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# Clonally Selected Shade-tolerant Mulberry (*Morus indica*) Genotype, CS-6 for Cultivation in Coconut Orchards

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## Abstract

The mulberry (*Morus* sp.) with its perennial nature and appropriate pruning methods, is more suitable for intercropping with coconut plantations, wherein wider space shall be utilized to gain an additional income per unit area. But the challenging task is that existing mulberry varieties, except Sahana are found unsuitable for cultivating as intercrops under coconut palms because of shade stress not only limits the growth and productivity of mulberries but also affects the nutritional value of foliage to use them as food for the silkworm, *Bombyx mori*. To overcome this constraint, a productive shade-tolerant mulberry variety is needed. To achieve this, fourteen mulberry genotypes were evaluated for their performance under partial shade (under coconut palms) and full sunlight (open field). The results revealed that mulberry genotypes grown under partial shade exhibited differential responses as shade-tolerance, shade-avoidance, and shade-intolerance syndromes. Characteristically, shade-tolerant mulberry genotypes (CS-3, CS-6, CS-7 and Sahana) have been shown to have statistically non-significant variation between open and partially shaded conditions in morphological, anatomical, biochemical and physiological traits, albeit leaf yield and quality production are consistent with those of full sunlight conditions. In contrast, shade-avoidant genotypes like CS-1, CS-4, CS-5, CS-9, CS-10, CS-11, M-5 and V-1 exhibited significant phenotypic plasticity in the above-stated traits, although their leaf yield and quality were considerably reduced under partial shade. The shade-intolerant genotypes, CS-2 and CS-8, demonstrated neither tolerance nor avoidance of shade and showed significant reductions in almost all traits studied, except for leaf petiole and internodal length. Furthermore, the shade-tolerant genotype CS-6 showed high resistance to powdery mildew, while CS-3, CS-7 and Sahana exhibited moderate resistance. Comparatively, the shade-avoidance (CS-1, CS-4, CS-5, CS-9, CS-10, CS-11, M-5, and V-1) and shade-intolerant (CS-2 and CS-8) genotypes were found to be more susceptible to the diseases under shade conditions. Notably, CS-6 displayed the highest leaf yield (405.43 g/harvest/plant) under shade, making it a promising candidate for intercropping in coconut plantations and a valuable resource for breeding programmes.

*Keywords* : Coconut orchards, Intercrop, Mulberry, Phenotypic plasticity, Shade-tolerance

The mulberry (*Morus* spp.: Moraceae), by and large, is being cultivated as a monocrop in sericulture-practicing countries and has been in use as feed for the monophagous silkworm, *Bombyx mori,* for the production of cocoons/silk. However, in the traditional sericulture belts of South India, it is often grown as an intercrop with various horticultural (e.g., coconut, areca nut, mango, sapota, guava, pomegranate) and forestry (e.g., sandal, Malabar neem, teak, silver oak) plants, while intercropping of mulberry with coconut palm has become the most popular one (Babu *et al.,* 2006 & Kumara *et al.,* 2024). The height of the coconut trees and the orientation of their leaves allow between 20 and 50 per cent of sunlight to reach the ground, creating a suitable environment for growing other annual and perennial plants, including mulberry (Nelliat *et al.,* 1974). The intercropping practice is considered an efficient system for resource utilization, ensuring better use of space, soil and water, provided the selection of the crop is appropriate (Singh and Datta, 2006 and Roopa *et al.,* 2022). Mulberry has been recommended as an intercrop in coconut orchards due to its lifespan of 15-25 years, providing a consistent source of income and acting as a financial buffer against fluctuating coconut prices (Dias, 1989). Besides, mulberry cultivation in coconut orchards offers ecological benefits, such as improving soil health and maintaining overall productivity (Reshma *et al.,* 2019 and John *et al.,* 2019). Despite these advantages, productivity and income from mulberry cultivation are invariably higher in open gardens compared to the shaded conditions of coconut (Shankar *et al.,* 1998 and Meerabai *et al.,* 2000). This is primarily because existing mulberry genotypes not only exhibit reduced leaf thickness under shade but also directly affect the yield and quality of the leaves (Babu *et al.,* 2006). Additionally, mulberry plants grown under shade are more susceptible to foliar diseases, powdery mildew in particular and infestation of mealy bugs, which decline the quantity and quality of the leaves for silkworm rearing (Gupta, 2001). While intercropping of mulberry with coconut offers numerous ecological and economic benefits, optimizing shade tolerance in mulberry genotypes is critical to improve productivity (Shukla *et al.,* 1989).

In this context, although quite a good number of mulberry genotypes have been developed and evaluated under coconut shade conditions to assess their yield attributes and suitability for silkworm rearing, the rate of success in the field is meager. However, among the seven genotypes screened, Sahana (K-2 x Kosen) and MR-2 are identified as relatively shade-tolerant (Balakrishna *et al.,* 2000 and Balakrishna *et al.,* 2002). The Sahana variety is characterized by medium branching, fast-growth with large, unlobed, dark green leaves and thrives well under 40 per cent shade. It also produces 40-44 MT of leaves/hectare/year under optimal irrigated conditions. With this significance, the Sahana genotype was recommended for intercropping in coconut orchards, trees older than 25 years in particular (Das *et al.,* 2010 and Thippeswamy *et al.,* 2014), but did not reach the expectation due to its lower leaf yield compared to the V-1, which yields 65-70 MT of leaves/hectare/year. Although the V-1 variety is shade-sensitive, it continues to be the preferred variety in many coconut plantations. As the Sahana genotype was derived from a hybrid of K-2 and Kosen (Balakrishna *et al.*, 2002) and possesses a poor yielding nature, we have explored naturally occurring clonally derived mulberry genotypes and analyzed them for their shade tolerance and leaf production for commercial exploitation in the coconut orchards.

