Assessment of Physiological Basis of Yield Variation in Small Millets under Rainfed Condition

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Physiological traits play an important role in crop growth and development. Comparative investigation on small millets, with respect different physiological traits such as leaf area index, leaf area duration, specific leaf weight, chlorophyll content, gas exchange parameters etc. and their relationship with grain yields were meager, and will be useful in small millets improvement. Therefore, this study aims to investigate the physiological traits and their relationship with grain yields five small millets (foxtail millet, proso millet, kodo millet, little millet and barnyard millet). Physiological traits such as leaf number, leaf area, specific leaf weight, chlorophylls a, b, and total chlorophyll, SPAD reading, photosynthetic rate and transpiration rate have reached their maximum value at grain development stage in all the crops, while leaf area index was the maximum at grain development stage, highest root length was achieved at maturity stage, and highest stomatal conductance was at flowering stage. Among different cultivars within the each crop, a cultivar having high leaf number, leaf area, leaf area index, leaf area duration, specific leaf weight, chlorophyll a, b, and total chlorophyll, chlorophyll fluorescence ratio, SPAD reading, photosynthetic rate, transpiration rate, stomatal conductance and root length, had produced higher grain yield. This shows importance of these traits in for enhanced yields in small millets.

Keywords
Small millets, Physiological traits, Photosynthetic rate, Stomatal

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Introduction

Small millets such as finger millet, foxtail millet, proso millet, kodo millet, little millet and barnyard millets are considered as important nutri-rich and climate-smart crops and are adapted to diverse environments (Vetriventhan et al., 2015 and Upadhyaya et al., 2008). Small millets play an important role in diversifying agriculture, supporting traditional farming systems and improving food and nutritional security particularly in marginal lands. Small millets are grown in India, China, Russia, Japan, USA and other African and East Asian countries. In India, the cultivation of small millets are cultivated in limited area of 2.32 m ha and occupy about 9.7 lakhs ha with a production of 4.67 lakhs tons, with a productivity of 480 kg/ha (averaged between 2006-2010).
Potential yields of up to 3 tons in small millets were reported (http://www.aicrpsm.res.in/Reports.html), indicating a large yield gap, and great opportunity to enhance productivity following improved crop management practices and cultivation of high yielding cultivars. Comparative investigation on small millets, with respect different physiological traits such as leaf area index, leaf area duration, specific leaf weight, chlorophyll content, etc. and their relationship with grain yields were meager, and will be useful in small millets improvement. Therefore, this study aims to investigate the physiological traits and their relationship with grain yields.

**Materials and Methods**

The experiment was conducted at Tamil Nadu Agricultural University, Coimbatore situated at 11Nº and 77Eº longitude with an altitude of 426.7 m above mean sea level. This study included two cultivars each of barnyard millet (Co 1 and Co 2) and kodo millet (Co 3, APK), three cultivars each of proso millet (Co 3, Co 4 and Co 5), little millet (Co 2, Co 3 and Co 4) and foxtail millet (Co 5, Co 6 and Co 7). Together, 13 cultivars of five small millets were planted in randomized complete block design with three replications. The experiment received NPK in the form of urea, single super phosphate and muriate of potash, respectively at the rate of 44: 22: 15 kg/ha. Full dose of P was applied as basal, whereas, N was applied in two splits, one as basal and another at 30 days after sowing (DAS). Potassium in the form of Muriate of potash was applied at 20th and 40th DAS. The observations on physiological traits and gas exchange parameters were recorded at seedling (20-25 DAS), vegetative (30-35 DAS), flowering (40-55 DAS), grain development (60-70 DAS) and grain maturation (75-85 DAS) stages of the crop. All the observations were made from ten randomly selected plants from each replication of all the treatments. The physiological traits such as number of leaves, leaf area, leaf area index (LAI), leaf area duration (LAD), specific leaf weight (SLW), root length, Chlorophyll a, b and total chlorophyll content were estimated. The number of leaves per plant was determined by counting the leaves from the base to the tip of the plant. Leaf area for the whole sampling unit was measured by using Leaf Area Meter (Licor Model 3100) and expressed as cm² plant⁻¹. The Leaf Area Index (LAI) was calculated by employing the formula of Williams (1946).

\[
LAI = \frac{leaf \ area \ per \ plant}{ground \ area \ occupied \ by \ the \ plant}
\]

Leaf Area Duration (LAD =

\[
\frac{L_1+L_2}{2} (t_2 - t_1)
\]

where, \(L_1 = LAI \text{ at first stage}, \ L_2 = LAI \text{ at second stage}, \ t_1 - t_2 = \text{Time interval in days}\)

was determined using the formula of Power et al. (1967) and expressed in days. Specific leaf weight (SLW = \(leaf \ dry \ weight/leaf \ area\)) was determined by using the formula given by Pearce et al. (1968) and expressed as mg cm⁻².

The plant was uprooted with minimum damage to the roots and the root length from the cotyledonary node to the root tip was measured and expressed as cm. Chlorophyll a, b and total chlorophyll content, were estimated in a fully expanded young leaf as per the method of Arnon (1949) and expressed as mg g⁻¹ fresh weight. Chlorophyll index in leaves was measured using SPAD meter. Photosynthetic rate, transpiration rate and stomatal conductance was measured following portable Photosynthesis System (PPS) (Model LI-6400 of LICOR Inc., Lincoln, Nebraska, USA) equipped with a halogen lamp (6400-02B LED) positioned on the cuvette. Totally,
three measurements were taken in the same leaf. The fully expanded young leaf was inserted in a 3 cm² leaf chamber and PPFD at 1200 µmol photons m⁻² s⁻¹ and relative humidity (50-55%) were set. The readings were taken between 11.00 am to 12.30 pm. Using PPS, the following gas exchange parameters were recorded and the values expressed as in parentheses.

