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RESEARCH

Assessing the Resilience of Diverse Millet Species under Nitrogen and Moisture Co-limited Conditions

M.K.S. Jayarathna[1], R.M.B. Amanda Bandara[2], D.M.S.B. Dissanayaka[1*]

[1]*Department of Crop Science, Faculty of Agriculture, University of Peradeniya, 20400 Peradeniya*
[2]*Department of Horticulture & Landscape Gardening, Faculty of Agriculture & Plantation Management, Wayamba University of Sri Lanka, Makandura, Sri Lanka*

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Dissanayaka, D.M.S.B.
https://orcid.org/0000-0003-2221-5507

ABSTRACT

Crop yields are highly susceptible to various abiotic stresses, which are expected to intensify under global climate change. Millets are recognized as potential candidates to enhance food and nutritional security for a growing global population under a changing climate. Nitrogen (N) deficiency and drought are among the leading abiotic stresses affecting crop production. This study aimed to explore the growth, reproductive biomass, N uptake, and N use efficiency of three millet species under N-deficient and drought conditions. In a pot experiment, one variety of each of finger millet (*Eleusine coracana* L. Gaertn), proso millet (*Panicum miliaceum* L.), and foxtail millet (*Setaria italica* L.) were cultivated under two moisture regimes (80% field capacity as well-watered and 40% field capacity as drought treatment) coupled with two N levels (no N application and recommended N application by the Department of Agriculture, Sri Lanka). Across all four treatment combinations, proso millet had significantly lower tissue N concentration in roots, shoots, and panicles compared to finger millet and foxtail millets. Finger millet demonstrated a significant increase in root dry weight and root mass ratio across all four treatments compared to the other two millets. In a given N treatment, each millet species produced similar panicle dry weights regardless of the two moisture regimes, indicating their greater ability in biomass allocation to reproductive structure. However, N-deficient conditions significantly reduced panicle biomass in finger and foxtail millets, whereas proso millet maintained similar panicle dry weights across two N levels, demonstrating its ability to withstand N-deficit conditions. The study confirms that all three varieties of millet species can perform better under moisture-limited conditions, with proso millet variety being well-adapted to environments where moisture and N limitations co-exist.

* Corresponding author - samanthad@agri.pdn.ac.lk

INTRODUCTION

The rapidly increasing global population in the era of climate change necessitates more efficient utilization of agricultural resources such as water, fertilizers, and land in fostering sustainable crop production to ensure global food security (Kyalo Willy *et al*., 2019; Fernandes *et al*., 2022). Nitrogen (N) and water are among the most crucial resources influencing crop growth and yield (Araus *et al*., 2020; Machado *et al*., 2022). Nitrogen is a critical nutrient influencing crop growth and yield, yet it is often the limiting factor in many crop production systems, particularly those with low-input supplies. The agricultural sector consumes approximately 80% of the total available freshwater, which is becoming increasingly scarce. It also uses large quantities of N fertilizers, often exceeding the crops' N demand (FAO 2015; Esteban *et al*., 2016; Liang *et al*., 2019). Excessive N fertilization leads to environmental issues, such as nitrate leaching, which is globally acknowledged as a significant public and economic concern. This over-fertilization can increase eutrophication in freshwater ecosystems, acidify agricultural soils, and contribute to greenhouse gas emissions, further intensifying global climate change (Esteban *et al*., 2016; Liang *et al*., 2018; Fernandes *et al*., 2022). Numerous studies have shown that drought or N-deficiency affects a wide range of morphological traits, such as leaf area, leaf weight ratio, root growth, root hydraulic conductivity, and long-term root anatomical changes (Du *et al*., 2018; Moles *et al*., 2018; Machado *et al*., 2022). Moreover, drought stress and N-deficiency significantly affect metabolic pathways, disrupting water relations and impairing photosynthesis. This impairment could result from stomatal closure and/or metabolic damage (Gonzalez-Dugo *et al*., 2010; Ding *et al*., 2018).

The majority of the world's population relies on cereals as their staple food, with wheat (*Triticum aestivum* L.), rice (*Oryza sativa* L.), and corn (*Zea mays* L.) being the preferred choices. Consequently, developing improved varieties and designing new approaches for enhancing crop stress tolerance have become a priority, and most crop improvement efforts are focused on staple cereals (Gupta *et al*., 2017). Modern techniques in crop improvement, such as genomics-assisted breeding and genetic engineering, play crucial roles in unraveling the complexities of stress response and tolerance, and in implementing strategies for boosting crop productivity. However, one potential solution to address these challenges involves identifying and enhancing native crops that exhibit high adaptability to local climates, possess substantial nutritional value, and can effectively withstand biotic and/or abiotic stresses. While it is challenging to find a single crop that meets all these criteria, the wide variety and diversity of underutilized food crops, such as millets, offer a range of climate-resilient options for resource-poor farming communities (Shukla *et al*., 2015).