## Material and Methods

### Plant Material

Eleven naturally occurring variants of mulberry were collected from more than 20-year-old mulberry gardens of the cultivar M-5 (Kanva 2) grown in coconut orchards. These clonal selections were carefully chosen and named as CS-1 (Clonal Selection-1), CS-2, CS-3, CS-4, CS-5, CS-6, CS-7, CS-8, CS-9, CS-10 and CS-11. For the screening trials, the M-5 genotype (the original cultivar from which the variants were derived) was used as a control, along with the shade-tolerant genotype Sahana and the shade-sensitive genotype Victory-1 (V-1).

### Establishment and Maintenance of the Evaluation Plot

Using Line Quantum Sensor (LI-191R), light measurement was carried out to assess the photosynthetically active radiation (PAR) under coconut palm shade. The intensity of light under the shade ranges from 48.59 per cent (657. 97 µmol $m^{-2}$ $s^{-1}$) to 51.44 per cent (697.97 µmol $m^{-2}$ $s^{-1}$)

recorded in open land, which was 1,356.07 µmol $m^{-2}$ $s^{-1}$ at 11 a.m. on a typical sunny day in June.

For experiments, six-month-old saplings were planted following the Randomized Block Design (RBD) with 3 replications (6 plants/genotype/replication) with 3ft x 3ft spacing and grown under the mature coconut palms canopy (variety Kalpa Samrudhi, 16 years old with 7m x 7m spacing). Concurrently, for comparative analysis, the same genotypes were planted in full sunlight next to the shaded plot (Fig. 1). The recommended package of practices was followed for both the mulberry plots (FYM @ 20 MT and NPK @ 350:140:140 kg/ha/yr) as well as coconut trees (FYM @ 50 kg and NPK @ 500 g, 320 g, 1200 g /palm/yr). Plants receive irrigation once every 6 days during dry conditions. After a year of establishment, the plants were harvested eight times at intervals of 65-70 days following shoot pruning.

### Morpho-Anatomical and Physio-Biochemical Analysis

Morphological, growth, yield and anatomical parameters of the mulberry were recorded following standard protocols and descriptors (Sahay *et al.,* 2016). To assess the physiological parameters, the net photosynthetic rate (Pn), stomatal conductance (gs), transpiration rate (Tr) and intercellular $CO_2$ concentration (Ci) were measured using 5th and 6th order leaves. All these measurements in triplicate were recorded in the field between 10 and 11 a.m. using a portable photosynthetic meter (Licor-6200). The efficiency of intrinsic water use was estimated according to Cregg *et al.* (2000). Biochemical analyses were conducted using 7th to 9th order mulberry leaves employing standard protocols. Protein estimation was performed following the Lowry *et al.* (1951) method; carbohydrate content was estimated according to the Plummer (1971) protocol; chlorophyll content was determined using the method of Hiscox and Israelstam (1979); and phenolic content was estimated as per the Malick and Singh (1980) protocol. The statistical analysis of the data was performed using the 't-test' to compare the values of each parameter between the shade and open conditions.

### Analysis of Phenotypic Plasticity

The phenotypic plasticity index (PI) was calculated for growth and yield, leaf anatomy, physiology and biochemical parameters separately (Grewell *et al.,* 2016). The difference between the maximum and



Fig. 1 : a) Open sunlight-grown mulberry genotypes; b) Coconut shade-grown mulberry genotypes

minimum values was divided by the maximum value to produce the index. Higher PI values, which are closer to one, imply that the variable is more plastic (Cheplick, 1995). The mean plasticity index (PI) was derived by averaging the plasticity index of individual groups such as growth and yield, leaf anatomy, physiology and biochemical traits.

### Screening for Resistance to Powdery Mildew Disease

Considering the natural infection of powdery mildew (*Phyllactinia corylea* [Pers.] Karst), continuous evaluation of its incidence was carried out throughout the year using the same shade experiment plot, without applying any control measures. For each genotype (6 plants/genotype/replication), four branches from different directions were selected and tagged for observation. The total number of leaves on each branch, along with the number of infected leaves, was recorded to calculate the disease incidence rate. All the infected leaves were categorized into different grades of infection using the 0-5 grading scale as described by Sharma and Gupta (2005). In this scale, 0=No infection, 1=0–5% leaf lamina covered by the symptoms, 2=6–25% leaf lamina covered by the symptoms, 3=26–50% leaf lamina covered by the symptoms, 4=51–75% leaf lamina covered by the symptoms, 5=76-100% leaf lamina covered by the symptoms. Per cent of disease index (PDI) was calculated according to the formula (McKinney, 1923).

$$\text{Per cent disease index} = \frac{\text{Sum of all numerical rating}}{\text{Total no. of leaves counted} \times \text{Maximum grade}} \times 100$$

The degree of disease resistance in mulberry genotypes was assessed based on the Per cent Disease Index (PDI) and classified as follows: 0 PDI = Immune/Completely Resistant, 0–5.0 PDI = Resistant, 5.1–20.0 PDI = Moderately Resistant, 20.1–50.0 PDI = Susceptible and 50.1-100 PDI = Highly Susceptible (Sharma and Gupta, 2005).

## Results and Discussion

### Morphological Traits

In full sunlight, the leaf color of mulberry genotypes varied significantly across different genotypes. For instance, CS-1 had light green leaves with a strongly glossy surface, while CS-6 exhibited green leaves with a strongly glossy texture (Fig. 2c). Genotypes like CS-7, CS-10, Sahana and V-1 showed dark green leaves with a glossy surface, whereas CS-2 had green leaves with a glossy appearance (Fig. 2k) and CS-3, CS-4 and CS-8 also displayed green leaves with a glossy texture. M-5 and CS-9 had light green, non-glossy leaves, while CS-5 and CS-11 exhibited dark green leaves with a non-glossy surface (Fig. 2g). In shade conditions, there were noticeable changes in leaf color among the genotypes. For example, leaves turned dark green in CS-1, CS-3, CS-4, CS-6, CS-9, and M-5. In contrast, no significant changes in leaf color were observed in CS-2, CS-8 and Sahana, although the glossiness of leaves disappeared in CS-2, CS-8 and V-1 under shaded conditions.