- Transpiration rate (mmol H₂O m⁻² s⁻¹)
- Stomatal conductance (mmol H₂O m⁻² s⁻¹)
- Photosynthetic rate (µmol CO₂ m⁻² s⁻¹)

The data collected on the different parameters were statistically analyzed by the 'F' test for significance as suggested by Gomez and Gomez (2010). The critical difference (CD) was computed at 5% probability. Biochemical traits at different crop growth stages were compared following Newman and Keul’s test (Newman 1939; Keuls 1952) using the GenStat 17th edition (http://www.genstat.co.uk).

Results and Discussion

Physiological traits

Physiological traits such as leaf number, leaf area, leaf area index, leaf area duration, specific leaf weight, chlorophyll a, chlorophyll b and total chlorophyll content and SPAD reading (Soil Plant Analysis Development) were recorded at five different growth stages of small millets (Table 1). Leaf number of was the highest in little millet at grain development (13.20), grain maturation (11.93) and harvest (6.90) stages while barnyard millet had the maximum number of leaf at flowering (7.60) and grain development (8.20) stages. Among five crop growth stages, the maximum leaf was reached at grain development stage (5.60 in kodo millet to 13.20 in little millet) in all small millets investigated (Table 2). Leaf area, leaf area index and leaf area duration were maximum in barnyard millet in four out of five growth stages compared to other crops investigated (Table 1), and reached the highest leaf area during grain development stage, leaf area index at grain maturation stage and leaf area duration in either of grain development or grain maturation stages. Specific leaf weight was the highest in foxtail millet at all five growth stages, and it has reached the maximum at grain developmental stage in all the crops. Chlorophyll a, b and total chlorophyll contents reached the maximum at grain development stage in all the crops.

Chlorophyll b was the maximum in finger millet in first four stages while kodo millet had the highest chlorophyll b content at maturity. Chlorophyll a was the maximum at vegetative stage in barnyard millet, flowering stage in kodo millet, grain development and maturation stages in proso millet and at harvest in little millet. Total chlorophyll content was the maximum in kodo millet in all crop growth stages except at grain maturation stage and reached the maximum at flowering stage in all five crops. Foxtail millet had slightly higher chlorophyll fluorescence (Fv/Fm ratio) and in all crops, it is maximum at grain development stage and low at maturity stage. The SPAD reading was maximum in foxtail millet in vegetative to grain maturation stage while barnyard millet had the maximum SPAD value at harvest.

Gas exchange parameters

Gas exchange parameters such as photosynthetic rate, transpiration rate and stomatal conductance were recorded at vegetative, flowering, panicle initiation and maturation stages in 13 cultivars of five small millets. Photosynthetic rate was the maximum in proso millet at vegetative, flowering and grain maturity stage compared to other crops,
and it reached highest at grain development stage and significantly differed with other stages in all the crops. Transpiration rate was the maximum at vegetative stage and grain development stage in proso millet, flowering stage in barnyard millet and maturity stage in little millet, and it reached the maximum at grain development stage in all the crops and differed significantly. Stomatal conductance was maximum in proso millet at vegetative, grain development and maturity stages and was reached the highest at flowering stage in all five small millets studied.

**Relationship of physiological traits with grain yield**

Two cultivars each in barnyard and kodo millets, and three cultivars each in foxtail millet, proso, and little millets were used in this study. Flowering duration of these cultivars varied from 40 to 65 DAS. Except kodo millet, remaining four crops’ cultivars flowered within 52 DAS, and matured in less than 95 DAS. Grain yields of small millets cultivars varied from 1133 kg/ha (APK of kodo millet) to 3499 kg ha\(^{-1}\) (Co 7 of foxtail millet), and straw yield varied from 5083 kg ha\(^{-1}\) to 7666 kg/ha. Harvest index varied from 0.27 to 4.10 among cultivars. Harvest index was highest in kodo millet (0.39 to 0.41, mean 0.40) and was lowest in foxtail millet (0.27 to 0.32, mean of 0.28). The foxtail millet cultivars yielded an average of 3033 kg/ha followed by proso millet (2877 kg/ha), and least was in kodo millet (1575 kg/ha). Within each crop, a cultivar having high leaf number, leaf area, leaf area index, leaf area duration, specific leaf weight, chlorophyll a, b, and total chlorophyll, chlorophyll fluorescence ratio, SPAD reading and root length had produced higher grain yield (Table 3 to 7).

