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# Long-term integrated nutrient management enhances physiological efficiency and yield gains in pearl millet (*Pennisetum glaucum*)–wheat (*Triticum aestivum*)

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ABSTRACT

Long-term nutrient management practices critically influence soil health, crop physiological traits, and ultimately grain yield sustainability under semi-arid conditions. A long-term field experiment, established in 1985 was conducted on integrated nutrient management (INM) in a pearl millet (*Pennisetum glaucum* L.)–wheat (*Triticum aestivum* L.) cropping system. Physiological parameters, yield and photochemical quantum yield of pearl millet [rainy (*kharif*) 2021–2022 and 2022–2023] and wheat [winter (*rabi*) 2020–21 and 2021–22] were evaluated for two consecutive cropping seasons. Results showed that, the combination of inorganic fertilisers with organic sources significantly enhanced physiological performance over fertiliser-alone treatments. For instance, the highest assimilation rates in pearl millet (9.34 µmol/$m^2$/sec) and wheat (14.10 µmol/$m^2$/sec) were recorded under the integrated nutrient regime with 50% N substituted by FYM, representing a 53–96% increase over the control. Similarly, maximum stomatal conductance and relative water content were observed in treatments involving FYM and wheat straw combinations, reflecting improved plant water status and stress tolerance. Grain yield improvements were substantial: pooled yields in pearl millet increased, from 1,497 kg/ha (control) to 3,352 kg/ha (50% N via FYM + 50% inorganic), while wheat yields rose from 1,741 kg/ha to 5,108 kg/ha under the same treatment sequence (residual effect in wheat), showing a remarkable 193% increase. Treatments involving partial substitution of chemical fertilisers with organics consistently maintained high yields, demonstrating the synergistic effect of integrated nutrient use. Overall, the study highlights that INM significantly enhances physiological efficiency and grain productivity in pearl millet–wheat systems, offering a robust pathway for sustainable intensification in semi-arid agro-ecosystems.

**Keywords**: Grain yield, Physiological traits, Sustainable cropping systems

The global surge in food production, largely driven by the extensive use of chemical fertilisers, has come at the cost soil health, resulting in soil nutrient depletion and, ultimately compromising long-term crop yields. Given the growing population and increasing food demand, sustainable farming practices that prioritise soil health, nutrient management and organic matter integration are essential to ensure food security and environmental sustainability. Although integrated nutrient management (INM) has been widely advocated for improving nutrient-use efficiency (NUE) and sustaining crop productivity, a mechanistic understanding of long-term nutrient management effect on crop physiological processes remains limited. Crop productivity is strongly influenced by physiological traits such as chlorophyll content, photosynthetic activity, stomatal conductance, and plant water status, all of which are highly sensitive to environmental stresses, particularly drought (Caser *et al.* 2018). Decline in these physiological attributes reduce carbon assimilation and biomass production, ultimately limiting crop yield.

The impact of integrated nutrient management (INM) on soil properties, such as improved soil structure, enhanced water retention, and increased nutrient availability, is well-documented in scientific literature (Ahlawat *et al.* 2023). However, comparatively fewer studies have investigated the improvements in soil properties under long-term INM translate in to enhanced crop physiological performance and sustained productivity. While improved soil health is generally associated with better crop performance, the physiological mechanisms underpinning these responses remain inadequately understood. Therefore, the present study evaluated the long-term effects of INM on crop physiological traits and productivity in a pearl millet–wheat cropping system, providing insights into the physiological mechanisms underlying sustained productivity.

## MATERIALS AND METHODS

The experiment was conducted during rainy (*kharif*) season of 2021–2022 and 2022–2023 and winter (*rabi*)

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season of 2020–21 and 2021–22 at the Research Farm of the Department of Agronomy, CCS Haryana Agricultural University, Hisar (29°08'58" N, 75°40'51" E), Haryana. The long-term experiment was initiated during *kharif* 1985 and has been maintained under the same treatment structure since its establishment. The experimental site falls under a hot semi-arid climate (Köppen BSh), characterised by hot summers and cool winters. The mean annual rainfall was approximately 443 mm, of which nearly 80% was received during the south-west monsoon season (July–September). The soil had been classified as a *Typic Ustochrept*. Before the initiation of the long-term experiment, the surface soil (0–15 cm) had an organic carbon content of 2.9 g/kg, bulk density of 1.51 $Mg/m^3$ and available N, $P_2O_5$, and $K_2O$ contents of 128, 25.12, and 361 kg/ha, respectively. The field experiment was laid out in a randomised block design (RBD) with three replications comprising 11 nutrient management treatments (Table 1). Each experimental plot measured 10 m × 8 m, and the original treatment layout had been maintained throughout the experimental period.

Organic nutrient sources, including Farm Yard Manure (FYM), wheat straw and green manure, were applied annually 35–40 days before sowing (DBS) of pearl millet, based on their nitrogen (N) content. Wheat straw was shredded and incorporated into the soil, while dhaincha (*Sesbania* spp.) was grown as a green manure crop, harvested after 45 days, chopped, and then integrated into the soil. Inorganic fertilisers: urea (46% N), Single Super Phosphate (SSP, 16% $P_2O_5$) and Muriate of Potash (MOP, 60% $K_2O$) were applied to meet crop nutrient requirements.

The recommended dose of fertilisers (RDF) for pearl millet and wheat was 125 kg/ha N, 62.5 kg/ha $P_2O_5$, 30 kg/ha $K_2O$; and 150 kg/ha N, 60 kg/ha, $P_2O_5$ and 60 kg/ha $K_2O$, respectively with 1/2 nitrogen and complete dose of phosphorus and potassium at the time of sowing and the remaining nitrogen was applied post-irrigation. 9.3 t/ha FYM, 16.8 t/ha wheat straw, and 2.8 t/ha green manure were used to provide 50% of the N from organic sources while 4.6 t/ha FYM, 8.4 t/ha wheat straw, and 1.4 t/ha green manure were utilised for a 25% organic N substitute.

