aimed at improving yield and stress resilience in small millets.

Total dry matter production

Total dry matter production fundamentally linked to reproductive success and grain yield in small millets, reflecting the plant's overall capacity to assimilate and allocate resources during critical developmental stages. In *Eleusine coracana* (finger millet), higher dry matter accumulation during flowering and grain-filling stages correlates positively with increased grain yield under both irrigated and stress conditions (47). In *Setaria italica* (foxtail millet), genotypes with greater total dry matter production during the reproductive phase exhibit more efficient biomass partitioning toward panicle development, resulting in improved yield performance (48). Furthermore, under water stress, drought-tolerant genotypes of *Pennisetum glaucum* (pearl millet) sustain elevated levels of dry matter production by maintaining photosynthetic efficiency and delaying senescence (49). These insights highlight that enhancing dry matter production and its efficient allocation to reproductive organs can significantly boost productivity and resilience of small millets across varied environmental conditions.

Net assimilation rate

Net Assimilation Rate (NAR), which measures a plant's efficiency in converting light into dry matter per unit LA, is a crucial physiological trait influencing reproductive development and yield in small millets. In *Eleusine coracana* (finger millet), cultivars exhibiting higher NAR during the reproductive phase demonstrate improved grain filling and yield potential under rainfed conditions (50). In *Setaria italica* (foxtail millet), genotypes that maintain sustained NAR during heading and grain-filling stages achieve greater dry matter accumulation and a superior harvest index (51). Drought-tolerant varieties of *Paspalum scrobiculatum* (kodo millet) retain relatively stable NAR under stress, supporting better reproductive success and efficient biomass partitioning (52). The consistent link between NAR, photosynthetic activity and assimilate allocation to reproductive organs underscores its value as a selection criterion in breeding programs aimed at enhancing millet productivity and stress resilience.

Physiological and biochemical boundaries of small millets

Photosynthetic pigments

Chlorophyll is a photosynthetic pigment responsible for absorbing light energy required for the synthesis of carbohydrates. The chlorophyll content of plant tissues reflects the photosynthetic capacity of the plant (53). Generally, higher chlorophyll levels in leaves are accompanied by increased concentrations of associated pigments and proteins, which contribute to enhanced light capture and energy conversion. A strong relationship has been observed between leaf chlorophyll content and the rate of photosynthesis, indicating that elevated chlorophyll levels are a major factor contributing to improved yield performance (54). In *Setaria italica* (foxtail millet), genotypic variation in total chlorophyll content has been reported, with higher-yielding genotypes consistently exhibiting increased chlorophyll levels (55,56).

Chlorophyll fluorescence (Fv/Fm ratio)

Chlorophyll fluorescence is an important diagnostic tool in both fundamental and applied plant physiology. Fluorescence refers to the re-emission of excess energy absorbed by chlorophyll molecules via pathways such as light, heat dissipation and re-radiation. When a leaf transitions from darkness to bright light, chlorophyll fluorescence rises rapidly from a minimal level (Fo) to an intermediate inflection (I) and peaks at maximum fluorescence (Fm), before gradually declining through minor inflections to a level near the initial Fo (T). The difference between Fm and Fo is termed variable fluorescence (Fv), which reflects the efficiency of Photosystem II (PSII).

The chlorophyll fluorescence ratio F735/F700 has been reported to correlate strongly with chlorophyll content in various species, including *Fagus sylvatica* (beech) and certain wild plants (57). This phenomenon is influenced significantly by pigment composition and leaf optical properties (58). In green leaves, approximately 90 % of chlorophyll fluorescence emitted at 658 nm is reabsorbed by chlorophyll itself, which alters both intensity and spectral output (59). Given its sensitivity to changes in photosynthetic performance, chlorophyll fluorescence also serves as a reliable proxy for Calvin cycle activity in various crop and fruit-bearing species.

Gas exchange parameters

Stomatal characteristics significantly influence gas exchange between the plant and its environment, directly affecting both photosynthetic and transpiration efficiency. The resistance to diffusion of CO_2 and water vapor is regulated by stomatal density and aperture. Notably, changes in stomatal resistance have a greater effect on water vapor diffusion than on photosynthesis, as stomatal resistance contributes a larger proportion to total resistance in the case of water vapor movement compared to CO_2 diffusion (60). Since stomata serve as key regulators of both processes, variations in stomatal density among cultivars can greatly impact gas exchange rates. High-yielding genotypes of *Panicum sumatrense* (little millet) showed increased stomatal conductance at 60 DAS, likely due to higher stomatal density on the abaxial leaf surface, which enhanced CO_2 uptake and subsequently improved photosynthesis (61). The photosynthetic rate is influenced by light intensity and surrounding CO_2 concentration, but it is closely regulated by stomatal behaviour (62,63). In *Setaria italica* (foxtail millet), a positive relationship was observed between stomatal number and biological yield, highlighting the impact of stomatal traits on plant productivity (64). Moreover, the spatial arrangement of veins within the leaf influences the movement of photosynthates toward economically valuable plant parts.