**Table 1** Gas exchange parameters of small millets at different growth stages

| Crop            | Growth stage                  |   |   |   |   |
|-----------------|-------------------------------|---|---|---|---|
|                 | Vegetative state | Flowering | Grain development | Grain maturity |
| Barnyard millet | 29.90a                        | 35.45b     | 41.38c          | 27.85a         |
| Foxtail millet  | 22.90a                        | 35.67c     | 43.56d          | 27.30b         |
| Proso millet    | 30.97a                        | 35.80ab    | 38.41c          | 31.50ab        |
| Kodo millet     | 24.35a                        | 28.70a     | 38.12c          | 26.09a         |
| Little millet   | 27.67a                        | 31.37b     | 39.74           | 31.36b         |
| TranspirationRate |                             |   |   |   |   |
| Barnyard millet | 5.25a                         | 11.40b     | 12.77c          | 11.61b         |
| Foxtail millet  | 5.00a                         | 7.20b      | 13.07d          | 11.22c         |
| Proso millet    | 6.40a                         | 9.60b      | 14.74d          | 10.71c         |
| Kodo millet     | 5.10a                         | 8.00b      | 13.02d          | 10.88c         |
| Little millet   | 5.40a                         | 8.13b      | 13.74d          | 12.02c         |
| Stomatal conductance |                   |   |   |   |   |
| Barnyard millet | 0.32a                         | 1.42d      | 0.49b           | 0.79c          |
| Foxtail millet  | 0.24a                         | 1.09d      | 0.65b           | 0.80c          |
| Proso millet    | 0.32a                         | 1.36d      | 1.11b           | 1.23c          |
| Kodo millet     | 0.26a                         | 1.13d      | 0.58b           | 0.77c          |
| Little millet   | 0.27a                         | 1.12d      | 0.82b           | 1.03c          |

#Growth Stages: Mean values of a trait at different growth stages were compared using Neman and Kue's test (Newman 1939; Keuls 1952). The means followed by different letter for a given trait and crop at different stages indicating significant difference at 5% probability.
Table 2: Mean performance of small millets for different physiological traits at different growth stages

| Crop and trait       | Crop Stages# |          |          |          |          |
|----------------------|--------------|----------|----------|----------|----------|
|                      |              | Vegetative | Flowering | Grain development | Grain maturation | Harvest |
| Leaf number          |              | 3.60a     | 7.60b    | 8.20b    | 7.85b    | 6.45b    |
| Barnyard millet      |              | 4.80a     | 5.8bc    | 6.4c     | 5.9abc   | 5.1ab    |
| Foxtail millet       |              | 6.00ab    | 6.93ab   | 7.63b    | 6.53ab   | 5.5a     |
| Proso millet         |              | 4.52a     | 4.85a    | 5.60a    | 5.30a    | 4.80a    |
| Kodo millet          |              | 4.80a     | 7.40b    | 13.20c   | 11.93c   | 6.90b    |
| Little millet        |              | 540a      | 673b     | 819c     | 767bc    | 653b     |
| Leaf Area            |              | 335a      | 520b     | 756d     | 652c     | 587bc    |
| Barnyard millet      |              | 342a      | 571b     | 790b     | 715b     | 581b     |
| Foxtail millet       |              | 329a      | 535b     | 818c     | 705bc    | 598b     |
| Proso millet         |              | 334a      | 423ab    | 861d     | 689c     | 547bc    |
| Kodo millet          |              | 2.41a     | 2.99ab   | 3.42bc   | 3.64c    | 2.91b    |
| Little millet        |              | 1.49a     | 2.31b    | 2.90c    | 3.36d    | 2.61bc   |
| Leaf area Index (LAI)|              | 1.52a     | 2.54ab   | 3.18b    | 3.52b    | 2.58b    |
| Barnyard millet      |              | 1.13a     | 2.38b    | 3.13bc   | 3.64c    | 2.655v   |
| Foxtail millet       |              | 1.48a     | 1.88ab   | 3.06c    | 3.83d    | 2.43bc   |
| Proso millet         |              | 27.00a    | 32.05ab  | 32.73ab  | 35.28b   | 31.76b   |
| Kodo millet          |              | 19.00a    | 26.03b   | 31.28c   | 29.83bc  | 26.54b   |
| Leaf area duration (LAD)|         | 20.28a    | 28.58ab  | 28.58ab  | 33.47b   | 30.48ab  |
| Barnyard millet      |              | 17.52a    | 27.55b   | 33.83b   | 31.45b   | 27.59b   |
|                | Specific leaf weight (SLW) | Chlorophyll ‘a’ | Chlorophyll ‘b’ | Total Chlorophyll | Chlorophyll fluorescence (Fv/Fm ratio) |
|----------------|---------------------------|-----------------|-----------------|-------------------|---------------------------------------|
| **Little millet** | 16.82a 24.70b 34.43b 31.30b 26.81b |                |                 |                   |                                        |
| **Barnyard millet** | 7.22a 7.65ab 22.48d 16.31c 11.76a | 1.47ab 1.54ab 1.73b 1.34a 1.26a | 0.35ab 0.42ab 0.56b 0.46ab 0.29a | 1.66ab 1.78ab 1.92b 1.80ab 1.55a | 0.58b 0.72d 0.77e 0.68c 0.55a |
| **Foxtail millet** | 7.25a 8.19a 25.28d 18.59c 13.33b | 1.45b 1.60c 1.75c 1.33a 1.23a | 0.40a 0.44a 0.78a 0.61a 0.30a | 1.67ab 1.77bc 1.93c 1.74bc 1.53a |                                        |
| **Proso millet** | 6.98a 8.10a 24.70d 17.52c 12.65b | 1.357a 1.60b 1.78c 1.37a 1.233a | 0.18a 0.42a 0.52a 0.38a 0.18a | 1.53ab 1.80cd 1.91d 1.7bc 1.4a      |                                        |
| **Kodo millet** | 6.27a 7.45a 23.87c 16.07b 11.73ab | 1.43b 1.62b 1.72c 1.25a 1.19a | 0.31a 0.42a 0.54a 0.49a 0.39a | 1.70a 1.83a 2.03a 1.72a 1.58a |                                        |
| **Little millet** | 7.14a 7.61a 22.79d 16.94c 7.61a  | 1.41ab 1.51bc 1.60c 1.29a 1.28a | 0.25a 0.36a 0.36a 0.50a 0.30a | 1.63ab 1.82b 1.92b 1.63ab 1.48a |                                        |
| Crop Type       | Foxtail millet | Proso millet | Kodo millet | Little millet | SPAD       |
|----------------|---------------|--------------|-------------|---------------|-----------|
| Foxtail millet | 0.59b         | 0.71d        | 0.77e       | 0.69c         | 0.57a     |
| Proso millet   | 0.55a         | 0.69b        | 0.75c       | 0.67b         | 0.54a     |
| Kodo millet    | 0.58b         | 0.68d        | 0.75e       | 0.67c         | 0.55a     |
| Little millet  | 0.58b         | 0.72d        | 0.76e       | 0.68c         | 0.56a     |