Millets are increasingly recognized for their potential as climate-resilient crops, particularly in the face of global climate change and resource limitations. Their inherent tolerance to drought and nutrient-limitation makes them valuable for sustainable agriculture in arid and semi-arid regions (Kole *et al*., 2015). Being rich in dietary fibers, resistant starches, vitamins, essential amino acids, storage proteins, and other bioactive compounds, millets are known to be nutritionally superior to other major cereals (Amadou *et al*., 2013). These qualities make millets an ideal crop for cultivation in arid and semi-arid regions. Millets are composed of six primary small-grained cereal crops: finger millet (*Eleusine coracana* L. Gaertn), foxtail millet (*Setaria italica* L.), kodo millet (*Paspalum scrobiculatum* L.), proso millet (*Panicum miliaceum* L.), barnyard millet (*Echinochloa* spp.), and little millet (*Panicum sumatrense* L.). Each of these crops is recognized for its unique traits and nutritional benefits (Kumar *et al*., 2016a, b; Gupta *et al*., 2017). Millets require very little water for cultivation and can be grown in non-irrigated conditions or in regions with very low rainfall (200–500 mm/year). In contrast to crops like rice and wheat, which may ensure food security with a high production cost, millets provide multiple forms of security, including food, fodder, fiber, nutrition, health, environment, and livelihood at minimal cost, making them significant for agricultural security (Bandyopadhyay *et al*., 2017; Gupta *et al*., 2017). Furthermore, millets have been recognized as vital plant genetic resources for agriculture, providing food security to impoverished farmers in arid, infertile, and marginal lands, particularly in Asia and Africa. Their rapid maturation and ability to grow in all seasons make them ideal for more intensive cropping systems. Additionally, they can also be used as catch or relay crops alongside slower-maturing crops (Bandyopadhyay *et al*., 2017; Gupta *et al*., 2017).

Given the increasing global interest in millets as a sustainable and climate-resilient food source, it is important to understand their responses to multiple abiotic stresses that commonly limit crop productivity. Among these, N-deficiency and soil moisture limitation are two major constraints responsible for reduced yields in many cropping systems. Previous studies have largely focused on the individual effects of N-deficiency and drought stress on crop growth and productivity (Gonzalez-Dugo *et al*., 2010; Ding *et al*., 2018; Plett *et al*., 2020). However, the combined effects of N- and water-limitation, as well as the varietal variability in crop responses to these co-occurring stresses, remain relatively underexplored (Machado *et al*., 2024). Therefore, this study compared dry matter production, N uptake, organ-specific N allocation, and nitrogen use efficiency (NUE) among one variety each of finger millet, proso millet, and foxtail millet under simultaneous moisture- and N-limitations. This approach adds a novel dimension to the study and enables the evaluation of their potential for improving crop production in environments where both water and N constraints frequently occur.

MATERIALS AND METHODS

Experimental location

A pot experiment was carried out in a greenhouse at the Department of Crop Science, Faculty of Agriculture, University of Peradeniya, Sri Lanka. The experimental period was from December 2023 to March 2024. Throughout the trial period, the mean minimum and maximum temperatures were 24.2 ^{0}C and 32.5 ^{0}C, respectively.

Growth medium preparation and seed establishment

Reddish-brown earth soil was collected from the experimental field at the Faculty of Agriculture, University of Peradeniya. To produce a N-limited medium, soil was mixed with sand in a 2:1 ratio. Properties of the growth medium are indicated in Table 1. Pots measuring 25 cm in height and 20 cm in diameter were prepared using 300-gauge polythene, and each pot was filled with 15 kg of this potting medium. Finger millet, proso millet, and foxtail millet were the millet species used. Certified seeds of these three species were obtained from the Field Crop Research and Development Institute, Mahailuppallama, Sri Lanka. A nursery was set up to produce healthy, uniformly sized seedlings for pot establishment. Two weeks after the nursery was established, two healthy, uniform seedlings were transplanted into the pots according to the treatment plan.

Experimental design and treatment structure

A three-factor factorial experiment was performed using a Completely Randomized Design with three replicates per treatment. Each replicate comprised of a pot having two plants. The first factor was the millet species, consisting of three types: finger millet, proso millet, and foxtail millet. The second factor was the soil moisture level, with two conditions: 80% of field capacity (FC) considered as well-watered conditions and 40% of FC considered as drought conditions. The third factor was the N, with two levels: N applied according to the recommendation of the Department of Agriculture-Sri Lanka (N+), and no external N application (N0). In total, there were 12 treatment combinations.

Table 1. Chemical properties of the growth medium used in the experiment

Soil property	Value
pH	5.95 ± 0.21
EC (ds/m)	0.21 ± 0.01
Available phosphorus (mg/kg)	10.84 ± 0.52
Exchangeable Potassium (mg/kg)	21.53 ± 3.15
Total nitrogen (mg/kg)	2.50 ± 0.04

Data represent the mean of four replicates ± SE (standard errors)

Determination of the field capacity of the growth medium

Determination of the FC of soil was carried out as described by Senevirathne *et al*. (2025). Briefly, a pot was filled with 15 kg of air-dried growth medium and weighed. The pot was then flooded with water, left to soak for one day (approximately 24 hours), and allowed another day to drain excess water. The wet weight of the soil was recorded. The amount of water required to reach the soil's FC was determined from the weight difference. The volumetric water content of the soil was measured using a digital soil moisture meter (TDR 150 Soil Moisture Meter, Spectrum Technologies, Inc.). At the FC, the growth medium had a volumetric water content of 32%.