*Measurement of physiological parameters*: The physiological traits of wheat and pearl millet plants were assessed at the anthesis stage.

*Chlorophyll content*: Fresh green leaves were cut into small segments and immersed in 5 mL of dimethyl sulfoxide (DMSO) overnight for chlorophyll extraction. The absorbance of the extracted chlorophyll solution was then recorded at 665 nm and 645 nm using a spectrophotometer (Barnes *et al.* 1992).

*Relative water content*: Immediately after sampling, the fresh weight (FW) of leaf pieces was measured. The samples were then floated in deionized water for 4 hr to achieve full turgidity, after which the turgid weight (TW) was recorded. Finally, the leaves were oven-dried at 60°C for 48 h to obtain the dry weight (DW). Relative water content (RWC) was calculated using the formula:

$$RWC\ (\%) = (FW - DW) / (TW - DW) \times 100$$

*Photochemical quantum yield*: Photochemical quantum yield was measured at mid-day on intact plants using a portable chlorophyll fluorometer.

*Assimilation rate, transpiration rate, and stomatal conductance*: Measurements of assimilation rate, transpiration rate and stomatal conductance were recorded on intact leaves using an Infrared Gas Analyser.

The experimental data were statistically analysed using

Table 1 Treatment details

| Treatments | *Kharif* | *Rabi* |
|---|---|---|
| $T_1$ | Control (no fertiliser) | Control (no fertiliser) |
| $T_2$ | 50% recommended dose of NPK through fertilisers | 50% recommended dose of NPK through fertilisers |
| $T_3$ | 50% recommended dose of NPK through fertilisers | Recommended dose of NPK through fertilisers |
| $T_4$ | 75% recommended dose of NPK through fertilisers | 75% recommended dose of NPK through fertilisers |
| $T_5$ | Recommended dose of NPK through fertilisers | Recommended dose of NPK through fertilisers |
| $T_6$ | 50% recommended dose of NPK through fertilisers + 50% N through FYM | Recommended dose of NPK through fertilisers |
| $T_7$ | 75% recommended dose of NPK through fertilisers + 25% N through FYM | 75% recommended dose of NPK through fertilisers |
| $T_8$ | 50% recommended dose of NPK through fertilisers + 50% N through wheat straw | Recommended dose of NPK through fertilisers |
| $T_9$ | 75% recommended dose of NPK through fertilisers + 25% N through wheat straw | 75% recommended dose of NPK through fertilisers |
| $T_{10}$ | 50% recommended dose of NPK through fertilisers + 50% N through green manure | Recommended dose of NPK through fertilisers |
| $T_{11}$ | 75% recommended dose of NPK through fertilisers + 25% N through green manure | 75% recommended dose of NPK through fertilisers |

analysis of variance (ANOVA). Treatment effects were tested for significance using the F-test and differences between treatment means were compared using the critical difference (CD) test. Means were separated at the $p<0.05$ level through Duncan's Multiple Range Test (DMRT).

## RESULTS AND DISCUSSION

*Chlorophyll content*: In pearl millet (Table 2), the lowest chlorophyll content was recorded in $T_1$ (1.38 mg/g FW) and $T_2$ (1.46 mg/g FW), which can be attributed to the absence or inadequacy of external nutrient supplementation, particularly nitrogen, a key component of chlorophyll molecules. In contrast, the highest chlorophyll content was observed in $T_6$ (1.95 mg/g FW), where 50% of the recommended nitrogen was substituted with FYM. This likely reflects enhanced nutrient availability and uptake, as FYM not only supplies nitrogen but also improves microbial activity and soil organic matter, facilitating better root growth and nutrient absorption. Treatments $T_8$ (1.84 mg/g FW) and $T_{10}$ (1.81 mg/g FW) also showed high chlorophyll values, indicating that partial substitution of nitrogen through wheat straw and green manure can sustain or even enhance chlorophyll synthesis, likely due to improved soil moisture retention and slow nutrient release.

In wheat (Table 3), a similar pattern emerged. The lowest chlorophyll content was noted in $T_1$ (1.48 mg/g FW) and $T_2$ (1.56 mg/g FW), again reflecting nitrogen deficiency under control or minimally fertilised conditions. The highest value was recorded in $T_6$ (2.34 mg/g FW), reinforcing the superior performance of FYM in enhancing physiological traits through improved soil fertility and microbial dynamics. Other organic substitution treatments like $T_8$ (2.21 mg/g FW), $T_{10}$ (2.12 mg/g FW), and $T_{11}$ (1.87 mg/g FW) also exhibited high to moderately high chlorophyll levels, emphasising the importance of sustained nitrogen availability from organic sources. The purely mineral fertiliser treatments $T_3$ to $T_5$ ranged between 1.61 and 1.81 mg/g FW, supporting a decent chlorophyll concentration but not matching the performance of organic-enriched treatments.

Application of FYM and other organic inputs significantly enhances the water-holding capacity and nutrient availability of the soil (Ahlawat *et al.* 2023), thereby creating a favourable rhizosphere environment for sustained crop growth and physiological activity. This improved soil environment facilitates greater nutrient uptake and maintains leaf hydration thereby supporting sustained physiological activity and efficient photosynthesis. In addition, gradual mineralisation of organic amendments ensures a steady and prolonged release of nutrients, particularly nitrogen, which is an essential constituent of chlorophyll molecules and photosynthetic proteins, thereby promoting chlorophyll biosynthesis and maintaining photosynthetic capacity (Bhardwaj *et al.* 2023). Consequently, plants under INM practices exhibit higher chlorophyll content, improved photosynthetic efficiency, and greater resilience compared to those solely dependent on inorganic fertilisers. The present findings are consistent with earlier reports demonstrating that integrated application of organic and inorganic nutrient sources enhances chlorophyll content and photosynthetic performance through sustained nutrient availability and improved physiological functioning in cereal crops (Gorooei *et al.* 2023).