| Crop Type       | Foxtail millet | Proso millet | Kodo millet | Little millet | Root length (cm) |
|----------------|---------------|--------------|-------------|---------------|-----------------|
| Barnyard millet | 37.20b        | 43.60c       | 52.70d      | 35.50b        | 6.00a           |
| Foxtail millet  | 38.70b        | 46.93c       | 54.53d      | 38.47b        | 5.73a           |
| Proso millet    | 34.07b        | 43.47c       | 51.87d      | 33.70b        | 6.67a           |
| Kodo millet     | 35.20b        | 42.45bc      | 49.60c      | 33.60b        | 5.75a           |
| Little millet   | 35.47b        | 44.77c       | 52.77d      | 35.03b        | 5.55a           |

Growth Stages: Mean values of a trait at different growth stages were compared using Neman and Kuel’s test (Newman 1939; Keuls 1952). The means followed by different letter for a given trait and crop at different stages indicating significant difference at 5% probability.
### Table 3: Physiological traits - Number of leaves, Leaf area (cm$^2$) and Leaf area index of small millets at different growth stages

| Crop         | Number of leaves | Leaf area (cm$^2$) | Leaf area index |
|--------------|------------------|-------------------|----------------|
|              | I    | II    | III   | IV   | V    | I   | II   | III   | IV   | V    | I   | II   | III   | IV   | V    |
| Banyard millet |      |       |       |      |      |      |      |       |      |      |      |      |       |      |      |
| CO 1         | 3.4  | 7.2   | 7.6   | 7.0  | 6.3  | 510.43 | 656.29 | 790.66 | 744.21 | 614.54 | 1.35 | 2.17 | 2.54  | 3.04 | 2.46 |
| CO 2         | 3.8  | 8.0   | 8.8   | 8.7  | 6.6  | 570.88 | 689.77 | 849.18 | 791.49 | 691.88 | 1.43 | 2.63 | 3.10  | 3.37 | 2.60 |
| Foxtail millet |      |       |       |      |      |      |      |       |      |      |      |      |       |      |      |
| CO 5         | 4.4  | 5.4   | 6.3   | 6.0  | 4.8  | 305.12 | 470.96 | 729.44 | 610.73 | 588.15 | 1.77 | 2.82 | 3.89  | 4.14 | 2.68 |
| CO 6         | 4.7  | 5.6   | 6.0   | 5.9  | 5.0  | 330.15 | 499.61 | 740.61 | 651.83 | 579.38 | 1.36 | 2.09 | 2.71  | 3.24 | 2.61 |
| CO 7         | 5.4  | 6.6   | 6.8   | 5.8  | 5.6  | 370.65 | 588.11 | 797.14 | 694.32 | 594.88 | 1.47 | 2.22 | 2.90  | 3.29 | 2.58 |
| Proso millet  |      |       |       |      |      |      |      |       |      |      |      |      |       |      |      |
| CO 3         | 5.7  | 6.6   | 7.3   | 5.3  | 5.1  | 304.24 | 489.33 | 683.44 | 570.82 | 554.12 | 1.65 | 2.61 | 3.09  | 3.54 | 2.64 |
| CO 4         | 5.9  | 6.8   | 7.1   | 6.6  | 5.3  | 322.11 | 591.02 | 757.61 | 697.25 | 585.65 | 1.25 | 2.58 | 3.26  | 3.94 | 2.69 |
| CO 5         | 6.5  | 7.4   | 8.5   | 7.7  | 6.1  | 399.34 | 633.91 | 930.57 | 875.96 | 603.59 | 1.00 | 2.18 | 3.00  | 3.33 | 2.62 |
| Kodo millet   |      |       |       |      |      |      |      |       |      |      |      |      |       |      |      |
| CO 3         | 4.6  | 5.5   | 6.6   | 6.2  | 5.4  | 280.19 | 580.51 | 887.11 | 733.77 | 606.29 | 1.49 | 1.69 | 2.63  | 3.48 | 2.20 |
| APK          | 3.9  | 4.2   | 4.6   | 4.4  | 4.2  | 225.33 | 489.77 | 749.82 | 675.48 | 590.19 | 1.40 | 1.78 | 2.84  | 3.56 | 2.31 |
| Little millet |      |       |       |      |      |      |      |       |      |      |      |      |       |      |      |
| CO 2         | 4.1  | 7.1   | 12.0  | 10.5 | 6.1  | 335.61 | 380.14 | 783.59 | 590.77 | 494.11 | 1.56 | 2.17 | 3.71  | 4.44 | 2.79 |
| CO 3         | 3.7  | 7.4   | 13.2  | 12.3 | 6.9  | 315.19 | 399.46 | 800.11 | 640.08 | 519.36 | 2.27 | 2.92 | 3.31  | 3.51 | 2.73 |
| CO 4         | 6.6  | 7.7   | 14.4  | 13.0 | 7.7  | 350.15 | 488.27 | 999.87 | 835.14 | 627.37 | 2.54 | 3.07 | 3.52  | 3.77 | 3.08 |
| Mean         | 4.8  | 6.6   | 8.4   | 7.6  | 5.8  | 355.33 | 535.17 | 807.62 | 700.91 | 588.42 | 1.58 | 2.38 | 3.12  | 3.59 | 2.61 |
| SED          | 0.017| 0.018 | 0.048 | 0.044| 0.015| 1.521  | 1.567  | 1.437  | 1.518  | 0.794  | 0.006| 0.007 | 0.006 | 0.006| 0.003|
| CD (0.05)    | 0.036| 0.037 | 0.100 | 0.091| 0.032| 3.139  | 3.234  | 2.967  | 3.134  | 1.640  | 1.35 | 2.17 | 2.54  | 3.04 | 2.46 |