Fig. 2 : Shade-tolerant genotype, CS-6: a) Full sunlight-grown plant and its leaf (c), b) Shade-grown plant and its leaf (d); Shade-avoidance genotype, CS-5: e) Full sunlight-grown plant and its leaf (g), f) Shade-grown plant and its leaf (h); Shade-intolerant genotype, CS-2; i) Full sunlight-grown plant and its leaf (k), j) Shade-grown plant and its leaf (1).

**Table 1**

**Comparative analysis of growth and yield parameters in open- and shade-grown mulberry genotypes**

| Genotypes | No. of branches/plant | | | Average shoot length (cm) | | | Shoot girth (cm) | | | Inter-nodal length (cm) | | | Petiole length (cm) | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Open | Shade | | Open | Shade | | Open | Shade | | Open | Shade | | Open | Shade | |
| **CS-1** | 9.45±1.52 | 3.64±0.74 | ** | 106.74±11.70 | 158.29±16.68 | ** | 1.09±0.16 | 0.65±0.10 | ** | 5.99±0.47 | 7.37±0.65 | ** | 4.82±0.36 | 6.44±0.35 | ** |
| **CS-2** | 6.48±0.65 | 3.10±0.66 | ** | 99.68±7.77 | 29.22±10.31 | ** | 0.82±0.06 | 0.51±0.07 | ** | 5.00±0.74 | 4.26±0.90 | ** | 3.78±0.47 | 3.96±0.53 | ** |
| **CS-3** | 7.94±1.16 | 7.93±1.24 | NS | 91.58±11.72 | 92.13±5.42 | NS | 0.85±0.04 | 0.84±0.05 | NS | 6.64±0.51 | 7.14±0.54 | NS | 4.56±0.43 | 4.86±0.41 | NS |
| **CS-4** | 9.92±0.99 | 5.06±1.50 | ** | 87.65±13.10 | 124.16±6.16 | ** | 1.06±0.11 | 0.63±0.10 | ** | 4.68±0.81 | 8.75±0.68 | ** | 4.63±0.39 | 7.65±0.36 | ** |
| **CS-5** | 6.08±0.80 | 3.11±0.48 | ** | 96.90±7.66 | 167.93±37.34 | ** | 1.30±0.06 | 0.60±0.08 | ** | 6.20±0.76 | 8.53±0.97 | ** | 5.25±0.26 | 7.16±1.21 | ** |
| **CS-6** | 8.39±2.10 | 8.00±1.55 | NS | 109.06±11.68 | 112.36±10.14 | NS | 1.32±0.07 | 1.31±0.03 | NS | 5.21±0.69 | 5.38±0.77 | NS | 4.26±0.25 | 4.45±0.52 | NS |
| **CS-7** | 11.65±1.33 | 11.25±1.26 | NS | 132.12±14.48 | 133.56±47.66 | NS | 0.80±0.8 | 0.79±0.04 | NS | 5.01±1.03 | 5.11±0.67 | NS | 5.10±0.25 | 5.25±0.59 | NS |
| **CS-8** | 9.55±2.05 | 2.85±0.45 | ** | 82.66±14.51 | 27.20±13.49 | ** | 0.53±0.05 | 0.33±0.05 | ** | 5.63±0.95 | 5.00±1.20 | ** | 5.30±0.15 | 5.48±0.65 | NS |
| **CS-9** | 7.41±1.04 | 3.95±0.81 | ** | 80.01±11.49 | 77.01±14.84 | ** | 0.77±0.08 | 0.56±0.04 | ** | 6.30±0.79 | 7.58±0.60 | ** | 4.15±0.39 | 6.55±0.24 | ** |
| **CS-10** | 6.44±1.23 | 3.85±0.83 | ** | 104.38±12.48 | 159.06±34.37 | ** | 0.85±0.04 | 0.51±0.07 | ** | 4.70±0.48 | 6.40±0.20 | ** | 5.46±0.46 | 6.65±0.83 | ** |
| **CS-11** | 5.55±1.19 | 3.46±0.57 | ** | 95.96±6.17 | 179.29±36.21 | ** | 0.75±0.05 | 0.46±0.04 | ** | 5.03±0.46 | 6.90±0.67 | ** | 5.80±0.58 | 7.05±0.22 | ** |
| **M-5** | 10.76±0.88 | 6.88±1.80 | ** | 99.11±10.27 | 169.16±15.92 | ** | 0.85±0.03 | 0.61±0.07 | ** | 5.51±0.74 | 6.55±0.56 | ** | 4.35±0.42 | 5.48±0.81 | ** |
| **Sahana** | 5.33±1.16 | 4.68±1.06 | NS | 79.91±34.59 | 80.55±16.20 | NS | 0.81±0.04 | 0.80±0.06 | NS | 3.85±0.91 | 3.92±0.43 | NS | 4.27±0.42 | 4.69±0.82 | NS |
| **V-1** | 13.90±1.30 | 8.85±0.90 | ** | 133.50±8.94 | 227.90±40.15 | ** | 1.04±0.10 | 0.58±0.07 | ** | 5.40±0.85 | 9.31±0.66 | ** | 5.78±0.66 | 8.13±0.87 | ** |