Impose of drought treatment

All pots were initially adjusted to 80% FC. If the moisture level dropped, water was added to restore and maintain it within 80% FC. The drought treatment began at the start of flowering of each millet species to simulate water limitation during the reproductive stage, which is considered a critical period for yield formation. For the well-watered treatment, soil moisture was maintained at 80% FC throughout the growth period. In the drought treatment, the soil was allowed to dry out without irrigation until the moisture level dropped to 40% FC. After reaching 40% FC, soil moisture was maintained at that level until harvesting of the plants. Soil moisture was measured every two days using the digital soil moisture meter. When the moisture dropped below 40% FC, the required amount of water was calculated and added to the pots. The selected 40% field capacity level was intended to represent moderate drought stress under controlled conditions (Senevirathne *et al*., 2025).

Management of N and other nutrients

The fertilizer recommendation given for finger millet was applied to proso millet and foxtail millet due to the absence of specific fertilizer recommendations for these two millets from the Department of Agriculture – Sri Lanka. Nitrogen was only applied in the N+ treatment as per the recommendation of the Department of Agriculture, as a basal dressing at a rate of 65 kg/ha and as a topdressing after five weeks of seed establishment (three weeks after seedling transplanting) at a rate of 125 kg/ha. Phosphorus (P) and potassium (K) were applied using triple superphosphate and muriate of potash, respectively. All other management practices also adhered to the Department of Agriculture's recommendations.

Plant harvesting, dry weight measurements and N analysis

Three varieties of millet species were harvested at their physiological maturity. During harvesting, the shoot was cut at the base of the plant, and panicles were separated. The root system was carefully uprooted, washed, and used to measure root dry weight. All samples, including roots, shoots (stems and leaves), and panicles, were oven-dried at 70 ^{0}C until they reached a constant weight to determine dry weights (DW). After drying, the samples were ground and analyzed for tissue N concentrations using the Kjeldahl method (Nelson and Sommers, 1973). The concentration of N in the plant organs was multiplied by the DW of the same plant organ to estimate N content. Nitrogen content of different plant organs was then combined to determine total plant N uptake. Nitrogen use efficiency (NUE) in plant biomass formation was computed by dividing the total plant dry weight (g/plant) by the total N acquired (mg/g) by the plant (Jayamanna *et al*., 2022; Senevirathna *et al*., 2024).

Statistical analysis

Data were subjected to three-way analysis of variance in SAS/STAT software Version 9.1 to examine the impact of millet species, moisture level, N treatment, and their interactions on response variables (SAS Institute Inc. 1995). Results of the statistical analyses are summarized in Table 2. Comparisons between means were made using Tukey's Studentized Range Test. Means are presented with standard error, and significance is expressed at $p<0.05$.

RESULTS AND DISCUSSION

The experiment was conducted as a pot study; therefore, the findings are interpreted as basic insights obtained under controlled conditions, which can provide a foundation for future multi-locational evaluations.

Dry matter accumulation in different plant organs of millet species in response to moisture and N levels

There were numerous interaction effects of three factors: species (S), moisture (M), and N on dry weight of roots, shoot (stems and leaves), panicles, and total plant (Table 2). The moisture level was only significant for root DW and root mass ratio (RMR), whereas shoot, panicle, and total plant DW of each millet species remained unaffected by moisture level (Table 2). A significant three-way interaction (S x M x N) was found only for the root DW. Additionally, the two-way interaction of S x N predominantly influenced the dry matter accumulation in the root and total plant. The greatest root DW was recorded by finger millet cultivated under drought conditions (40% FC) coupled with N application (Table 3). Proso millet produced similar root dry weight irrespective of the four treatment combinations. Finger millet significantly increased its root DW under moisture-deficit conditions compared to well-watered conditions, but only when N was applied. For instance, with N application, the root DW of finger millet under drought stress was 33% higher than at 80% FC. Under each moisture regime, the root DW of each millet species did not differ significantly between the two N levels, except for the root DW of finger millet at 40% FC. Nitrogen supplementation under drought conditions increased root DW in finger millet by 51% compared with plants cultivated without external N input. Across two moisture regimes and N levels, root dry matter formation of millet species followed the order, finger millet > foxtail millet > proso millet (Table 3).

The highest shoot DW was observed in finger millet grown under well-watered conditions with N supplementation (Table 3). At both moisture levels, N application significantly enhanced shoot DW of finger millet and foxtail millet. For example, under well-watered conditions, shoot DW of finger millet increased by 95% in response to N application. The respective increment in moisture-deficit was 75%. When plants were cultivated with an external supply of N at 40% FC of soil moisture, shoot DW of finger millet was significantly lower than that recorded at 80% FC. However, there was no remarkable change in shoot DW between the two moisture regimes when finger millet plants were cultivated in soils where N was not applied. Likewise, at both 40% and 80% FCs, foxtail millet exhibited decreased shoot dry matter accumulation when there was no external N supplement, in contrast to the condition where N was applied. At 80% FC, there was a decrease in DW by approximately 43%, whereas at 40% FC, the reduction was around 45%. Nonetheless, within each N level, drought stress did not cause a significant reduction in the accumulation of dry matter in the shoot of foxtail millet. In contrast to finger millet and foxtail millet, proso millet demonstrated the ability to sustain a comparable level of shoot biomass accumulation across all combinations of moisture and N treatments in this study (Table 3).