I - Vegetative stage ; II – Flowering stage ; III – Grain development stage ; IV – Grain maturation stage ; V – Harvest stage
Table 4 Physiological traits - Leaf area duration (days), Specific Leaf Weight (mg /cm$^2$) and Root length (cm) of small millets at different growth stages

| Crop            | Leaf area duration (days) | Specific Leaf Weight (mg /cm$^2$) | Root length (cm) |
|-----------------|---------------------------|-----------------------------------|------------------|
|                 | I  | II | III | IV | I  | II | III | IV | V  | I  | II | III | IV | V  |
| Banyard millet  |    |    |     |    |    |    |     |    |    |    |    |     |    |    |
| CO 1            | 17.60 | 23.55 | 27.90 | 27.50 | 3.7 | 7.4 | 13.2 | 12.3 | 6.9 | 5.5 | 16.5 | 16.7 | 17.3 | 17.4 |
| CO 2            | 20.30 | 28.65 | 32.35 | 29.85 | 6.6 | 7.7 | 14.4 | 13.0 | 7.7 | 6.5 | 17.7 | 18.5 | 18.6 | 18.7 |
| Foxtail millet  |    |    |     |    |    |    |     |    |    |    |    |     |    |    |
| CO 5            | 22.95 | 33.55 | 40.15 | 34.10 | 4.7 | 5.6 | 6.0 | 5.9 | 5.0 | 5.2 | 7.2 | 15.5 | 16.6 | 16.7 |
| CO 6            | 17.25 | 24.00 | 29.75 | 29.25 | 5.4 | 6.6 | 6.8 | 5.8 | 5.6 | 5.5 | 8.9 | 15.6 | 16.4 | 16.5 |
| CO 7            | 18.45 | 25.60 | 30.95 | 29.35 | 5.7 | 6.6 | 7.3 | 5.3 | 5.1 | 6.5 | 13.5 | 16.3 | 16.5 | 16.6 |
| Proso millet    |    |    |     |    |    |    |     |    |    |    |    |     |    |    |
| CO 3            | 21.3 | 28.50 | 33.15 | 30.90 | 3.4 | 7.2 | 7.6 | 7.0 | 6.3 | 5.9 | 13.2 | 15.5 | 15.7 | 15.9 |
| CO 4            | 19.15 | 29.20 | 36.00 | 33.15 | 3.8 | 8.0 | 8.8 | 8.7 | 6.6 | 6.5 | 13.9 | 16.3 | 16.4 | 16.6 |
| CO 5            | 15.9 | 25.90 | 31.65 | 29.75 | 4.4 | 5.4 | 6.3 | 6.0 | 4.8 | 7.6 | 15.6 | 16.5 | 16.7 | 16.8 |
| Kodo millet     |    |    |     |    |    |    |     |    |    |    |    |     |    |    |
| CO 3            | 15.9 | 21.60 | 30.55 | 28.40 | 5.9 | 6.8 | 7.1 | 6.6 | 5.3 | 5.9 | 11.9 | 15.6 | 16.2 | 16.5 |
| APK             | 15.9 | 23.10 | 32.00 | 29.35 | 6.5 | 7.4 | 8.5 | 7.7 | 6.1 | 5.6 | 11.4 | 13.8 | 14.5 | 15.5 |
| Little millet   |    |    |     |    |    |    |     |    |    |    |    |     |    |    |
| CO 2            | 18.65 | 29.40 | 40.75 | 36.15 | 4.6 | 5.5 | 6.6 | 6.2 | 5.4 | 5.6 | 11.5 | 12.2 | 15.5 | 15.8 |
| CO 3            | 25.95 | 31.15 | 34.10 | 31.20 | 3.9 | 4.2 | 4.6 | 4.4 | 4.2 | 5.4 | 12.3 | 15.3 | 15.4 | 15.8 |
| CO 4            | 28.05 | 32.95 | 36.45 | 34.25 | 4.1 | 7.1 | 12.0 | 10.5 | 6.1 | 5.7 | 12.5 | 15.5 | 15.6 | 15.8 |
| Mean            | 19.79 | 27.47 | 33.52 | 31.02 | 4.8 | 6.6 | 8.4 | 7.6 | 5.8 | 355.33 | 535.17 | 807.62 | 700.91 | 588.42 |
| SED             | 0.063 | 0.063 | 0.042 | 0.017 | 0.018 | 0.048 | 0.044 | 0.015 | 1.521 | 1.567 | 1.437 | 1.518 | 0.794 |
| CD (0.05)       | 0.130 | 0.129 | 0.131 | 0.088 | 0.036 | 0.037 | 0.100 | 0.091 | 0.032 | 3.139 | 3.234 | 2.967 | 3.134 | 1.640 |