** and NS denote significant at the 1% ($p \leq 0.01$) levels of probability and Not Significant, respectively.

**Cont.. Table 1**
**Comparative analysis of growth and yield parameters in open- and shade-grown mulberry genotypes**

| Genotypes | Leaf area ($cm^2$) | | | Leaf specific wt. ($mg/cm^2$) | | | Leaf moisture content (%) | | | Leaf moisture retention ( % ) | | | Leaf yield / plant/ harvest (g) | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Open | Shade | | Open | Shade | | Open | Shade | | Open | Shade | | Open | Shade | |
| **CS-1** | 338.23±18.32 | 458.87±33.47 | ** | 16.92±0.79 | 8.82±0.55 | ** | 76.07±1.95 | 85.92±2.60 | ** | 66.07±3.02 | 50.34±0.26 | ** | 422.98±71.75 | 251.14±56.05 | ** |
| **CS-2** | 236.59±20.62 | 81.93±16.21 | ** | 14.23±0.70 | 7.50±0.31 | ** | 74.78±2.32 | 76.21±2.32 | ** | 59.78±2.59 | 40.35±0.32 | ** | 224.43±74.38 | 106.24±37.32 | ** |
| **CS-3** | 181.04±14.83 | 193.04±21.78 | NS | 15.71±0.62 | 15.30±0.26 | NS | 75.66±2.34 | 76.03±3.14 | NS | 68.66±3.08 | 67.71±2.45 | NS | 326.52±39.19 | 310.81±25.81 | NS |
| **CS-4** | 273.77±18.33 | 340.68±19.28 | ** | 16.28±0.50 | 9.51±0.26 | ** | 76.67±1.83 | 86.26±3.45 | ** | 66.67±3.84 | 50.32±0.23 | ** | 425.43±29.65 | 227.19±38.49 | ** |
| **CS-5** | 379.62±17.91 | 463.79±22.93 | ** | 17.36±0.60 | 8.37±0.30 | ** | 74.42±2.69 | 86.47±1.32 | ** | 64.42±3.29 | 50.40±0.24 | ** | 648.24±77.44 | 302.05±68.62 | ** |
| **CS-6** | 335.66±19.76 | 349.49±36.41 | NS | 20.09±0.51 | 19.93±0.87 | NS | 77.34±1.33 | 77.53±2.15 | NS | 73.34±2.05 | 73.90±2.28 | NS | 411.53±54.52 | 405.43±57.64 | NS |
| **CS-7** | 250.59±13.98 | 261.39±25.79 | NS | 16.40±0.27 | 16.02±0.45 | NS | 75.39±3.31 | 75.36±1.39 | NS | 71.39±2.67 | 70.35±2.82 | NS | 320.28±47.58 | 319.49±49.61 | NS |
| **CS-8** | 147.76±18.71 | 64.49±17.29 | ** | 14.47±0.32 | 6.29±0.16 | ** | 73.95±2.93 | 83.66±3.80 | ** | 63.95±2.08 | 41.33±2.43 | ** | 101.71±13.99 | 73.23±21.95 | ** |
| **CS-9** | 240.02±19.52 | 297.93±16.18 | ** | 15.63±0.27 | 8.33±0.16 | ** | 75.64±1.46 | 86.41±1.46 | ** | 65.64±2.73 | 60.60±0.32 | ** | 249.82±35.07 | 103.18±28.25 | ** |
| **CS-10** | 262.41±28.47 | 348.24±28.77 | ** | 16.51±0.22 | 9.33±0.18 | ** | 74.65±1.06 | 87.45±1.51 | ** | 64.65±3.22 | 65.98±3.97 | ** | 324.29±35.94 | 227.40±39.68 | ** |
| **CS-11** | 254.29±26.57 | 330.50±23.39 | ** | 15.53±0.33 | 8.46±0.33 | ** | 76.34±1.06 | 87.00±1.06 | ** | 66.34±2.30 | 62.13±3.20 | ** | 256.26±44.24 | 186.18±48.27 | ** |
| **M-5** | 148.24±13.48 | 211.20±10.96 | ** | 16.47±0.36 | 9.16±0.05 | ** | 72.78±2.25 | 84.20±1.00 | ** | 62.78±1.97 | 60.19±3.97 | ** | 328.27±26.74 | 125.31±41.46 | ** |
| **Sahana** | 261.43±34.78 | 278.54±17.08 | NS | 17.46±0.24 | 17.30±0.25 | NS | 76.38±2.41 | 77.71±2.46 | NS | 75.35±2.36 | 73.56±3.27 | NS | 316.85±55.37 | 311.06±29.78 | NS |
| **V-1** | 339.62±37.95 | 441.13±34.23 | ** | 18.58±0.29 | 10.43±0.27 | ** | 75.96±1.93 | 82.62±5.28 | ** | 73.05±2.03 | 54.97±1.42 | ** | 541.90±87.10 | 244.94±52.34 | ** |