*Assimilation rate*: In pearl millet, the lowest assimilation rate was observed under $T_1$ (control) at 6.09 μmol/m$^2$/sec,

Table 2 Effect of long term INM on chlorophyll content, assimilation rate, and photochemical quantum yield in pearl millet

| Treatments | Chlorophyll content (mg/g FW) | | | Assimilation rate (μmol/m$^2$/sec) | | | Photochemical quantum yield (Fv/Fm) | | |
|---|---|---|---|---|---|---|---|---|---|
| | 2021–22 | 2022–23 | Pooled | 2021–22 | 2022–23 | Pooled | 2021–22 | 2022–23 | Pooled |
| $T_1$ | 1.35 | 1.42 | 1.38$^{f}$ | 6.01 | 6.17 | 6.09$^{g}$ | 0.492 | 0.510 | 0.501$^{e}$ |
| $T_2$ | 1.42 | 1.51 | 1.46$^{ef}$ | 6.39 | 6.49 | 6.44$^{g}$ | 0.512 | 0.539 | 0.526$^{e}$ |
| $T_3$ | 1.49 | 1.54 | 1.52$^{de}$ | 6.98 | 7.08 | 7.03$^{f}$ | 0.530 | 0.587 | 0.559$^{de}$ |
| $T_4$ | 1.53 | 1.59 | 1.56$^{d}$ | 7.16 | 7.37 | 7.27$^{ef}$ | 0.571 | 0.596 | 0.584$^{cd}$ |
| $T_5$ | 1.62 | 1.71 | 1.67$^{c}$ | 7.21 | 7.62 | 7.42$^{de}$ | 0.598 | 0.615 | 0.607$^{bcd}$ |
| $T_6$ | 1.92 | 1.98 | 1.95$^{a}$ | 9.30 | 9.38 | 9.34$^{a}$ | 0.695 | 0.698 | 0.696$^{a}$ |
| $T_7$ | 1.78 | 1.80 | 1.79$^{b}$ | 7.79 | 7.81 | 7.80$^{c}$ | 0.621 | 0.627 | 0.624$^{bc}$ |
| $T_8$ | 1.82 | 1.86 | 1.84$^{b}$ | 8.19 | 8.55 | 8.37$^{b}$ | 0.650 | 0.673 | 0.662$^{ab}$ |
| $T_9$ | 1.68 | 1.73 | 1.71$^{c}$ | 7.66 | 7.67 | 7.67$^{cd}$ | 0.603 | 0.625 | 0.614$^{bcd}$ |
| $T_{10}$ | 1.80 | 1.81 | 1.81$^{b}$ | 7.82 | 8.12 | 7.97$^{c}$ | 0.630 | 0.665 | 0.648$^{ab}$ |
| $T_{11}$ | 1.65 | 1.72 | 1.69$^{c}$ | 7.28 | 7.62 | 7.45$^{de}$ | 0.600 | 0.623 | 0.612$^{bcd}$ |
| CD ($p$=0.05) | 0.07 | 0.07 | | 0.32 | 0.33 | | 0.027 | 0.026 | |

Values followed by similar letters in a column indicate non-significant difference ($p<0.05$) according to Duncan Multiple Range test (DMRT) for separation of means. Refer to Table 1 for treatment details.

while the highest was recorded under $T_6$ (9.34 µmol/m$^2$/sec), where 50% nitrogen was supplied through FYM (Table 2). This substantial increase can be attributed to improved soil organic matter and microbial activity under FYM application, which enhance root health, nutrient availability and ultimately photosynthetic capacity. Other treatments incorporating organic sources, $T_8$ (wheat straw, 50% N replacement); $T_{10}$ (green manure, 50% N replacement); and $T_7$ (FYM, 25% N replacement) also exhibited elevated assimilation rates (8.37, 7.97, and 7.80 µmol/m$^2$/sec, respectively), suggesting that even partial integration of organics supports sustained physiological activity. These treatments likely improved leaf area development, chlorophyll content and enzymatic efficiency. In contrast, purely inorganic treatments like $T_2$ and $T_3$ had relatively lower assimilation rates (6.44 and 7.03 µmol/m²/sec), indicating that while mineral nutrients provide immediate benefits, their long-term effect on soil health and photosynthetic potential may be limited.

A similar pattern was evident in wheat (Table 3), where $T_6$ again registered the highest assimilation rate of 14.10 µmol/m$^2$/sec, reinforcing the photosynthetic benefits of FYM-enriched nutrition. Treatments $T_8$, $T_{10}$, and $T_7$ closely followed with assimilation values of 13.54, 13.19, and 12.10 µmol/m$^2$/sec, highlighting the synergistic effects of combining organic residues with mineral fertilisers. These higher values reflect the improved stomatal conductance and chloroplast functioning under organically-amended conditions. In contrast, treatments relying solely on chemical fertilisers, such as $T_3$, $T_4$, and $T_5$, recorded moderate rates (11.25, 10.63, and 11.37 µmol/m²/sec, respectively), and the lowest was again seen in $T_1$ (control) at 7.20 µmol/m$^2$/sec, underscoring the importance of nutrient input in driving photosynthesis.

The significantly higher assimilation rates observed under long-term INM indicate that the benefits of FYM and crop residue incorporation extend beyond improved soil fertility to enhanced photosynthetic functioning. In addition to increasing chlorophyll concentration, the gradual mineralisation of organic amendments ensures a sustained supply of nitrogen throughout the crop growth period, thereby supporting the synthesis of chlorophyll, Rubisco and other photosynthetic proteins which collectively determine leaf photosynthetic capacity (Wang *et al.* 2016). Nitrogen is particularly important because a substantial proportion of leaf nitrogen is invested in the photosynthetic apparatus, and inadequate nitrogen availability directly reduces carbon assimilation by limiting Rubisco activity and photosynthetic enzyme content (Evans 1989). Furthermore, long-term INM improves soil biological activity, root growth and nutrient acquisition, while enhanced soil moisture retention helps maintain stomatal conductance and facilitates greater $CO_2$ diffusion into the mesophyll, thereby minimising both stomatal and biochemical limitations to photosynthesis (Reddy *et al.* 2004, Flexas *et al.* 2004). Consequently, substitution of 25–50% mineral nitrogen through FYM and crop residues substantially enhanced assimilation rates in both pearl millet and wheat, demonstrating that balanced nutrient management improves photosynthetic efficiency through coordinated enhancement of soil health, nitrogen use efficiency and carbon assimilation, ultimately leading to greater crop productivity.