I - Vegetative stage ; II – Flowering stage ; III – Grain development stage ; IV – Grain maturation stage ; V – Harvest stage
Table 5 Physiological traits - Chlorophyll ‘a’ (mg g⁻¹), Chlorophyll ‘b’ (mg g⁻¹) and Total Chlorophyll (mg g⁻¹) content of small millets at different growth stages

| Crop              | Chlorophyll ‘a’ (mg g⁻¹) | Chlorophyll ‘b’ (mg g⁻¹) | Total Chlorophyll (mg g⁻¹) |
|-------------------|--------------------------|--------------------------|---------------------------|
|                   | I  | II | III | IV | V  | I  | II | III | IV | V  | I  | II | III | IV | V  | I  | II | III | IV | V  | I  | II | III | IV | V  | I  | II | III | IV | V  |
| Banyard millet    |    |    |     |    |    | 1.43 | 1.47 | 1.62 | 1.32 | 1.20 | 0.31 | 0.36 | 0.50 | 0.42 | 0.28 | 1.63 | 1.73 | 1.88 | 1.74 | 1.48 |
| CO 1              |    |    |     |    |    | 1.51 | 1.60 | 1.83 | 1.37 | 1.32 | 0.39 | 0.48 | 0.61 | 0.49 | 0.30 | 1.69 | 1.82 | 1.95 | 1.86 | 1.62 |
| Foxtail millet    |    |    |     |    |    | 1.39 | 1.51 | 1.65 | 1.28 | 1.19 | 0.37 | 0.41 | 0.58 | 0.57 | 0.31 | 1.60 | 1.72 | 1.89 | 1.85 | 1.50 |
| CO 5              |    |    |     |    |    | 1.45 | 1.55 | 1.78 | 1.31 | 1.22 | 0.38 | 0.45 | 0.70 | 0.31 | 0.20 | 1.66 | 1.78 | 1.92 | 1.62 | 1.42 |
| CO 6              |    |    |     |    |    | 1.51 | 1.75 | 1.83 | 1.41 | 1.28 | 0.44 | 0.45 | 1.05 | 0.95 | 0.39 | 1.75 | 1.82 | 1.97 | 1.74 | 1.67 |
| Foxtail millet    |    |    |     |    |    | 1.34 | 1.66 | 1.73 | 1.33 | 1.22 | 0.17 | 0.46 | 0.51 | 0.32 | 0.11 | 1.51 | 1.72 | 1.87 | 1.65 | 1.33 |
| CO 7              |    |    |     |    |    | 1.39 | 1.40 | 1.78 | 1.37 | 1.20 | 0.18 | 0.41 | 0.25 | 0.24 | 0.18 | 1.57 | 1.81 | 1.91 | 1.61 | 1.38 |
| Kodo millet       |    |    |     |    |    | 1.34 | 1.73 | 1.82 | 1.41 | 1.28 | 0.17 | 0.46 | 0.51 | 0.32 | 0.11 | 1.52 | 1.88 | 1.95 | 1.72 | 1.61 |
| Proso millet      |    |    |     |    |    | 1.41 | 1.66 | 1.76 | 1.30 | 1.18 | 0.35 | 0.51 | 0.64 | 0.59 | 0.48 | 1.68 | 1.77 | 1.95 | 1.85 | 1.66 |
| CO 3              |    |    |     |    |    | 1.45 | 1.57 | 1.68 | 1.20 | 1.20 | 0.27 | 0.33 | 0.43 | 0.38 | 0.30 | 1.72 | 1.90 | 2.11 | 1.58 | 1.50 |
| Kodo millet       |    |    |     |    |    | 1.31 | 1.48 | 1.56 | 1.22 | 1.21 | 0.21 | 0.30 | 0.37 | 0.16 | 0.10 | 1.52 | 1.78 | 1.93 | 1.38 | 1.31 |
| CO 3              |    |    |     |    |    | 1.43 | 1.50 | 1.54 | 1.29 | 1.31 | 0.25 | 0.34 | 0.60 | 0.46 | 0.17 | 1.68 | 1.84 | 1.90 | 1.75 | 1.48 |
| Little millet     |    |    |     |    |    | 1.49 | 1.56 | 1.70 | 1.36 | 1.31 | 0.28 | 0.45 | 0.79 | 0.88 | 0.34 | 1.74 | 1.83 | 1.94 | 1.76 | 1.65 |
| Mean              | 1.41 | 1.57 | 1.71 | 1.32 | 1.04 | 0.29 | 0.41 | 0.60 | 0.49 | 0.27 | 1.64 | 1.80 | 1.94 | 1.70 | 1.51 | I  | II | III | IV | V  | 1  | 2  | 3  | 4  | 5  |
| SED               | 0.0011 | 0.0017 | 0.0016 | 0.0011 | 0.0008 | 0.0015 | 0.0010 | 0.0034 | 0.0038 | 0.0018 | 0.0014 | 0.0009 | 0.0010 | 0.0022 | 0.0021 |
| CD (0.05)         | 0.0022 | 0.0035 | 0.0033 | 0.0022 | 0.0017 | 0.0030 | 0.0021 | 0.0071 | 0.0078 | 0.0078 | 0.0029 | 0.0019 | 0.0020 | 0.0045 | 0.0042 |