** and NS denote significant at the 1% ($p \leq 0.01$) levels of probability and Not Significant, respectively.

**TABLE 2**
**Comparative analysis of leaf anatomical parameters in open- and shade-grown mulberry genotypes**

| Genotypes | Leaf thickness (μm) | | | Upper cuticle thickness (μm) | | | Spongy parenchyma tissue (μm) | | | Stomatal frequency (no./mm²) | | | No. of chloroplast/stomata | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Open | Shade | | Open | Shade | | Open | Shade | | Open | Shade | | Open | Shade | |
| **CS-1** | 112.83±4.95 | 85.16±2.85 | ** | 5.28±0.14 | 3.41±0.23 | ** | 40.55±1.47 | 27.16±1.47 | ** | 673.45±21.07 | 425.16±15.84 | ** | 7.26±0.40 | 12.00±1.41 | ** |
| **CS-2** | 63.01±1.78 | 43.66±2.42 | ** | 3.31±0.19 | 1.78±0.40 | ** | 26.16±1.03 | 20.00±0.63 | ** | 741.83±29.62 | 755.00±14.75 | ** | 8.45±0.51 | 6.16±0.75 | ** |
| **CS-3** | 96.16±1.16 | 94.50±4.41 | NS | 5.03±0.53 | 4.48±0.78 | NS | 36.33±1.09 | 34.50±5.24 | NS | 576.66±44.00 | 781.00±20.75 | NS | 15.55±0.81 | 15.33±0.82 | NS |
| **CS-4** | 86.18±1.47 | 64.51±2.42 | ** | 4.73±0.48 | 3.33±0.12 | ** | 32.36±1.87 | 24.16±1.94 | ** | 762.33±26.49 | 774.00±28.29 | NS | 7.48±0.54 | 13.16±0.75 | ** |
| **CS-5** | 76.83±2.13 | 54.00±2.52 | ** | 3.95±0.66 | 2.36±0.15 | ** | 29.56±1.41 | 22.33±1.21 | ** | 756.52±37.78 | 538.16±26.29 | ** | 9.31±0.40 | 13.50±2.16 | ** |
| **CS-6** | 173.52±1.51 | 162.29±2.30 | NS | 8.11±0.52 | 7.63±0.43 | NS | 68.33±1.36 | 66.50±2.73 | NS | 443.26±32.89 | 449.83±41.12 | NS | 16.93±1.87 | 17.00±0.89 | NS |
| **CS-7** | 116.12±2.36 | 112.83±7.26 | NS | 6.46±0.40 | 5.86±0.87 | NS | 45.16±1.64 | 44.33±2.42 | NS | 578.31±45.59 | 582.16±8.10 | NS | 15.19±0.75 | 15.66±0.51 | NS |
| **CS-8** | 53.83±4.44 | 30.33±6.02 | ** | 2.95±0.46 | 1.73±0.57 | ** | 23.54±1.63 | 15.00±1.78 | ** | 357.16±24.52 | 362.16±16.86 | NS | 6.48±0.54 | 3.00±1.26 | ** |
| **CS-9** | 75.73±0.75 | 56.66±1.75 | ** | 4.71±0.47 | 2.61±0.14 | ** | 28.66±2.13 | 23.33±4.08 | ** | 656.83±28.99 | 430.50±13.60 | ** | 8.73±0.40 | 13.16±0.98 | ** |
| **CS-10** | 112.52±1.37 | 84.33±3.44 | * | 5.48±0.18 | 3.26±0.12 | ** | 46.16±1.04 | 34.50±3.27 | ** | 731.17±11.66 | 529.66±23.26 | ** | 12.16±2.09 | 14.83±1.16 | ** |
| **CS-11** | 82.16±4.21 | 55.83±2.56 | ** | 4.55±0.17 | 2.48±0.11 | ** | 33.56±1.72 | 22.33±1.21 | ** | 759.36±19.97 | 422.66±10.65 | ** | 11.34±0.81 | 14.66±1.03 | ** |
| **M-5** | 96.52±2.07 | 75.84±2.48 | ** | 5.53±0.14 | 3.33±0.16 | ** | 34.53±1.72 | 23.00±3.03 | ** | 574.56±37.42 | 390.66±60.90 | ** | 10.55±0.51 | 15.00±0.89 | ** |
| **Sahana** | 110.16±9.98 | 104.66±3.50 | NS | 5.95±0.47 | 5.65±0.39 | NS | 47.16±1.32 | 45.83±3.76 | NS | 826.33±67.21 | 831.33±11.87 | NS | 14.83±0.40 | 15.33±0.81 | NS |
| **V-1** | 157.66±1.86 | 89.00±6.66 | ** | 6.50±0.14 | 4.28±0.11 | ** | 52.66±1.36 | 26.50±3.39 | ** | 685.00±13.34 | 450.00±27.75 | ** | 10.66±0.51 | 15.00±0.89 | ** |

** and NS denote significant at the 1% ($p \leq 0.01$) levels of probability and Not Significant, respectively.

**Cont… Table 2**

**Comparative analysis of leaf anatomical parameters in open- and shade-grown mulberry genotypes**

| Genotypes | Stomatal length (μm) | | | Trichomes density ($mm^2$) | | |
|---|---|---|---|---|---|---|
| | Open | Shade | | Open | Shade | |
| **CS-1** | 33.28±0.04 | 35.33±0.01 | ** | 36.56±2.85 | 22.16±1.16 | ** |
| **CS-2** | 28.00±0.05 | 33.33±1.16 | ** | 44.33±3.72 | 56.16±1.47 | ** |
| **CS-3** | 37.58±1.59 | 38.16±1.62 | NS | 14.52±2.42 | 14.00±1.41 | NS |
| **CS-4** | 41.83±0.19 | 45.16±0.63 | ** | 37.65±1.78 | 14.33±1.36 | ** |
| **CS-5** | 37.00±0.58 | 44.33±0.25 | ** | 45.33±3.14 | 23.66±1.75 | ** |
| **CS-6** | 29.16±1.75 | 30.83±0.43 | NS | 6.16±1.94 | 5.00±1.54 | NS |
| **CS-7** | 39.33±0.58 | 40.66±1.70 | NS | 9.83±1.16 | 10.00±2.09 | NS |
| **CS-8** | 25.16±0.06 | 21.16±2.31 | ** | 57.24±1.78 | 74.00±2.28 | ** |
| **CS-9** | 32.33±1.45 | 40.00±1.89 | ** | 44.66±2.58 | 24.16±2.13 | ** |
| **CS-10** | 43.50±0.93 | 48.33±0.55 | ** | 36.83±2.13 | 17.16±3.76 | ** |
| **CS-11** | 34.33±2.21 | 39.37±0.96 | ** | 46.33±2.33 | 25.00±2.36 | ** |
| **M-5** | 29.66±0.94 | 36.83±1.35 | ** | 36.56±1.87 | 14.66±1.21 | ** |
| **Sahana** | 38.16±0.78 | 39.50±1.53 | NS | 14.50±2.07 | 14.23±2.31 | NS |
| **V-1** | 38.00±1.82 | 45.00±1.78 | ** | 33.33±4.71 | 21.33±2.33 | ** |

** and NS denote significant at the 1% ($p \leq 0.01$) levels of probability and Not Significant, respectively.

The growth habit also exhibited considerable variability between genotypes under different light conditions. In full sunlight, the growth nature was erect in genotypes such as CS-1, CS-2 (Fig. 2i), CS-3, CS-4, CS-6 (Fig. 2a), CS-7, CS-10, CS-11, M-5 and V-1. Sahana and CS-9 displayed a semi-erect growth habit, while CS-5 had a spreading growth form (Fig. 2e). Under shaded conditions, several genotypes displayed a shift towards a spreading growth habit, including CS-1, CS-3, CS-4, CS-9, CS-10, CS-11, M-5 and V-1, indicating a plastic response to reduced light availability. However, the growth form remained constant in CS-3, CS-6 (Fig. 2), CS-7 and Sahana, which exhibited the same growth pattern regardless of the light conditions.