Photosynthetic efficiency is a critical factor in grain yield determination, as it supplies the essential assimilates and energy required for growth and reproductive development. In *Panicum sumatrense*, the photosynthetic rate measured at flowering was found to be the highest among all yield-contributing traits (65-67). Additionally, leaf chlorophyll content has a strong positive correlation with photosynthetic rate, serving as a key determinant of crop productivity. Higher chlorophyll content is associated with increased photosynthesis and ultimately improved yield performance (68). Photosynthetic surface area per unit ground area offers valuable insight into the plant's total photosynthetic potential. High-yielding genotypes of *Panicum miliaceum* (proso millet) demonstrated elevated photosynthetic rates compared to their lower-yielding counterparts. These high-performing genotypes were also characterized by greater abaxial stomatal density, increased vein density, higher photosynthetic rate, elevated total chlorophyll content, higher RNase activity, greater stomatal conductance and moderate transpiration rates in *Panicum sumatrense* (69). Together, these attributes reinforce the importance of integrating stomatal and photosynthetic parameters in small millet breeding programs aimed at enhancing yield potential and environmental resilience.

Soluble protein

Soluble protein content serves as a biochemical indicator of photosynthetic activity by reflecting the levels of ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco), the primary enzyme responsible for CO_2 fixation during photosynthesis. Rubisco content per unit LA shows a strong positive correlation with soluble protein levels, indicating that leaves with higher protein content typically possess greater photosynthetic capacity (70). A similar positive relationship has been observed between seed yield and soluble protein content, underscoring the relevance of this trait for reproductive success in small millets. In the leaves of *Panicum miliaceum* (broomcorn millet), soluble protein content increases initially and then declines during the later stages of the dry season, coinciding with leaf senescence (71). Likewise, in *Setaria italica* (foxtail millet), soluble protein levels rise from 14 days after anthesis before gradually decreasing as the plant reaches maturity under dry season stress. These dynamic changes highlight the role of soluble proteins in supporting photosynthetic efficiency and yield formation during reproductive development in small millets (72).

Total carbohydrates

Carbohydrate content varies significantly among plant tissues. The distribution of carbohydrates between source and sink tissues has important implications for plant metabolism and growth. Feedback inhibition of photosynthesis can occur when carbohydrate accumulates in the leaves due to reduced translocation or utilization by sink organs. At the molecular level, carbohydrate metabolism is tightly regulated by sugar-sensing proteins that detect sucrose and hexoses and trigger downstream gene expression changes. Therefore, the overall carbohydrate economy in plants is sensitive to carbohydrate-mediated regulation mechanisms (73). In source tissues like leaves, sucrose synthesized in the cytosol may either be exported to sink tissues or stored in vacuoles (74). Furthermore, a shorter interveinal distance in C_4 grasses, such as maize and sorghum, facilitates faster transport of carbohydrates, aiding in efficient source-sink communication (75,76). *Eleusine coracana* (finger millet) shows tolerance to mild salinity stress (100 mM NaCl) by enhancing growth parameters such as plant height, LA and biomass, as well as increasing nitrate reductase activity and total reducing carbohydrates, all contributing to improved yield under stress (77). In cereals like sorghum and millets, starch constitutes the major form of carbohydrate storage, while soluble carbohydrates, pentosans, cellulose and hemicellulose occur in smaller quantities. In sorghum, normal endosperm types contain 23-30 % amylose, while waxy varieties typically contain less than 5 % amylose (78).