I - Vegetative stage ; II – Flowering stage ; III – Grain development stage ; IV – Grain maturation stage ; V – Harvest stage
### Table 6: Chlorophyll fluorescence (Fv/Fm ratio), SPAD values, Yield potential and harvest index of small millets

| Crop            | Chlorophyll fluorescence (Fv/Fm ratio) | SPAD values | Yield potential and Harvest index |
|-----------------|----------------------------------------|-------------|----------------------------------|
|                 | I          | II         | III        | IV         | V          | I          | II         | III        | IV         | V          | Days to 50% flowering | Plant height | Days to maturation (days) | Grain yield (Kg/ha) | Harvest index |
| Banyard millet  |            |            |            |            |            |            |            |            |            |            |                         |              |                        |                    |              |
| CO 1            | 0.581      | 0.723      | 0.774      | 0.679      | 0.552      | 36.2       | 41.5       | 50.6       | 34.7       | 24.8       | 52                       | 113          | 95                       | 2197            | 0.35          |
| CO 2            | 0.583      | 0.725      | 0.778      | 0.682      | 0.555      | 38.2       | 45.7       | 54.8       | 36.3       | 26.5       | 48                       | 120          | 92                       | 3091            | 0.38          |
| Foxtail millet  |            |            |            |            |            |            |            |            |            |            |                         |              |                          |                  |               |
| CO 5            | 0.586      | 0.708      | 0.770      | 0.692      | 0.569      | 35.2       | 45.1       | 51.1       | 38.8       | 22.1       | 43                       | 106          | 89                       | 2716            | 0.27          |
| CO 6            | 0.589      | 0.715      | 0.772      | 0.695      | 0.572      | 38.4       | 47.2       | 54.0       | 37.5       | 20.4       | 43                       | 106          | 87                       | 2883            | 0.28          |
| CO 7            | 0.592      | 0.714      | 0.775      | 0.697      | 0.574      | 42.5       | 48.5       | 58.5       | 39.1       | 26.7       | 40                       | 111          | 83                       | 3499            | 0.31          |
| Proso millet    |            |            |            |            |            |            |            |            |            |            |                         |              |                          |                  |               |
| CO 3            | 0.526      | 0.663      | 0.731      | 0.675      | 0.521      | 32.8       | 44.2       | 49.6       | 30.4       | 17.2       | 47                       | 105          | 94                       | 2883            | 0.39          |
| CO 4            | 0.562      | 0.669      | 0.748      | 0.664      | 0.537      | 33.1       | 40.6       | 51.3       | 34.5       | 16.4       | 45                       | 106          | 93                       | 2666            | 0.39          |
| CO 5            | 0.567      | 0.674      | 0.769      | 0.673      | 0.558      | 36.3       | 45.6       | 54.7       | 36.2       | 15.3       | 44                       | 113          | 90                       | 3083            | 0.4           |
| Kodo millet     |            |            |            |            |            |            |            |            |            |            |                         |              |                          |                  |               |
| CO 3            | 0.575      | 0.681      | 0.752      | 0.674      | 0.543      | 37.4       | 46.4       | 52.5       | 35.9       | 22.1       | 60                       | 96           | 115                      | 2016            | 0.41          |
| APK             | 0.577      | 0.683      | 0.755      | 0.677      | 0.546      | 33.0       | 38.5       | 46.7       | 31.3       | 23.2       | 65                       | 94           | 122                      | 1133            | 0.39          |
| Little millet   |            |            |            |            |            |            |            |            |            |            |                         |              |                          |                  |               |
| CO 2            | 0.575      | 0.720      | 0.760      | 0.675      | 0.558      | 34.2       | 42.2       | 50.7       | 33.5       | 24.7       | 48                       | 103          | 86                       | 2466            | 0.35          |
| CO 3            | 0.578      | 0.723      | 0.764      | 0.679      | 0.560      | 35.1       | 44.5       | 52.4       | 36.2       | 25.4       | 47                       | 105          | 83                       | 2499            | 0.36          |
| CO 4            | 0.581      | 0.726      | 0.769      | 0.682      | 0.561      | 37.1       | 47.6       | 55.2       | 35.4       | 26.2       | 43                       | 106          | 80                       | 2774            | 0.38          |
| Mean            | **0.574**  | **0.701**  | **0.763**  | **0.680**  | **0.554**  | **36.11**  | **44.43**  | **52.47**  | **35.37**  | **22.38**  | **48**                   | **107**       | **93**                    | **2608**        | **0.36**      |
| SED             | 0.0003     | 0.0004     | 0.0002     | 0.0002     | 0.0002     | 0.044      | 0.048      | 0.049      | 0.041      | 0.064      | 0.117                    | 0.113         | 0.201                    | 9.630           | 0.001         |
| CD (0.05)       | 0.0006     | 0.0008     | 0.0004     | 0.0004     | 0.0005     | 0.091      | 0.099      | 0.101      | 0.086      | 0.113      | 0.241                    | 0.234         | 0.413                    | 19.87           | 0.002         |