*Photochemical quantum yield*: The pooled data demonstrated significant variation in photochemical quantum yield (Fv/Fm) among different nutrient management treatments in both pearl millet and wheat, indicating that photosynthetic efficiency is strongly influenced by the

Table 3 Effect of long term INM on chlorophyll content, assimilation rate, and photochemical quantum yield in wheat

| Treatments | Chlorophyll content (mg/g FW) | | | Assimilation rate (µmol/m$^2$/sec) | | | Photochemical quantum yield (Fv/Fm) | | |
|---|---|---|---|---|---|---|---|---|---|
| | 2020–21 | 2021–22 | Pooled | 2020–21 | 2021–22 | Pooled | 2020–21 | 2021–22 | Pooled |
| $T_1$ | 1.45 | 1.52 | 1.48$^{h}$ | 7.10 | 7.29 | 7.20$^{g}$ | 0.696 | 0.707 | 0.702$^{c}$ |
| $T_2$ | 1.51 | 1.60 | 1.56$^{g}$ | 8.36 | 8.54 | 8.45$^{f}$ | 0.706 | 0.718 | 0.712$^{c}$ |
| $T_3$ | 1.76 | 1.82 | 1.79$^{f}$ | 11.06 | 11.43 | 11.25$^{d}$ | 0.742 | 0.751 | 0.747$^{cd}$ |
| $T_4$ | 1.58 | 1.64 | 1.61$^{g}$ | 10.70 | 10.56 | 10.63$^{e}$ | 0.728 | 0.741 | 0.735$^{d}$ |
| $T_5$ | 1.77 | 1.84 | 1.81$^{f}$ | 11.28 | 11.45 | 11.37$^{d}$ | 0.50 | 0.755 | 0.753$^{bc}$ |
| $T_6$ | 2.30 | 2.37 | 2.34$^{a}$ | 14.03 | 14.16 | 14.10$^{a}$ | 0.771 | 0.777 | 0.774$^{a}$ |
| $T_7$ | 1.97 | 2.00 | 1.99$^{d}$ | 12.17 | 12.02 | 12.10$^{c}$ | 0.760 | 0.767 | 0.764$^{abc}$ |
| $T_8$ | 2.19 | 2.22 | 2.21$^{b}$ | 13.22 | 13.86 | 13.54$^{b}$ | 0.764 | 0.771 | 0.768$^{ab}$ |
| $T_9$ | 1.87 | 1.93 | 1.90$^{e}$ | 11.99 | 12.19 | 12.09$^{c}$ | 0.758 | 0.765 | 0.762$^{abc}$ |
| $T_{10}$ | 2.11 | 2.13 | 2.12$^{c}$ | 12.94 | 13.43 | 13.19$^{b}$ | 0.761 | 0.771 | 0.766$^{abc}$ |
| $T_{11}$ | 1.83 | 1.91 | 1.87$^{e}$ | 11.29 | 11.82 | 11.56$^{d}$ | 0.753 | 0.762 | 0.758$^{abc}$ |
| CD ($p$=0.05) | 0.09 | 0.08 | | 0.50 | 0.52 | | 0.032 | 0.032 | |

Values followed by similar letters in a column indicate non-significant difference ($p$<0.05) according to Duncan Multiple Range test (DMRT) for separation of means. Refer to Table 1 for treatment details.

nature and balance of nutrient inputs. In pearl millet, (Fv/Fm) ranged from a minimum of 0.501 under the control treatment ($T_1$) to a maximum of 0.696 under $T_6$ (50% N through FYM + 50% RDF) (Table 2). Similarly, in wheat, (Fv/Fm) values ranged from 0.702 ($T_1$) to 0.774 ($T_6$), highlighting a consistent trend across both crops (Table 3). The consistently lowest (Fv/Fm) under control indicates that nutrient deficiency hampers the efficiency of photosystem II, possibly due to limited chlorophyll synthesis and impaired electron transport chain activity.

The crops treated with only fertilisers ($T_2$, $T_3$, $T_4$, $T_5$) recorded moderate (Fv/Fm) values of 0.526–0.607 in pearl millet and 0.712–0.753 in wheat. This suggests that although inorganic fertilisers improve photosynthetic performance over control, they are outperformed by integrated treatments involving organic nutrient sources. Treatments each incorporating 50% N from different organic sources ($T_6$, $T_8$, and $T_{10}$) consistently showed superior (Fv/Fm), with pearl millet values of 0.696, 0.662, and 0.648, and wheat values of 0.774, 0.768, and 0.766, respectively.

Interestingly, treatments with 25% N from organic sources ($T_7$, $T_9$, $T_{11}$) also showed improved (Fv/Fm) over sole fertiliser treatments, with pooled values between 0.612–0.624 in pearl millet and 0.758–0.764 in wheat. This reflects a dose-dependent response to organic integration, where even partial organic substitution supports microbial activity and soil structure, thereby improving nutrient synchrony and plant physiological responses.

Nitrogen deficiency critically impairs protein synthesis, triggering photodamage at the PSII reaction center and leading to photoinhibition, as evidenced by declining Fv/Fm ratios (Lawlor and Cornic 2002). This reduction reflects both PSII inactivation and diminished excitation energy transfer from light harvesting complex II (LHCII), exacerbated under water deficit due to reduced LHCII content (Govindjee 2004). Remarkably, the integration of organic amendments, especially at a 50% nitrogen substitution level, substantially boosts photochemical efficiency driven by improved nitrogen availability (Ahlawat *et al.* 2023), enhanced soil moisture conservation, sustained nutrient release, and a more active rhizosphere environment.

