

Physiological superiority of millet crops for climate resilience

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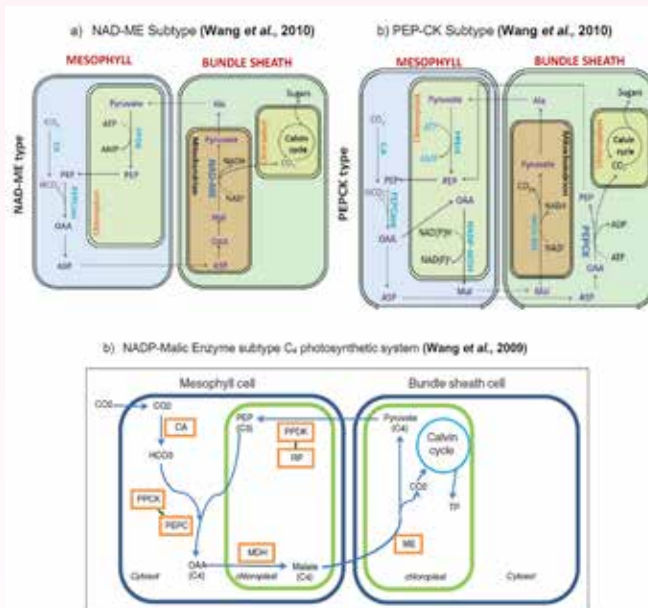
Milletts are the most important category of grain crops. They are a group of small-seeded grasses that are highly tolerant to environmental stresses and have high physiological efficiency. They are an important food security crop in many parts of the world, especially in Africa and Asia. Milletts have several key adaptive traits that make them well-suited for climate resilience, including their short growing season, deep root system and ability to tolerate high temperatures and drought conditions. The importance of these crops in terms of their physiological and anatomical make up is highlighted in this article, which needs to be utilized for selection of superior and high yielding germplasm for competing the yield potential of other major cereals.

Keywords: Climate smart crops, Kranz anatomy, Stress tolerance, Water use efficiency

IN the era of severe climate vulnerabilities and vagaries that affect crop production and productivity, an effective and sustainable solution for the farmers is to adapt to climate smart crops. Millet crops which include sorghum (jowar), pearl millet (bajra), finger millet (ragi), foxtail millet (kangani), barnyard millet (sanwa), proso millet (chenna), little millet (kutki) and kodo millet (kodo) are the promising crops that can cope with changing climate, sustain productivity and exhibit resilience to abiotic stresses. Their rich nutritional properties and health benefits have enabled their revival and cultivation in the recent years. Milletts are considered as nutri-cereals as they hold abundant nutritional benefits, food and fodder value, ecological benefits, reduced reliance on chemical fertilizers and are less sensitive to yield declines with lower inputs. The UN Food and Agriculture Organization reports state that “Compared to the more commonly known cereals such as wheat, rice or corn, milletts are capable of growing under drought conditions, under non-irrigated conditions even in very low rainfall regimes, having a low water footprint”.

Almost all the millet crops are well known for their hardiness which can withstand prolonged periods of drought, high temperatures and still yield grains and fodder. Hence, they are considered as climate smart crops. They are physiologically and anatomically superior over C_3 crops like rice and wheat to harness the available resources like light, water and other inputs. This

necessitates to understand the underlying physiological traits and anatomical make up of these crops, that makes them climate suitable crops. These crops have evolved in arid, low-latitude conditions and are in general more drought tolerant, sustain elevated temperatures, are less affected by increasing atmospheric carbon dioxide



The NADP-ME type of C_4 pathway in sorghum and millets: CA, carbonic anhydrase; MDH, malic dehydrogenase; PE, malic enzyme; OAA, oxaloacetate; PEPCK, phosphoenolpyruvate carboxylase; PEPCK, PEPCK; PEPCK, pyruvate orthophosphate dikinase; PEPCK, PEPCK; PEPCK, PEPCK; TP, triose phosphate.

Fig 1a,b,c: Three primary decarboxylase enzymes that are recruited in C_4 photosynthesis

C_4 photosynthetic system operating in millet crops

Table 1. Key traits in millet crops contributing for abiotic stress tolerance

Morpho-physiological/ molecular traits	Response to stress conditions	References
Earliness, plasticity to flower as per pattern of rainfall	Early life cycle completion confers escape from water stress, temperature stress at critical growth stages	Bidinger <i>et al.</i> (2007)
Small leaf area, waxy leaves and better leaf venation	Higher photo-assimilation, transpiration efficiency and water use efficiency	Bandyopadhyay <i>et al.</i> (2017)
Early, dense and deep root system with higher water uptake efficiency	Avoids early drought and deep roots, helps in terminal drought	Li and Brutnell (2011), Kumar and Panneerselvam (2014), Passot <i>et al.</i> (2016)
Higher photosynthesis	Due to C ₄ cycle and Kranz anatomy, millets have high water use efficiency under warm temperature, due to operation of MDH (Malate dehydrogenase) and PPDK (pyruvate orthophosphate dikinase) genes	Sage and Zhu (2011)
Enhanced level of secondary metabolites and osmolytes	Higher levels of antioxidants and osmolytes	Lata <i>et al.</i> (2011)
Functional genes expressed under abiotic stress	LEA (Late embryogenesis abundant protein), ARDP (ABA-responsive DRE binding protein), DREB (dehydration responsive element binding protein), NAC transcription factor, Aldose reductase, Glutamine synthetase, Pyrroline-5-carboxylate reductase, OPR (12-oxophytodienoic acid reductase), WD-40, PHGPX phospholipid hydroperoxide glutathione peroxidase), NAC transcription factors, bHLH transcription factor, Dehydrin 7, Heat shock factor, Ascorbate peroxidase, β -carbonic anhydrase, Glutathione reductase, Dehydroascorbate reductase	Bandyopadhyay <i>et al.</i> (2017)

levels, and have no/negligible GHGs emission which has been lost in major cereals as a result of intensive selection. A deeper understanding of the physiology of these millet crops is discussed in this article.