**Growth, Yield and Anatomical Features**

Significant variability was observed for growth and yield traits between mulberry genotypes grown in open versus shaded conditions. Traits such as plant height, shoot girth, number of branches per plant, internodal distance, petiole length, leaf area, leaf-specific weight, leaf moisture content and its retention capacity showed notable differences between plants grown in shaded and open environments (Table 1). Similarly, key leaf anatomical traits (Fig. 3), including leaf thickness,

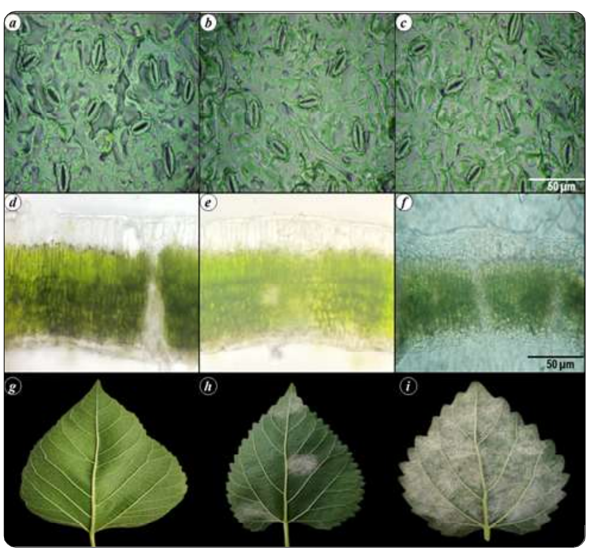

Fig. 3 : Stomatal view of CS-6 (a), CS-5 (b) and CS-2 (C) genotypes; Leaf cross sectional view of CS-6 (d), CS-5 (e) and CS-2 (f) genotypes; Leaves of powdery mildew resistant (g: CS-6), moderately resistant (h: CS-3) and highly susceptible (i: CS-1) genotypes

spongy tissue thickness, upper cuticle thickness, stomatal number, chloroplast number, stomatal size, and trichome density, demonstrated significant plasticity (Table 2).

Interestingly, four genotypes, *viz.,* CS-3, CS-6, CS-7, and Sahana, showed better leaf yield under shaded conditions among the 14 genotypes with similar performance observed for these same genotypes in open conditions. Notably, the CS-6 genotype demonstrated exceptional performance under shaded conditions, achieving a leaf yield of 405.43 g per plant/harvest, which was 30.33 per cent higher than the shade-tolerant variety Sahana. Additionally, CS-6 consistently exhibited the highest leaf thickness of 162.29 µm under shade conditions compared to the other genotypes. Importantly, the leaf yield and leaf thickness in CS-6 were more consistent across both shaded and open conditions. Under full sunlight, however, the V-1 variety out performed others, producing the highest leaf yield of 541.90 g per plant, though it showed inferior performance in shaded environments.

**Physio-Biochemical Characteristics**

The CS-6 emerged as the top performer under shaded conditions, exhibiting the highest values across several key parameters, which include a net photosynthetic rate of 13.16 µmol ($CO_2$) $m^{-2}$ $s^{-1}$, water use efficiency (WUE) of 23.97 µmol ($CO_2$) $mmol^{-1}$ ($H_2O$), stomatal conductance of 26.9 mol $m^{-2}$ $s^{-1}$ and intercellular $CO_2$ concentration of 6.11 µmol ($CO_2$) $m^{-2}$ $s^{-1}$ (Table 3). The biochemical content of protein, carbohydrates, phenol and chlorophyll in the leaves of CS-1, CS-2, CS-5, CS-8, CS-9, CS-10, CS-11, M-5 and V-1 grown in open and shade-grown conditions revealed significant variability. However, no significant difference was noticed in the genotypes CS-3, CS-6, CS-7 and Sahana, as they are more stable in their biochemical composition regardless of light availability (Table 4).

**Phenotypic Plasticity Index**

The expression of phenotypic plasticity recorded was highest in the genotypes CS-1, CS-2, CS-4, CS-5,

**TABLE 3**

**Comparative analysis of physiological parameters in open- and shade-grown mulberry genotypes**

| Genotypes | Photosynthetic rate [µmol ($CO_2$) $m^{-2}$ $s^{-1}$] | | | Intrinsic water use efficiency [µmol ($CO_2$) $mmol^{-1}$ ($H_2O$)] | | | Stomatal conductance [mol $m^{-2}$ $s^{-1}$] | | | Transpiration rate [mmol $H_2O$ $m^{-2}$ $s^{-1}$] | | | Intercellular $CO_2$ concentration [µmol ($CO_2$) $m^{-2}$ $s^{-1}$] | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Open | Shade | | Open | Shade | | Open | Shade | | Open | Shade | | Open | Shade | |
| **CS-1** | 10.32 | 9.66 | ** | 22.32 | 20.26 | ** | 25.36 | 23.7 | ** | 18.39 | 16.32 | ** | 6.11 | 4.63 | ** |
| **CS-2** | 9.63 | 6.12 | ** | 20.14 | 16.26 | ** | 27.17 | 21.9 | ** | 19.56 | 13.23 | ** | 5.99 | 3.23 | ** |
| **CS-3** | 12.3 | 11.49 | ** | 23.56 | 22.17 | ** | 26.14 | 21.5 | ** | 19.16 | 16.66 | ** | 6.17 | 5.36 | ** |
| **CS-4** | 10.14 | 9.47 | ** | 23.68 | 20.97 | ** | 27.25 | 23.71 | ** | 18.33 | 17.45 | ** | 5.96 | 4.11 | ** |
| **CS-5** | 10.36 | 9.10 | ** | 22.51 | 20.57 | ** | 24.52 | 22.8 | ** | 17.25 | 15.96 | ** | 5.94 | 3.96 | ** |
| **CS-6** | 13.52 | 13.16 | NS | 24.12 | 23.97 | NS | 27.71 | 26.9 | NS | 20.69 | 18.33 | ** | 7.11 | 6.11 | ** |
| **CS-7** | 12.96 | 11.44 | ** | 24.13 | 22.56 | ** | 26.39 | 25.4 | ** | 19.14 | 17.15 | ** | 6.59 | 5.23 | ** |
| **CS-8** | 9.54 | 6.26 | ** | 20.79 | 16.70 | ** | 26.41 | 20.4 | ** | 19.36 | 14.52 | * | 6.51 | 3.33 | ** |
| **CS-9** | 12.47 | 9.51 | ** | 22.47 | 20.22 | ** | 25.44 | 23.5 | ** | 20.11 | 17.26 | ** | 6.15 | 4.56 | * |
| **CS-10** | 11.22 | 10.3 | ** | 23.97 | 21.49 | ** | 24.32 | 22.5 | ** | 18.71 | 16.52 | ** | 5.36 | 4.21 | ** |
| **CS-11** | 8.78 | 7.44 | ** | 21.47 | 19.64 | ** | 24.36 | 22.1 | ** | 19.16 | 17.46 | ** | 6.12 | 4.36 | ** |
| **M-5** | 12.56 | 10.17 | ** | 21.56 | 18.63 | ** | 26.71 | 23.7 | ** | 19.36 | 15.36 | ** | 5.91 | 3.36 | ** |
| **Sahana** | 12.12 | 11.56 | ** | 23.77 | 22.26 | ** | 27.96 | 26.1 | ** | 19.5 | 16.23 | ** | 6.13 | 5.79 | ** |
| **V-1** | 14.11 | 10.32 | ** | 25.57 | 21.16 | ** | 28.35 | 24.4 | ** | 21.36 | 18.88 | ** | 8.12 | 5.39 | ** |