The dry weight of panicles was significantly influenced by the millet species, N level and their interaction, while the moisture treatment showed no impact on panicle dry weight (Table 2). In each moisture level, N treatment had a remarkable impact on determining the panicle DW of both finger millet and foxtail millet (Table 3). For example, when finger millet was cultivated under well-watered conditions without external N supplementation, its panicle DW decreased by 47% compared to the N-supplied condition. The relevant reduction under drought stress was 46%. A similar pattern was observed in foxtail millet, which reduced its panicle DW by 46% under well-watered conditions and by 47% under moisture-limited conditions when N was limited. However, either moisture level or N treatment could not significantly impact dry matter accumulation in the panicles of proso millet. The same pattern was observed in the total plant dry matter of all three millet species. Comparison of the total plant dry matter across two moisture regimes and two N applications showed that finger millet has the highest capacity for dry matter accumulation compared to the other two millet species. When averaged across moisture and N treatments, finger millet produced approximately 188% and 46% greater biomass than proso millet and foxtail millet, respectively. Similarly, there was a 98% increase in plant DW of foxtail millet compared to proso millet (Table 3). When examining RMR (root DW relative to total plant DW), significant main effects and two-way interactions between S x M and M x N were observed (Table 3). In all three millet species, there was a tendency for RMR to increase when the plants were cultivated under moisture-deficient conditions compared to well-watered conditions.

For most plant species, growth and root traits are impaired by drought, regardless of N availability, with a more pronounced effect under low-N conditions. It is well-documented that root traits play a crucial role in plant productivity during drought (Steinemann *et al*., 2015; Zheng *et al*., 2017), and the application of sufficient amounts of nutrients can potentially mitigate the adverse impacts of water-deficit by enhancing root growth and water use efficiency (Luo *et al*., 2013; Tran *et al*., 2014; Ding *et al*., 2015). For example, N application stimulated root growth and enhanced root plasticity under drought conditions, maintaining plant growth and dry matter production (Tran *et al*., 2014). Furthermore, under drought conditions, root parameters such as root length, root surface area, number of root tips, fine root length, and fine root surface area were all increased with adequate N supplementation (Song *et al*., 2019). Similarly, the tendency to enhance root biomass of finger millet under drought with N supplementation (Table 3) suggests that optimal N nutrition may partially alleviate the adverse effects of drought stress on root development, thereby improving N nutrition under moisture-limited conditions. However, the present experiment was conducted in pots, which can strongly restrict root growth and alter natural soil water and nutrient dynamics. Consequently, the responses observed in this study may not fully represent root growth behavior under field conditions. Therefore, further research under field-based experimental settings, where root growth is not physically constrained as in pot experiments, is necessary to validate and better understand these responses.

Previous studies have demonstrated that plants exhibit higher dry matter distribution and accumulation under well-watered conditions than under moisture-stressed conditions, resulting in greater crop yields in environments with adequate moisture. Contrary to this common phenomenon in most crop species cultivated worldwide, a significant reduction of DW was not observed in any millet species in response to moisture limitation (Table 3). The results of this study are in line with Matsuura and An (2019), who demonstrated strong dehydration tolerance of foxtail millet and proso millet to severe soil drying. In their study, both species maintained a similar number of grains per panicle across well-watered and water-stressed conditions and did not reduce dry matter production and the partitioning of dry matter to the panicle after heading in response to the severe soil drying, where soil moisture dropped to 20% FC. In the present study, in each N level, all three millet species maintained similar dry weight irrespective of the two moisture regimes (Table 3). However, in each moisture regime, N-limitation marked a significant reduction of plant dry matter for finger millet and foxtail millet, indicating that these two species cannot tolerate N-deficit conditions in the growing environment. Therefore, even under drought conditions, finger millet could end up with significantly lower biomass yield if N is limited. This may be attributed to the role of N in mitigating the adverse effects of drought stress in millet plants, as adequate N supply can enhance osmoregulation, reduce lipid peroxidation, and improve key physiological processes under drought stress (Nematpour *et al*., 2019).

In contrast to the behavior of finger millet and foxtail millet, proso millet sustained a similar level of plant biomass accumulation across all combinations of moisture and N treatments (Table 3), indicating its ability to perform better in moisture- and N co-limited conditions. Low nutrient requirement, a short growing season, and highly efficient C4 photosynthesis are key traits that enable proso millet to adapt well to dry-land farming, particularly in the semi-arid areas (Kole *et al*., 2015; Rajput *et al*., 2016). In addition, the relatively lower plant biomass observed in proso millet compared with the other two millet species evaluated in this study may reduce its N demand for biomass production and physiological functioning. Together, these characteristics contributed to the superior performance of proso millet under conditions of simultaneous moisture- and N-limitation. The results of the present study indicate that, compared with finger millet and foxtail millet, proso millet may represent a more suitable candidate for crop production systems in resource-poor drylands where water- and N-limitations frequently co-occur. In this experiment, panicle dry weight was used as an indicator of reproductive biomass, allowing a comparative assessment of drought effects across treatments. However, additional parameters such as grain yield, grain number per panicle, and harvest index would provide a more comprehensive evaluation of crop productivity under combined moisture- and N-limitations. Furthermore, because the present experiment primarily focused on plant growth, N dynamics, and reproductive biomass, future studies incorporating detailed physiological measurements would be valuable for improving the understanding of the mechanisms underlying drought responses in millet species.