Millets as model crops for climate-resilience

Millet crops have a characteristic Kranz anatomy with C₄ pathway that is photosynthetically efficient in utilizing the light, water and CO₂, ultimately resulting in higher biomass and yield. Millet crops possess several morpho-physiological and agronomically superior traits (Table 1), viz. short life cycle (12–14 weeks from seed to seed), short stature, smaller leaf area, source-sink efficient leaf venation features, deeper root systems and hardness to stress conditions which makes them powerful model

system for dissecting C₄ photosynthesis. The short growing season length in almost all millets enables them to escape unpredictable late summer droughts, or serve as a rescue crop if another grain crop fails. Drought tolerance of millets, and other C₄ grasses express a set of unique, likely to be linked to ancestral evolution of dehydration pathways that can survive under severe drought stress typically specific to seed desiccation.

The photosynthetic enzymes, viz. carbonic anhydrase (CAH), malate dehydrogenase (MDH), malic enzyme (ME), phosphoenolpyruvate carboxylase (PEPC), phosphoenolpyruvate carboxylase kinase (PPCK) and pyruvate orthophosphate dikinase (PPDK) are reported to be maximum in all the millet species and these crops operate all the C₄ subtype pathways. Further, millets

Table 2. Photosynthetic efficiency of millet crops over other high input crops

Character	C ₄ Plant	C ₃ Plant
First CO ₂ acceptor	Phosphoenolpyruvate carboxylase	RuBP carboxylase
Type of chloroplast	Dimorphic chloroplast-Kranz anatomy present, two types of cells contain chloroplast (Mesophyll and Bundle Sheath)	Monomorphic-only one type of cell contains chloroplast, Kranz anatomy absent
Carbon pathway	Both Calvin cycle (bundle sheath) and Hatch-Slack cycle (mesophyll)	Calvin cycle in mesophyll cells
Photorespiratory C ₂ cycle	Absent	Present
CO ₂ compensation point	0–10 ppm	50–150 ppm
CO ₂ assimilation rate in intense light	50–70 mg CO ₂ /dm ² /hr	15–35 mg CO ₂ /dm ² /hr
Temperature optimum for photosynthesis and growth	30–45°C	10–25°C
Transpiration ratio	500 (about 500 molecules of water are lost for every molecule of CO ₂ fixed by photosynthesis)	250 (about 500 molecules of water are lost for every molecule of CO ₂ fixed by photosynthesis)
Water use efficiency	4.2–13.4 kg yield/ha/mm of rain	4.5–10.7 kg yield/ha/mm of rain
Rainfall requirement	200–500 mm	500–900 mm

greatly benefit from the C_4 photosynthetic trait as the Kranz anatomy increases the concentration of CO_2 in the bundle sheath, suppresses photo-respirative loss (around 80%) depending on the environment and increases the carboxylase activity of RuBisCO. RuBisCO of C_4 plants works efficiently at elevated CO_2 levels, have enhanced photosynthetic rates at warm conditions, confers higher water use efficiency (WUE) and nitrogen use efficiency (NUE) which are ~ 1.5–4-fold higher than crops having C_3 photosynthesis. In addition to WUE and NUE, the other benefits from C_4 photosynthesis are improved growth, higher biomass allocation and partitioning, and lower hydraulic conductivity per unit leaf area. These traits, make them next-generation crops with the potential to build climate-resilience and achieve sustainable yield. Realizing the stress tolerance potential of millets, using millet as a model crop is a promising option for developing climate-resilient crop species.

Some of the key photosynthetic efficient components of C_4 crops over C_3 crops are given in Table 2. To fully harness the underlying genetic potential using high-throughput phenotypic screening, conventional/molecular breeding/transgenic approaches and technologies are needed to exploit the inherent key traits in stress tolerance across millet crops.

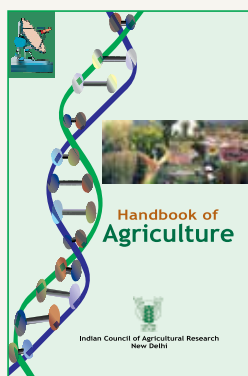
Despite their adaptability and climate resilience traits among other cereal crops, there is a dearth of studies to unveil mechanisms that confer stress tolerance. Further, resilient traits must be utilized for selection of superior and high yielding germplasm for competing the yield potential of major cereals like rice and wheat.

SUMMARY

Millets hold enormous potential for sustainable food and nutritional security. The underlying physiological characteristics highlight millets as a crop of choice for the global population, especially under the threat of climate change. Thus, highlighting the need for climate smart crops, farmers switching to cultivation of millets from water intensive crops will achieve an assured yield of around 8–10 quintal per acre with low input costs. Further, choosing millets over rice and wheat can help to accomplish the sustainable development goals (SDGs) – mainly SDG 2 (zero hunger), SDG 3 (good health and well-being), SDG 12 (sustainable consumption and production) and most importantly SDG 13 (climate action).

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TECHNICAL SPECIFICATIONS

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