** and NS denote significant at the 1% ($p \leq 0.01$) levels of probability and Not Significant, respectively.

TABLE 4

**Comparative analysis of biochemical parameters in open- and shade-grown mulberry genotypes**

| Genotypes | Protein (%) | | | Carbohydrate (%) | | | Chlorophyll a (mg/g) | | | Chlorophyll b (mg/g) | | | Phenol (mg/g) | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Open | Shade | | Open | Shade | | Open | Shade | | Open | Shade | | Open | Shade | |
| **CS-1** | 26.36±0.10 | 18.22±0.12 | ** | 14.21±0.02 | 10.28±0.16 | ** | 3.18±0.03 | 2.22±0.07 | ** | 1.19±0.04 | 2.14±0.01 | ** | 5.89±0.54 | 4.48±0.08 | ** |
| **CS-2** | 24.46±0.36 | 19.55±0.29 | ** | 13.35±0.45 | 7.14±0.11 | ** | 2.71±0.31 | 1.50±0.29 | ** | 1.22±0.07 | 0.77±0.22 | ** | 4.16±0.10 | 3.16±0.04 | ** |
| **CS-3** | 25.62±0.62 | 24.56±0.35 | NS | 14.24±0.03 | 13.61±0.55 | NS | 3.15±0.11 | 2.81±0.19 | NS | 2.36±0.47 | 2.13±0.25 | NS | 7.40±0.10 | 7.20±0.20 | NS |
| **CS-4** | 25.29±0.11 | 19.38±0.31 | ** | 14.53±0.31 | 10.39±0.29 | ** | 3.12±0.13 | 2.23±0.15 | ** | 1.28±0.08 | 2.23±0.15 | ** | 6.33±0.05 | 4.46±0.57 | ** |
| **CS-5** | 25.77±0.60 | 18.87±0.12 | ** | 14.41±0.42 | 9.24±0.08 | ** | 3.21±0.09 | 2.46±0.05 | ** | 1.18±0.11 | 2.22±0.05 | ** | 6.20±0.02 | 4.57±0.56 | ** |
| **CS-6** | 27.22±0.09 | 26.57±0.87 | NS | 15.33±0.11 | 14.93±0.57 | NS | 3.88±0.02 | 3.19±0.57 | NS | 2.29±0.07 | 2.33±0.02 | NS | 7.87±0.06 | 7.20±0.51 | NS |
| **CS-7** | 26.28±0.17 | 25.77±0.92 | NS | 14.36±0.14 | 13.18±0.68 | NS | 3.18±0.03 | 3.14±0.00 | NS | 2.11±0.10 | 2.16±0.05 | NS | 7.14±0.02 | 6.81±0.58 | NS |
| **CS-8** | 22.79±0.55 | 14.58±0.50 | ** | 13.17±0.04 | 8.22±0.07 | ** | 2.57±0.18 | 1.70±0.17 | ** | 1.56±0.10 | 0.56±0.06 | ** | 5.49±0.32 | 4.21±0.01 | ** |
| **CS-9** | 23.50±0.51 | 18.34±0.99 | ** | 13.28±0.25 | 9.18±0.04 | ** | 3.17±0.08 | 2.60±0.26 | ** | 1.35±0.08 | 2.36±0.01 | ** | 6.34±0.34 | 4.90±0.64 | ** |
| **CS-10** | 24.67±0.62 | 19.11±0.52 | ** | 14.45±0.14 | 10.31±0.21 | ** | 3.25±0.13 | 2.53±0.22 | ** | 1.26±0.04 | 2.10±0.10 | ** | 6.28±0.03 | 4.01±0.56 | ** |
| **CS-11** | 23.63±0.42 | 18.44±0.26 | ** | 14.28±0.02 | 10.36±0.33 | ** | 3.66±0.32 | 2.32±0.09 | ** | 1.50±0.06 | 2.16±0.07 | ** | 6.33±0.07 | 3.49±0.54 | ** |
| **M-5** | 25.52±0.39 | 19.96±0.34 | ** | 13.25±0.21 | 10.41±0.41 | ** | 3.24±0.02 | 2.33±0.02 | ** | 1.24±0.01 | 2.23±0.08 | ** | 6.50±0.31 | 4.31±0.04 | ** |
| **Sahana** | 24.11±0.87 | 23.53±0.53 | NS | 14.17±0.06 | 13.51±0.33 | NS | 3.22±0.05 | 3.18±0.06 | NS | 1.84±0.03 | 1.96±0.66 | NS | 6.73±0.01 | 6.46±0.56 | NS |
| **V-1** | 25.43±0.61 | 20.16±0.02 | ** | 14.64±0.25 | 10.80±0.39 | ** | 3.18±0.07 | 2.23±0.32 | ** | 1.29±0.10 | 2.16±0.06 | ** | 6.12±0.00 | 4.03±0.58 | ** |