Organ-specific N allocation in millet species under different moisture and N treatment combinations

Nitrogen concentrations of roots, shoots, and panicles were significantly affected by species, moisture level, and N treatment. A significant two-way interaction between millet species and N level was observed for both root and panicle N concentrations (Table 2). N-limitation in soil resulted in a considerable drop in N content in the root, shoot, and panicle of finger millet under both well-watered and drought conditions (Figure 1). However, except for root N content under N-added conditions, drought stress had no huge impact on the N content of plant organs of finger millet. Regardless of the moisture and N treatments, proso millet was able to maintain similar organ N content in the present study. Similar to the response of finger millet, foxtail millet also decreased the N content of the shoot and panicle in response to N-limitation, but not to moisture treatment (Figure 1). When averaged across the two millet species, finger millet and foxtail millet showed a 53% and 60% decline, respectively, in N content of the shoot and panicle under well-watered conditions when subjected to N-limitation. Similarly, the respective reductions under drought stress were 56% and 61% (Figure 1).

Table 2. Significance of different sources of variability

Parameter	Source of variability						
	S	M	N	S x M	S x N	M x N	S x M x N
Root dry weight (g/plant)	***	***	ns	ns	***	***	***
Shoot dry weight (g/plant)	***	ns	***	ns	*	ns	ns
Panicle dry weight (g/plant)	***	ns	***	ns	***	ns	ns
Total plant dry weight (g/plant)	***	ns	***	ns	***	ns	ns
Root mass ratio	***	***	***	ns	***	**	ns
Root N concentration (mg-N/g-DW)	*	*	***	ns	**	ns	ns
Shoot N concentration (mg-N/g-DW)	*	*	***	ns	ns	ns	ns
Panicle N concentration (mg-N/g-DW)	*	*	***	ns	*	ns	ns
Root N content (mg-N/Plant)	*	ns	***	ns	**	ns	ns
Shoot N content (mg-N/Plant)	*	ns	***	ns	**	ns	ns
Panicle N content (mg-N/Plant)	*	ns	***	ns	**	ns	ns
Plant N uptake (mg-N/pot)	*	ns	***	ns	**	ns	ns
N use efficiency (g-DW/mg-N)	*	ns	***	ns	**	ns	ns

Significant effects are indicated for species (S), moisture (M), nitrogen (N) treatments, and their interactions (ns, no significant difference; *, P<0.05; **, P<0.01; ***, P<0.001).

Table 3. Dry weight (DW) of different plant organs and root mass ratio of three millet species cultivated under different moisture and nitrogen levels. Values represent the mean of three replicates ± SE (Standard error)

Species	Moisture	Nitrogen	Dry weight (g/plant)				Root Mass Ratio
			Root DW	Shoot DW	Panicle DW	Total Plant DW	
Finger millet	80% FC	N+	4.21 ± 0.08^{b}	12.5 ± 0.51^{a}	8.7 ± 0.62^{a}	25.5 ± 1.15^{a}	0.17 ± 0.01^{b}
		N0	3.85 ± 0.08^{b}	6.4 ± 0.34^{d}	4.6 ± 0.28^{c}	14.9 ± 0.62^{c}	0.26 ± 0.01^{a}
	40% FC	N+	5.61 ± 0.02^{a}	10.7 ± 0.19^{b}	8.6 ± 0.36^{a}	24.9 ± 1.34^{a}	0.23 ± 0.01^{a}
		N0	3.71 ± 0.04^{b}	6.1 ± 0.16^{d}	4.6 ± 0.14^{c}	14.3 ± 0.74^{c}	0.26 ± 0.01^{a}
Proso millet	80% FC	N+	0.33 ± 0.04^{f}	2.5 ± 0.13^{e}	4.3 ± 0.03^{c}	7.1 ± 0.12^{c}	0.05 ± 0.00^{f}
		N0	0.41 ± 0.02^{f}	2.3 ± 0.03^{e}	4.2 ± 0.24^{c}	6.9 ± 0.28^{c}	0.06 ± 0.00^{ef}
	40% FC	N+	0.54 ± 0.02^{ef}	2.2 ± 0.03^{e}	4.1 ± 0.09^{c}	6.9 ± 0.09^{c}	0.08 ± 0.00^{cdef}
		N0	0.51 ± 0.08^{ef}	2.2 ± 0.09^{e}	4.1 ± 0.12^{c}	6.7 ± 0.17 ^{c}	0.07 ± 0.01^{cdef}
Foxtail millet	80% FC	N+	1.13 ± 0.07^{cd}	8.3 ± 0.43^{c}	7.5 ± 0.29^{ab}	16.9 ± 0.78^{ab}	0.07 ± 0.01^{def}
		N0	1.01 ± 0.01^{de}	5.8 ± 0.13^{d}	4.0 ± 0.23^{c}	10.9 ± 0.82^{c}	0.09 ± 0.01^{cde}
	40% FC	N+	1.59 ± 0.2 ^{c}	8.0 ± 0.32^{c}	7.0 ± 0.34^{b}	16.6 ± 0. 53^{b}	0.10 ± 0.02^{cd}
		N0	1.12 ± 0.09^{cd}	5.5 ± 0.17^{d}	3.7 ± 0.19^{c}	10.3 ± 0.45^{c}	0.11 ± 0.01^{c}