Abnormal starch accumulation in the leaf can act as a senescence trigger, although this effect depends on whether carbohydrate levels exceed a critical threshold. In certain experiments, lower leaves of de-eared plants (plants without ear development) accumulated significantly more starch than those of intact control plants. Despite this increase, these leaves did not exhibit premature senescence or histochemical signs of degeneration, suggesting that other compensatory mechanisms may prevent senescence if the critical concentration threshold is not reached. These responses can be influenced by genotype and environmental factors. Following ear removal, carbohydrate concentrations in upper leaves increased markedly, with more than double the total carbohydrate content and several times more starch compared to those in intact plants at final harvest (79). In *Zea mays*, starch usually accumulates in modest amounts in bundle sheath cells. However, under altered source-sink conditions, the buildup of non-structural carbohydrates may disrupt normal leaf physiological functions, potentially inducing early senescence. Furthermore, studies have indicated that this feedback inhibition mechanism is part of a larger stress-adaptation response and its extent may vary depending on plant developmental stage and stress type. Overall, carbohydrate balance within source tissues plays a pivotal role in determining the progression of senescence, particularly under stress or altered sink demand conditions (80).

Nitrate reductase action

Nitrate Reductase (NRase) activity is the rate-limiting enzyme in nitrogen metabolism and plays a key role in the regulation of this metabolic process in crops (81). Consequently, NRase is closely linked to plant growth and development. Studies have identified NRase as the essential enzyme in the nitrate reduction pathway. Research on groundnut showed that leaf NRase activity declines sharply during the post-flowering stage (82). NRase catalyses the conversion of nitrate to nitrite, which is considered the rate-limiting step in the assimilation of nitrate into proteins. The amount of nitrate reduced reflects the plant's nitrogen uptake efficiency. Environmental factors influence the rate of NRase activity. A decrease in NRase activity is often accompanied by an increase in free amino acids and a decline in protein synthesis. NRase activity has been associated with total yield and nitrogen content in plants.

The activity of NRase is vital for nitrogen assimilation in plants. A positive correlation between NRase activity and grain yield has been observed in foxtail millet (83). NRase activity tends to be higher in tissues with elevated photosynthetic rates, indicating its role in the photosynthetic adaptation of little millet. High-yielding genotypes consistently exhibit higher NRase activity, as confirmed in foxtail millet. NRase activity varies significantly among proso millet genotypes during the flowering stage. Under low NaCl stress (100 mM), finger millet shows tolerance through increased plant height, LA, biomass, NRase activity and total reducing carbohydrate content, resulting in improved growth and biomass accumulation for enhanced yield under salinity conditions (84).

Catalase and peroxidase compound movement

In peroxisomes, catalases play a crucial role in the removal of harmful hydrogen peroxide (H_2O_2), which is continuously produced during photorespiration (85). Increased catalase activity helps in the dismutation of H_2O_2, a key molecule involved in triggering senescence. This rise in catalase activity may result from enhanced superoxide dismutase activity. Both catalases and peroxidases are enzymes associated with chlorophyll metabolism. A greater decline in catalase activity has been observed in drought-sensitive jute lines compared to drought-tolerant ones (86).

In rice, catalase activity increases during the early stages of drought. In maize, catalase activity initially rises under drought stress but decreases sharply with prolonged or severe stress. Similar patterns have been observed in other studies also (86,87).

Variation in catalase activity has been recorded in wheat seedlings under drought conditions. Differences in catalase isozyme activity in wheat were also reported. These changes in catalase isozyme patterns result from the expression of different catalase genes. Class III catalase genes are upregulated during stress, while Class I catalase genes respond negatively. Class II catalase is typically present across all plants.

Conclusion

Millets demonstrate a remarkable combination of physiological, biochemical and agronomic traits that contribute to their resilience under drought and rainfed conditions, underscoring their significance in the era of climate change. Their inherent adaptations including deep rooting systems, efficient LA development, heightened antioxidant responses and stress-induced enzymatic activities enable them to maintain productivity in environments where conventional cereals often struggle. Yet, these climate-smart crops continue to be overlooked in mainstream breeding programs and policy frameworks. To realize their full potential in enhancing food and nutritional security, especially in semi-arid and low-input systems, it is imperative to focus on genetic enhancement, molecular breeding approaches and innovative agronomic strategies. Strengthening their cultivation through dedicated research, effective extension services and robust value chain development will pave the way for more sustainable and climate-resilient agricultural systems.

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Authors' contributions

SR and SK conducted the literature survey and contributed to drafting the sections on reproductive development and stress physiology in millets. JAS supported the drafting and editing of the manuscript. RS and LPJ contributed to the section on phenological traits and data interpretation. SR and RSP were responsible for compiling and synthesizing information on hormonal regulation and reproductive traits under abiotic stress. RSP also participated in structuring the manuscript and reviewing critical references. AM conceived the review topic, guided the overall structure and scientific direction and coordinated the writing process. All authors read and approved the final manuscript.

Compliance with ethical standards

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