*Stomatal conductance*: In pearl millet, the lowest stomatal conductance was observed in $T_1$ (control) and $T_2$, recording 0.13 mol/m²/sec and 0.14 mol/m²/sec, respectively (Table 4). These lower values likely indicate restricted stomatal aperture due to suboptimal nutrient availability, which can limit $CO_2$ uptake and reduce photosynthetic performance. Conversely, the highest value was observed in $T_6$ (0.30 mol/$m^2$/sec), where 50% nitrogen was substituted with FYM. The enhanced stomatal conductance here could be attributed to improved soil structure, moisture retention, and microbial activity from FYM application, facilitating better root function and stomatal behaviour. Other treatments such as $T_8$ (0.27 mol/$m^2$/sec), $T_{10}$ (0.25 mol/$m^2$/sec), $T_7$ (0.24 mol/$m^2$/sec), and $T_{11}$ (0.22 mol/$m^2$/sec) also displayed moderate to high conductance, demonstrating that partial substitution of nitrogen through organics (wheat straw and green manure) promotes balanced plant physiological responses. Treatments with only inorganic fertilisation like $T_3$, $T_4$, and $T_5$ showed intermediate conductance levels (0.16 mol/$m^2$/sec, 0.20 mol/$m^2$/sec, and 0.21 mol/$m^2$/sec, respectively), further supporting the premise that mineral nutrition alone, while beneficial, may not fully optimise physiological performance over the long term.

Table 4 Effect of long term INM on stomatal conductance, transpiration rate, and relative water content in pearl millet

| Treatments | Stomatal conductance (mol/$m^2$/sec) | | | Transpiration rate (mmol/$m^2$/sec) | | | Relative water content (%) | | |
|---|---|---|---|---|---|---|---|---|---|
| | 2021–22 | 2022–23 | Pooled | 2021–22 | 2022–23 | Pooled | 2021–22 | 2022–23 | Pooled |
| $T_1$ | 0.13 | 0.13 | 0.13$^{e}$ | 3.89 | 4.02 | 3.96$^{f}$ | 53.15 | 54.40 | 53.78$^{g}$ |
| $T_2$ | 0.13 | 0.14 | 0.14$^{e}$ | 4.34 | 4.36 | 4.35$^{e}$ | 59.72 | 60.37 | 60.05$^{f}$ |
| $T_3$ | 0.16 | 0.16 | 0.16$^{de}$ | 5.14 | 5.29 | 5.22$^{d}$ | 60.28 | 61.33 | 60.80$^{ef}$ |
| $T_4$ | 0.20 | 0.20 | 0.20$^{cd}$ | 5.25 | 5.32 | 5.29$^{d}$ | 61.01 | 62.80 | 61.91$^{def}$ |
| $T_5$ | 0.20 | 0.21 | 0.21$^{bcd}$ | 5.46 | 5.83 | 5.65$^{c}$ | 62.07 | 64.51 | 63.29$^{cde}$ |
| $T_6$ | 0.30 | 0.29 | 0.30$^{a}$ | 6.15 | 6.28 | 6.22$^{a}$ | 70.02 | 71.45 | 70.74$^{a}$ |
| $T_7$ | 0.24 | 0.24 | 0.24$^{bc}$ | 5.91 | 6.05 | 5.98$^{b}$ | 65.05 | 67.04 | 66.05$^{bc}$ |
| $T_8$ | 0.26 | 0.27 | 0.27$^{ab}$ | 6.09 | 6.26 | 6.18$^{ab}$ | 68.04 | 69.10 | 68.57$^{ab}$ |
| $T_9$ | 0.22 | 0.22 | 0.22$^{bc}$ | 5.67 | 5.88 | 5.78$^{c}$ | 64.51 | 65.70 | 65.11$^{c}$ |
| $T_{10}$ | 0.24 | 0.25 | 0.25$^{abc}$ | 5.99 | 6.11 | 6.05$^{ab}$ | 67.50 | 69.05 | 68.28$^{ab}$ |
| $T_{11}$ | 0.21 | 0.23 | 0.22$^{bc}$ | 5.48 | 5.92 | 5.70$^{c}$ | 63.08 | 65.52 | 64.30$^{cd}$ |
| CD ($p$=0.05) | 0.01 | 0.01 | | 0.24 | 0.25 | | 2.75 | 2.82 | |

Values followed by similar letters in a column indicate non-significant difference ($p$<0.05) according to Duncan Multiple Range test (DMRT) for separation of means. Refer to Table 1 for treatment details.

Table 5 Effect of long term INM on stomatal conductance, transpiration rate, and relative water content in wheat