Values in a column not followed by a common letter are significantly different (P < 0.05). *FC* Field capacity, *N+* N applied condition, *N0* N not-applied condition

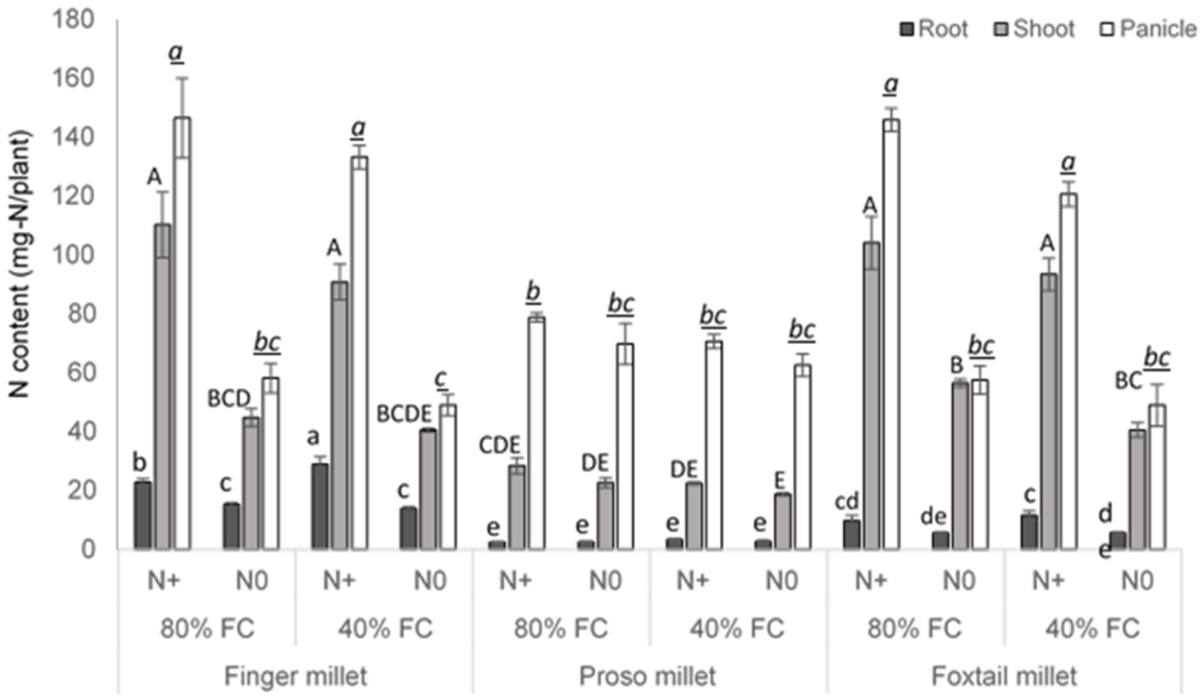

Figure 1: Nitrogen content of different plant organs (root, shoot, and panicle) of three millet species cultivated under different moisture and N levels. Means followed by the same letters are not significantly different at p<0.05. Error bars represent the standard error (S.E.; n = 3). Statistical analysis was conducted separately for each plant organ. *FC*:Field capacity, *N+*:N applied condition, *N0*:N not-applied condition

In all three millet species, the percentage allocation of N in the roots did not significantly vary across different combinations of moisture and N (Figure 2). Among the three millet species, finger millet had the highest percentage of N allocated to the roots compared to proso millet and foxtail millet. Proso millet and foxtail millet shared the similarity in the percentage allocation of N in the root system. The lowest percentage of N allocation in the shoot was recorded in proso millet, which did not significantly vary under different treatment combinations of moisture and N. Both finger millet and foxtail millet allocated a remarkably greater fraction of N to the shoot in comparison with proso millet (Figure 2). However, the percentage of N allocation in these two species did not vary across different treatment combinations. N allocation to panicle in terms of percentage from the total plant N was greatest in proso millet and was significantly different from those of the other two species (Figure 2). This ability of greater N allocation to panicles would partly explain the N-deficiency tolerance of proso millet. In the case of P, it has been well-documented that plants adapted to P-impoverished habitats accumulate significantly greater fractions of P in their reproductive structures, including seeds, while maintaining very low P content in leaves (Lambers *et al.*, 2015), which facilitates early establishment of seedlings in P-deficient lands.