I - Vegetative stage; II – Flowering stage; III – Grain development stage; IV – Grain maturation stage; V – Harvest stage
Table 7 Gas exchange parameters of small millets at different growth stages

| Stages            | Vegetative stage | Flowering stage | Grain development stage | Maturity stage |
|-------------------|------------------|-----------------|-------------------------|---------------|
| Crop              | PR   | TR   | SC   | PR   | TR   | SC   | PR   | TR   | SC   | PR   | TR   | SC   |
|                   |      |      |      |      |      |      |      |      |      |      |      |      |
| Barnyard millet   |      |      |      |      |      |      |      |      |      |      |      |      |
| CO1               | 29.3 | 5.1  | 0.31 | 34.2 | 11.3 | 1.4  | 40.1 | 12.66| 0.47 | 27.16| 11.53| 0.78 |
| CO2               | 30.5 | 5.4  | 0.33 | 36.7 | 11.5 | 1.43 | 42.66| 12.88| 0.52 | 28.54| 11.68| 0.8  |
| Foxtail millet    |      |      |      |      |      |      |      |      |      |      |      |      |
| CO5               | 21.5 | 4.8  | 0.21 | 33.7 | 6.7  | 1.09 | 42.13| 12.84| 0.56 | 25.21| 10.87| 0.71 |
| CO6               | 22.7 | 5    | 0.23 | 36.6 | 7.2  | 1.08 | 43.46| 13.14| 0.62 | 26.81| 11.23| 0.81 |
| CO7               | 24.5 | 5.2  | 0.27 | 36.7 | 7.7  | 1.11 | 45.1 | 13.94| 0.68 | 29.87| 11.55| 0.88 |
| Proso millet      |      |      |      |      |      |      |      |      |      |      |      |      |
| CO3               | 30.2 | 6.3  | 0.31 | 34.3 | 9.1  | 1.31 | 35.32| 14.11| 1.05 | 30.8 | 10.31| 1.21 |
| CO4               | 30.8 | 6.4  | 0.32 | 35.6 | 9.4  | 1.35 | 37.41| 14.67| 1.1  | 31.53| 10.56| 1.22 |
| CO5               | 31.9 | 6.5  | 0.32 | 37.5 | 10.3 | 1.41 | 42.5 | 15.45| 1.19 | 32.17| 11.26| 1.27 |
| Kodo millet       |      |      |      |      |      |      |      |      |      |      |      |      |
| APK               | 23.5 | 5    | 0.25 | 27.6 | 7.8  | 1.1  | 37.13| 12.81| 0.54 | 25.67| 10.45| 0.73 |
| CO3               | 25.2 | 5.2  | 0.27 | 29.8 | 8.2  | 1.16 | 39.1 | 13.23| 0.62 | 26.5 | 11.32| 0.81 |
| Little millet     |      |      |      |      |      |      |      |      |      |      |      |      |
| CO2               | 26.5 | 5.2  | 0.26 | 30.4 | 7.8  | 1.08 | 38.22| 12.64| 0.76 | 30.14| 11.65| 1.01 |
| CO3               | 27.5 | 5.4  | 0.27 | 31.5 | 8.1  | 1.1  | 39.41| 13.65| 0.82 | 31.64| 11.74| 1.03 |
| CO4               | 29   | 5.6  | 0.3  | 32.2 | 8.5  | 1.19 | 41.58| 14.95| 0.89 | 32.3 | 12.67| 1.05 |
| Mean              | 27.16| 5.5  | 0.28 | 33.6 | 8.74| 1.22 | 40.32| 13.61| 0.75 | 29.1 | 11.29| 0.94 |
| SED               | 0.056| 0.009| 0.0006| 0.051| 0.025| 0.002| 0.046| 0.015| 0.004| 0.042| 0.01| 0.003 |
| CD (0.05)         | 0.115| 0.019| 0.0013| 0.105| 0.05 | 0.005| 0.096| 0.031| 0.008| 0.086| 0.021| 0.007 |

PR - Photosynthetic Rate  TR – Transpiration rate  SC – Stomatal conductance
Small millets are climate resilient crops, and are less affected by insect pests and diseases and abiotic stress. However, small millets cultivation and consumption has been declined mainly due to limited productivity, high drudgery involved in their processing and negative perceptions of small millets as a food for the poor. In this study, we assessed the physiological traits at different growth stages and their relationship with grain yield. Understanding the physiological traits in crops plants at different stages helps to understand their adaptations and crop characteristics. Leaf area is the fundamental determinant of the rate of photosynthesis of any plant and the optimum leaf area development aids in effective interception of light energy and facilitates higher dry matter production.

The nature of the foliage cover is an important factor in determining the efficiency with which the available solar radiation is used in primary production (Loomis and Williams, 1969). The leaf area index is an important measure of canopy structure because crop morphology, leaf orientation and distribution influence LAI. Leaf area duration is the integral of leaf area index over time. Formation of optimum photosynthetic area and maintenance of photosynthetically active leaves for a longer duration, especially during the reproductive phase of crop, are essential for increasing the photosynthetic rate, dry matter accumulation and grain yield (Watson, 1958).

Reduction in transpiration rate under water deficit conditions leads to reduce the photosynthetic rate by inhibition of CO₂ entry into the chloroplast through the stomata. The chlorophyll fluorescence is an important measurement of photosynthetic efficiency of crops. The high Fv/ Fm ratio is proportional to quantum yield and showing high degree of photosynthesis (Gitelson et al., 1999). Fluorescence yield will be high when PS II reaction centre is least damaged by photoinhibition. In this study, Several physiological traits such as leaf number, leaf area, specific leaf weight, chlorophylls a, b, and total chlorophyll, SPAD reading, photosynthetic rate and transpiration rate have reached their maximum value at grain development stage in all the crops, while leaf area index was the maximum at grain development stage, highest root length was achieved at maturity stage, and highest stomatal conductance was at flowering stage. Among different cultivars within the each crop, a cultivar having high leaf number, leaf area, leaf area index, leaf area duration, specific leaf weight, chlorophyll a, b, and total chlorophyll, chlorophyll florescence ratio,
SPAD reading, photosynthetic rate, transpiration rate, stomatal conductance and root length, had produced higher grain yield. This shows importance of these traits in for enhanced yields in small millets.

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