| Treatments | Stomatal conductance (mol/m$^2$/sec) | | | Transpiration rate (mmol/m$^2$/sec) | | | Relative water content (%) | | |
|---|---|---|---|---|---|---|---|---|---|
| | 2020–21 | 2021–22 | Pooled | 2020–21 | 2021–22 | Pooled | 2020–21 | 2021–22 | Pooled |
| $T_1$ | 0.20 | 0.19 | 0.20$^{f}$ | 5.60 | 5.78 | 5.69$^{f}$ | 60.15 | 60.33 | 60.24$^{d}$ |
| $T_2$ | 0.21 | 0.22 | 0.22$^{f}$ | 5.87 | 5.89 | 5.88$^{ef}$ | 61.10 | 64.45 | 62.78$^{d}$ |
| $T_3$ | 0.27 | 0.29 | 0.28$^{e}$ | 5.99 | 6.16 | 6.08$^{e}$ | 70.63 | 72.54 | 71.59$^{c}$ |
| $T_4$ | 0.30 | 0.30 | 0.30$^{de}$ | 6.37 | 6.46 | 6.42$^{d}$ | 70.99 | 71.61 | 71.30$^{c}$ |
| $T_5$ | 0.31 | 0.32 | 0.32$^{cde}$ | 6.65 | 6.73 | 6.69$^{cd}$ | 71.12 | 73.88 | 72.50$^{bc}$ |
| $T_6$ | 0.45 | 0.44 | 0.45$^{a}$ | 7.68 | 7.98 | 7.83$^{a}$ | 75.86 | 77.41 | 76.64$^{a}$ |
| $T_7$ | 0.36 | 0.36 | 0.36$^{bc}$ | 7.31 | 7.31 | 7.31$^{b}$ | 71.82 | 74.02 | 72.92$^{bc}$ |
| $T_8$ | 0.39 | 0.41 | 0.40$^{ab}$ | 7.55 | 7.92 | 7.74$^{a}$ | 75.32 | 76.50 | 75.91$^{ab}$ |
| $T_9$ | 0.35 | 0.35 | 0.35$^{bcd}$ | 7.25 | 7.43 | 7.34$^{b}$ | 71.36 | 73.96 | 72.66$^{bc}$ |
| $T_{10}$ | 0.36 | 0.38 | 0.37$^{bc}$ | 7.32 | 7.84 | 7.58$^{ab}$ | 74.57 | 76.08 | 75.33$^{ab}$ |
| $T_{11}$ | 0.35 | 0.34 | 0.35$^{bcd}$ | 6.90 | 6.96 | 6.93$^{c}$ | 71.14 | 73.91 | 72.53$^{bc}$ |
| CD ($p$=0.05) | 0.02 | 0.02 | | 0.30 | 0.31 | | 3.07 | 3.14 | |

Values followed by similar letters in a column indicate non-significant difference ($p$<0.05) according to Duncan Multiple Range test (DMRT) for separation of means. Refer to Table 1 for treatment details.

A similar trend was observed in wheat (Table 5), where $T_6$ again registered the highest stomatal conductance (0.45 mol/m$^2$/sec), indicating enhanced gas exchange and transpiration potential under FYM-based nutrition. This was closely followed by $T_8$ (0.40 mol/m$^2$/sec), $T_{10}$ (0.37 mol/m$^2$/sec), $T_9$ (0.35 mol/m$^2$/sec), and $T_{11}$ (0.35 mol/m$^2$/sec), suggesting that organic matter additions, even at 25% nitrogen substitution favourably influence stomatal functioning, possibly by reducing physiological stress and improving plant water status. In contrast, $T_1$ and $T_2$ had the lowest conductance values (0.20 and 0.22 mol/m$^2$/sec, respectively), again highlighting the adverse effect of nutrient deprivation on stomatal dynamics. The inorganic-only treatments $T_3$, $T_4$, and $T_5$ exhibited moderate conductance (0.28 mol/m$^2$/sec, 0.30 mol/m$^2$/sec, and 0.32 mol/m²/sec, respectively), indicating reasonable but not optimal physiological performance.

Under low nitrogen availability, the sharp decline in stomatal conductance under increasing water stress highlights the role of drought-induced stomatal closure in limiting $CO_2$ diffusion from the atmosphere to the mesophyll cells (Reddy *et al.* 2004, Wang *et al.* 2016). The present data clearly demonstrate that the integration of organic nutrient sources particularly FYM, significantly enhances stomatal conductance in both pearl millet and wheat. This improvement likely stems from superior nitrogen provisioning and better soil moisture retention.

*Transpiration rate*: In pearl millet (Table 4), pooled transpiration values ranged from 3.96 mmol/m²/sec under $T_1$ (control: no fertiliser) to a maximum of 6.22 mmol/m²/sec under $T_6$, where 50% of nitrogen was substituted with FYM. This elevated rate in $T_6$ suggests that organic amendments not only supply nutrients gradually but also enhance soil physical properties, such as porosity and moisture retention, which directly influence transpiration dynamics. Treatments $T_8$ and $T_{10}$, involving 50% nitrogen substitution through wheat straw and green manure respectively, also recorded high values of 6.18 and 6.05 mmol/m$^2$/sec, indicating that integration of organics boosts physiological activity. Similarly, $T_7$ and $T_9$, with mixed sources of nutrients, showed moderate values (5.98 and 5.78 mmol/m$^2$/sec), reflecting a balanced improvement in root-soil interaction. In contrast, chemically dominated treatments such as $T_2$ and $T_3$ recorded lower transpiration values (4.35 and 5.22 mmol/m²/sec), likely due to limited improvements in soil biological and structural quality, which are crucial for sustained water uptake.

A comparable pattern was observed in wheat (Table 5). The lowest transpiration rate of 5.69 mmol/m$^2$/sec under $T_1$ (control) rose steadily across treatments with higher organic inclusion, peaking at 7.83 mmol/m$^2$/sec in $T_6$. The pronounced effect in $T_6$ highlights the role of FYM in improving rhizosphere conditions, including microbial colonisation and nutrient buffering, thereby sustaining higher transpiration. Treatments $T_8$ (7.74 mmol/m$^2$/sec), $T_{10}$ (7.58 mmol/m²/sec), and $T_9$ (7.34 mmol/m$^2$/sec) also showed consistently high transpiration, underscoring the physiological relevance of integrating crop residues and green manure. By contrast, treatments focused solely on mineral fertilisation, such as $T_3$ and $T_4$, remained comparatively lower (6.08 and 6.42 mmol/m$^2$/sec), suggesting a ceiling to the benefits provided by inorganic inputs alone. Furthermore, organic sources likely contribute to better osmotic balance and deeper rooting, both of which

are critical for maximising transpiration, especially under moisture-limited conditions typical of semi-arid regions.