Total plant N uptake and N use efficiency in plant biomass production of millet species under different moisture and N levels

Nitrogen uptake by plants per pot and N use efficiency (NUE) in plant biomass production of millet species were affected by the species, N treatment, and their interaction (Table 2). Soil moisture level had no significant impact on total plant N uptake and NUE for biomass production. Irrespective of the moisture treatment, finger millet and foxtail millet recorded comparatively greater plant N uptake compared to proso millet under N-added conditions (Figure 3). When averaged across the two moisture treatments, finger millet and foxtail millet had respectively 158% and 135% plant N uptake compared to proso millet in N-added conditions. When N was not supplied to the growth medium, all millet species tended to maintain similar plant N uptake from the pot. Across two moisture regimes, finger millet cultivated under N-limited conditions had 58% reduction in N uptake than that grown with N supplement. The relevant reduction for foxtail millet was 53%. Among the three millets, proso millet did not exhibit a significant response to N addition or moisture treatment and maintained similar N uptake across all treatment combinations (Figure 3). N-limited conditions enhanced the use efficiency of acquired N in plant biomass production by both finger millet and foxtail millet (Figure 4). Similar to its N uptake behavior, proso millet had similar NUE across all treatment combinations. Moisture stress had no significant impact on NUE of any of the three millet species used in the study (Figure 4). The lower total N uptake by finger millet and foxtail millet under N-limited conditions led to their higher NUE in plant biomass production, indicating that plants with reduced N uptake utilized acquired N more efficiently in biomass production. These findings indicate that plants tend to enhance N use efficiency for biomass production when they cannot acquire sufficient amounts of nutrients from their growing environment. This phenomenon has been observed in several plant species, including widely cultivated crops around the world (Maillard *et al*., 2015; Nitschke *et al*., 2017; Nieves-Cordones *et al*., 2020).

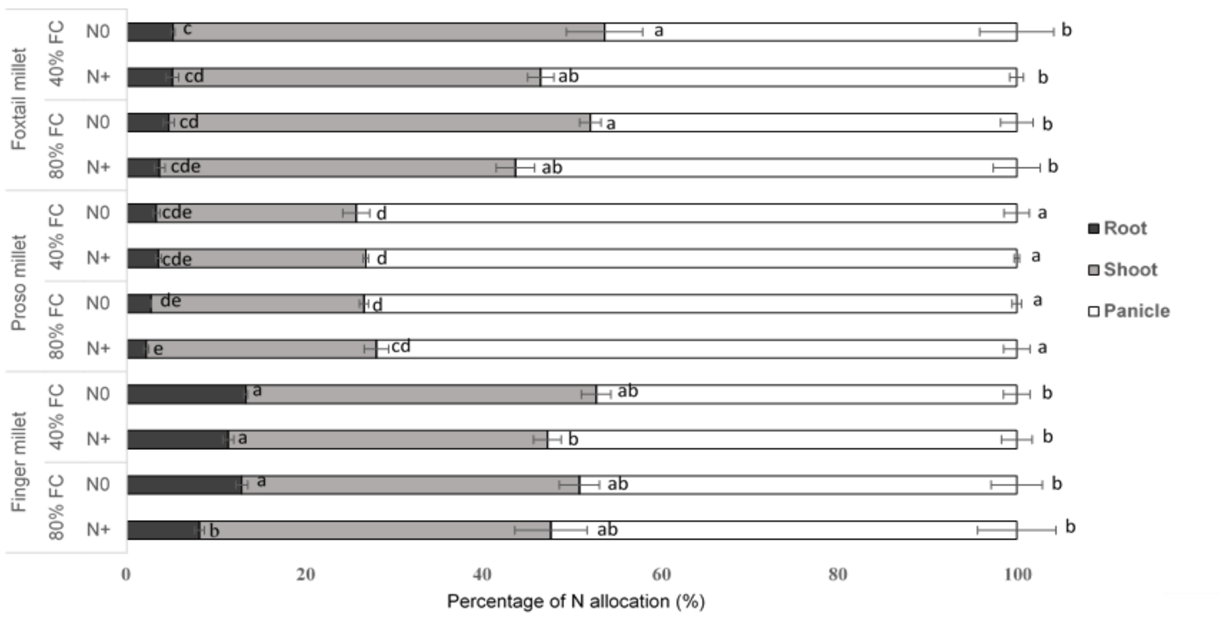

Figure 2. Percentage of N allocation to different plant organs (roots, shoots, and panicles) from total plant N of three millet species cultivated under different moisture and N levels. Means followed by the same letters in each plant organ are not significantly different at *P>0.05*. Error bars represent the standard error (S.E.; n = 3). Statistical analysis was conducted separately for each plant organ. *FC:* Field capacity, *N+*:N applied condition, *N0*:N not-applied condition