In the present study, treatments receiving 25–50% nitrogen substitution through organic sources consistently maintained higher transpiration rates than the sole inorganic fertiliser treatments in both pearl millet and wheat. This improvement can be attributed to the long-term beneficial effects of INM on soil physical properties, root proliferation, moisture retention and balanced nutrient availability, which collectively facilitate continuous water uptake and sustain stomatal functioning. Previous studies have likewise demonstrated that organic amendments improve plant water relations and gas-exchange characteristics by enhancing soil conditions and root activity, thereby supporting higher transpiration and photosynthetic performance (Wang *et al.* 2017, Halim *et al.* 2018). Furthermore, plants growing under favourable soil moisture conditions maintain stomatal opening and transpiration, whereas drying soil induces root-to-shoot signalling, including abscisic acid-mediated stomatal regulation that restricts water loss (Saradadevi *et al.* 2017, Wang *et al.* 2021). Therefore, the higher transpiration observed under long-term INM in the present study reflects improved plant water status and sustained physiological activity, which promote evaporative cooling, efficient nutrient transport, and enhanced photosynthetic productivity, ultimately contributing to greater crop resilience.

*Relative water content*: In pearl millet, the pooled data indicate a clear gradient of RWC across treatments. The lowest RWC (53.78%) was observed in $T_1$ (Control), highlighting the direct impact of nutrient deficiency, particularly nitrogen on the plant's water uptake and retention capacity (Table 4). As nitrogen supports better root growth and cell turgidity, its absence likely led to poor hydration. Slight improvements were recorded in $T_2$ (60.05%) and $T_3$ (60.80%), suggesting that even partial mineral fertilisation improves water balance in plants. The highest RWC was observed in $T_6$ (70.74%), where 50% of nitrogen was substituted with FYM. FYM likely enhanced soil moisture retention and root health, thereby enabling better water absorption. Treatments $T_8$ (68.57%) and $T_{10}$ (68.28%), involving organic sources like wheat straw and green manure, also showed significantly higher RWC, supporting the idea that organic matter improves soil porosity, water-holding capacity, and microbial activity, all contributing to improved plant hydration. Treatments $T_7$, $T_9$, and $T_{11}$ also demonstrated moderate-to-high RWC, validating the benefits of integrated nutrient management over mineral fertilisers alone ($T_4$ and $T_5$ with RWC values around 61–63%). Although the observed RWC values indicate that pearl millet experienced a certain degree of water stress, they should be interpreted in the context of the anthesis stage, cultivation under semi-arid conditions and the prevailing weather conditions at the time of sampling; therefore, the higher RWC under INM reflects an improved ability to maintain plant water status relative to the sole inorganic fertiliser treatments. A similar pattern was noted in wheat (Table 5), with $T_1$ (60.24%) and $T_2$ (62.78%) again showing the lowest RWC due to inadequate nutrient supply. The highest RWC was recorded in $T_6$ (76.64%), reiterating the superior performance of FYM in maintaining cellular hydration under field conditions. Treatments $T_8$ (75.91%), $T_{10}$ (75.33%), and $T_{11}$ (72.53%) followed closely, highlighting the long-term benefits of adding organic matter for water conservation. Purely mineral fertilised plots like $T_3$–$T_5$ also maintained decent hydration (RWC between 71.30% and 72.50%), though not matching the organically supplemented ones. The superior RWC under integrated treatments reflects improved soil structure, better root-soil contact, and enhanced biological activity, enabling plants to withstand brief periods of water stress.

Previous studies have demonstrated that water deficit conditions significantly reduce the relative water content (RWC) of crops, with pronounced declines observed in durum wheat genotypes at anthesis and grain filling stages (Bogale *et al.* 2011). Similarly, RWC under well-watered conditions consistently recorded the highest values, which decreased markedly under mild and severe drought stress (Wasaya *et al.* 2021). In the present study, the incorporation of organic inputs, particularly FYM, markedly improved the RWC in both pearl millet and wheat. The application of FYM enhanced the soil's water-holding capacity, stabilised the rhizosphere moisture environment, and reduced the onset of plant water stress. This favourable water regime contributed to better drought tolerance, improved physiological stability, and enhanced plant vigour even under semi-arid conditions.

*Grain yield*: The grain yield of pearl millet exhibited considerable variation across treatments with pooled mean values ranging from 1,497 kg/ha under $T_1$ (control) to 3352 kg/ha under $T_6$ (Fig. 1). The lowest yield recorded in $T_1$ was expected due to the absence of fertiliser application, leading to nutrient deficiencies and thus poor crop productivity. Conversely, the highest yield under $T_6$ reflects the beneficial effect of INM involving a combination of chemical fertilisers and organics, promoting better soil health and nutrient availability. Treatments $T_8$ (3,255 kg/ha) and $T_{10}$ (3,180 kg/ha) also performed significantly well, indicating that partial substitution of fertilisers with organics sustained high productivity. Intermediate yields were observed in treatments $T_4$ (2,886 kg/ha) and $T_5$ (2,974 kg/ha), showing moderate improvements over control. Notably, the gradual improvement in yield with increasing fertiliser and organic inputs highlights the crucial role of balanced fertilisation strategies in sustaining pearl millet production.

In wheat, grain yield followed a similar trend, with pooled yields ranging from 1,741 kg/ha in $T_1$ to an impressive 5,108 kg/ha in $T_6$ (Fig. 1). The control treatment ($T_1$) again recorded the lowest yield, reaffirming the importance of nutrient supplementation. Treatments $T_6$ (5,108 kg/ha) and $T_8$ (4,971 kg/ha) belonged to the highest yield groups, suggesting that wheat responded even more positively than pearl millet to combined nutrient management. Treatments $T_{10}$ (4,930 kg/ha) and $T_7$ (4,744 kg/ha) also attained statistically at-par yields. On the other hand, treatments such as $T_4$ (4,428 kg/ha) and $T_5$ (4,619 kg/ha) were placed

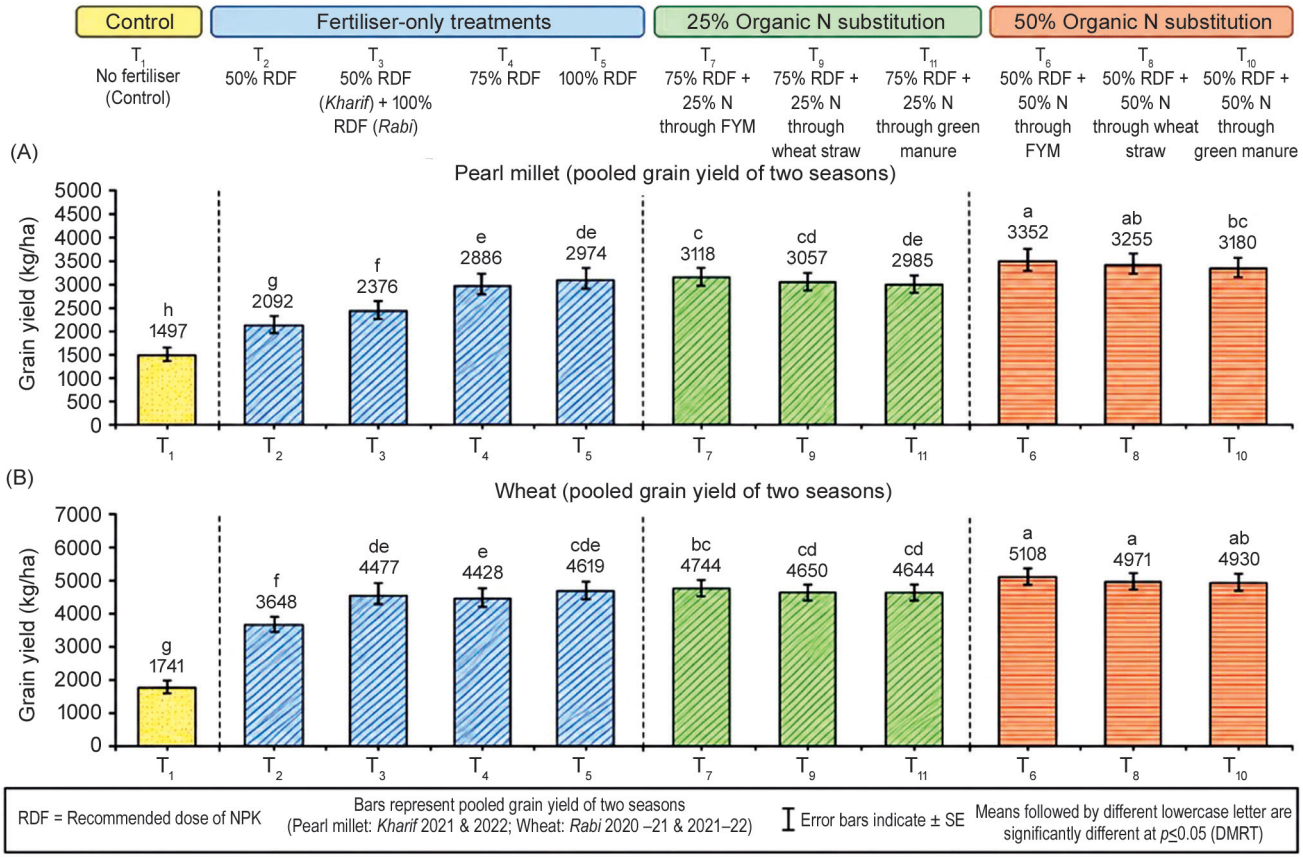


Fig. 1 Grain yield of pearl millet and wheat.

in intermediate groups, reflecting moderate benefits from fertiliser application alone without organic amendments. The consistent pattern across both crops highlights that treatments combining fertilisers and organic sources were superior to fertiliser-alone treatments.

Enhanced nitrogen availability plays a critical role in sustaining higher chlorophyll content, which directly translates into greater light absorption, elevated $CO_2$ assimilation, and ultimately higher net assimilation rates (Reddy *et al.* 2004, Pandey and Shukla 2015). In addition to nutrient availability, the long-term application of organic inputs, particularly FYM and crop residues, significantly improves soil physical properties (Ahlawat *et al.* 2023), notably increasing the soil's water-holding capacity. This enhancement ensures a more stable and prolonged moisture supply throughout the growing season, even under fluctuating environmental conditions. Improved soil moisture status not only delays the onset of drought stress but also promotes higher stomatal conductance, facilitating efficient $CO_2$ diffusion into leaf tissues and maintaining superior RWC within the plant system (Wasaya *et al.* 2021). Consequently, these integrated improvements culminate in substantially higher grain yields.

The present long-term study demonstrated that INM substantially improved physiological efficiency, plant water relations, and grain productivity of the pearl millet–wheat cropping system under semi-arid conditions. Among the nutrient management practices evaluated, substitution of 50% inorganic nitrogen with FYM consistently recorded the highest chlorophyll content, photosynthetic rate, stomatal conductance, transpiration rate, RWC, photochemical quantum yield and grain yield in both crops. Compared with the control, this treatment increased grain yield by 124% in pearl millet and 193% in wheat, demonstrating the cumulative benefits of long-term INM. Furthermore, replacing 25–50% of fertiliser nitrogen with organic sources consistently enhanced crop productivity compared with the recommended dose of inorganic fertilisers alone, with yield advantages of up to 12.7% in pearl millet and 10.6% in the succeeding wheat after 50% nitrogen substitution through FYM in pearl millet. These findings demonstrate that integrating organic manures with inorganic fertilisers enhances nutrient-use efficiency and sustains crop productivity beyond conventional fertilisation. Therefore, replacing 25–50% of the recommended nitrogen with locally available organic sources, particularly FYM where available, can be recommended as a practical nutrient management strategy for pearl millet–wheat systems in semi-arid regions to improve productivity, maintain soil health and promote long-term sustainability.

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