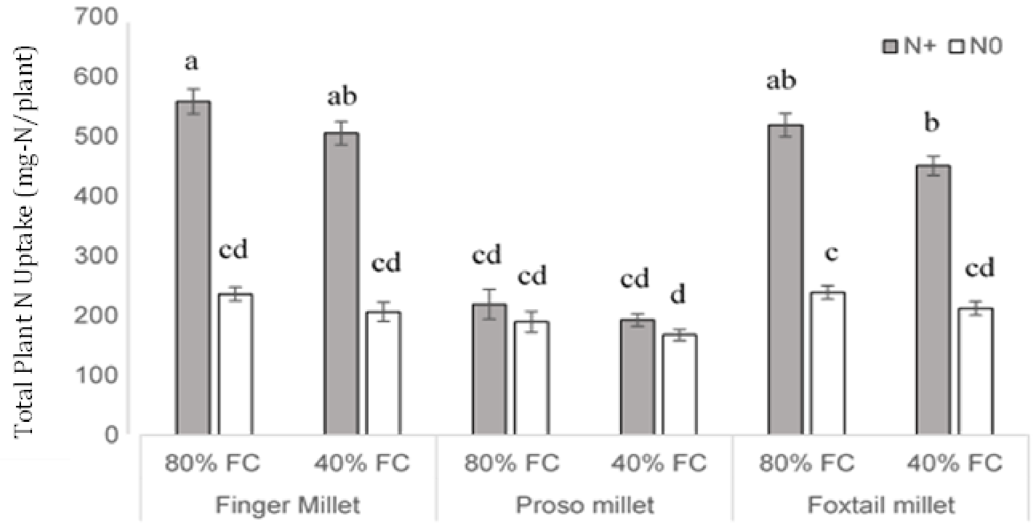

Figure 3. Total plant N uptake by three millet species cultivated under different moisture and N levels. Means followed by the same letters are not significantly different at *P*<0.05. Error bars represent the standard error (S.E.; n = 3). *FC:*Field capacity, *N+*:N applied condition, *N0*:N not-applied condition

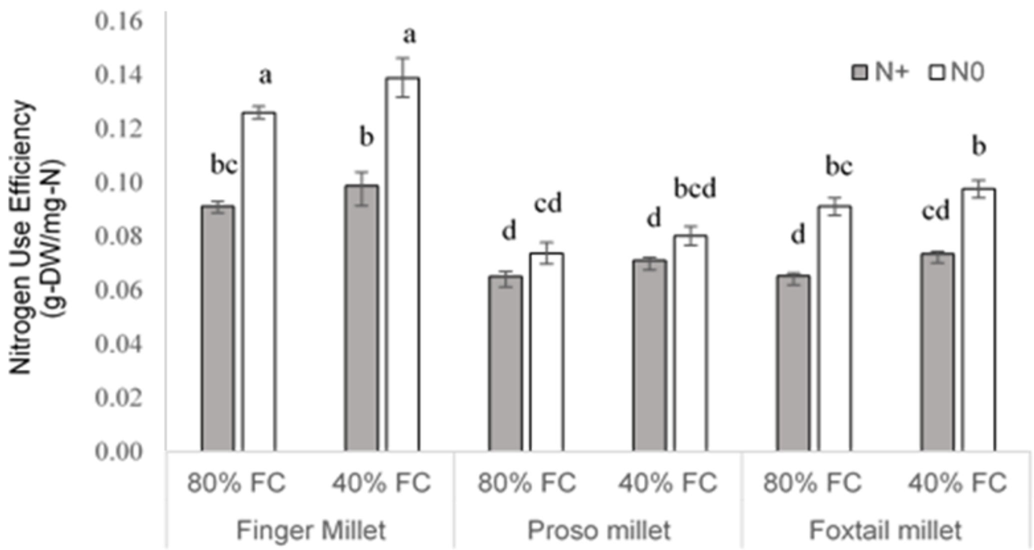

Figure 4. Nitrogen use efficiency in biomass formation by three millet species cultivated under different moisture and N levels. Means followed by the same letters are not significantly different at *P*>0.05. Error bars represent the standard error (S.E.; n = 3). *FC:* Field capacity, *N+:* N applied condition, *N0:* N not-applied condition

CONCLUSIONS

All three millet varieties produced comparable panicle dry weights across two moisture regimes, indicating their ability to maintain panicle biomass under 40% FC, similar to that observed under 80% FC. Selected varieties of finger millet and foxtail millet showed a significant reduction in panicle dry weight under N-limited conditions, whereas the proso millet variety maintained a similar panicle dry weight despite N-limitation, indicating its ability to perform better under N-deficiency. Total plant N uptake of finger millet and foxtail millet decreased due to N-limitation under both moisture regimes. In contrast, proso millet showed no significant change in N uptake in response to either N addition or moisture treatment and was able to maintain consistent N uptake across all treatment combinations. Finger millet and foxtail millet demonstrated greater NUE compared to proso millet, which had a similar NUE across moisture and N treatments. The findings confirm that all three varieties of millet species are tolerant to moisture-limited conditions, with proso millet being particularly well-adapted to environments where moisture and N limitations co-occur. However, the study did not explore the physiological mechanisms underlying improved N uptake by proso millet irrespective of the moisture and N-deficiency, and improved NUE, particularly in varieties of finger millet and foxtail millet under N-limited conditions. As millets are known to be climate-smart future crops, further exploration into physiological mechanisms governing improved N uptake and NUE by millets under co-limitation of N and moisture will help to improve the mechanistic understanding of drought stress tolerance of millets. Furthermore, future studies incorporating a wider range of genotypes would be valuable for validating these findings.

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