** and NS denote significant at the 1% ($p \leq 0.01$) levels of probability and Not Significant, respectively.

CS-9, CS-10, CS-11, M-5 and V-1 and low in CS-2 and CS-8. Notably, there was no expression of phenotypic plasticity in the shade-tolerant genotypes such as CS-3, CS-6, CS-7 and Sahana, depicting stable phenotypic traits regardless of shading condition. Among the various traits analyzed, the growth and yield traits exhibited the highest plasticity index of 0.25, followed by physiological traits at 0.24, leaf anatomical traits at 0.22 and biochemical traits at 0.21 (Fig. 4).

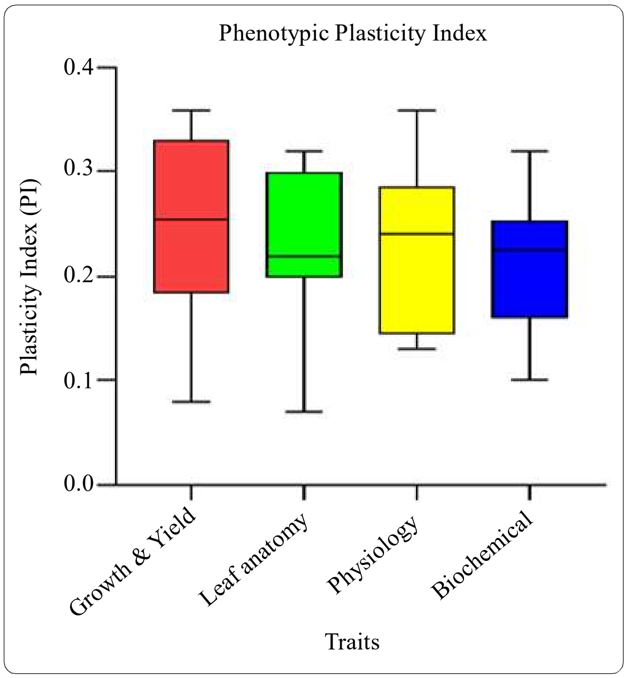


Fig. 4 : Boxplots showing phenotypic plasticity index (PI) distribution for each of the measured traits among the four identified groups.

## Screening for Resistance to Powdery Mildew

Screening was conducted on eleven clonally selected genotypes (CS-1 to CS-11), along with the M-5, V-1, and Sahana varieties, under coconut palms to assess their resistance to the fungal pathogen *Phyllactinia corylea* (Pers.) Karst. Disease occurrence was observed from July to March in the shade plot, while in the open mulberry garden, it was recorded from November to February during the study period. The percentage of disease index (PDI) was used to evaluate the degree of resistance. The results revealed that CS-6 exhibited high resistance to powdery mildew (Fig. 3g), with a PDI of 2.37. Genotypes CS-3, CS-7, and Sahana displayed moderate resistance (Fig. 3h), with PDI values ranging from 8.42 to 18.51. In contrast, CS-1, CS-2, CS-4, CS-5, CS-8, CS-9, CS-10, CS-11, M-5 and V-1 were highly susceptible (Fig. 3i), with PDI values ranging from 54.16 to 82.27 (Table 5)

**Table 5**

**Disease responses in different mulberry genotypes**

| Genotypes | Per cent Disease Index (PDI) | Disease response |
|---|---|---|
| CS-1 | 64.23 | Highly susceptible |
| CS-2 | 54.16 | Highly susceptible |
| CS-3 | 16.29 | Moderately resistant |
| CS-4 | 74.11 | Highly susceptible |
| CS-5 | 59.64 | Highly susceptible |
| CS-6 | 2.37 | Resistant |
| CS-7 | 8.42 | Moderately resistant |
| CS-8 | 71.36 | Highly susceptible |
| CS-9 | 88.27 | Highly susceptible |
| CS-10 | 77.92 | Highly susceptible |
| CS-11 | 68.41 | Highly susceptible |
| M-5 | 55.74 | Highly susceptible |
| Sahana | 18.51 | Moderately resistant |
| V-1 | 73.54 | Highly susceptible |

Shade tolerance is known for plants' ability to survive and thrive under low light conditions (Lambers *et al.,* 1998). In natural environments, shade is primarily caused by two signaling factors: a low proportion of red light to far-red light (R:FR) and low photosynthetically active radiation (PAR) (Franklin and Whitelam, 2005 and Vandenbussche *et al.,* 2005). All plants can acclimatize to shaded environments, altering their growth strategies to make the most use of the available light (Lambers *et al.,* 1998). In coconut plantations, the amount of light reaching the ground changes significantly over time. During the first five years, the area beneath the coconut canopy receives the maximum amount of solar energy and as the coconut trees mature, they cast increasingly intense shade. By attaining 20 years of age, dense shading severely limits the growth of other plants and at 50 years, the canopy height allows enough light for the cultivation of intercrops. The other important factor for intercropping is the root distribution of the coconut trees, typically confined to a 2-meter radius around the base or about 25 per cent of the total area. This limited root spread leaves 75-80 per cent of the land area available for farming other crops, such as mulberry, which can take advantage of the less shaded and root-restricted spaces (Bavappa *et al.,* 1986). Considering these advantages and using ~75-80 per cent of the land area available under the coconut plantation, we have made a systematic investigation not only to identify naturally occurring mulberry variants but also to evaluate their potential, which can survive and thrive under low light conditions to propagate them as intercropping.

A set of eleven naturally occurring variants of mulberry with respect to morphometric traits (Basavaiah *et al.,* 1994 and Dandin *et al.,* 1996), named CS-1, CS-2, CS-3, CS-4, CS-5, CS-6, CS-7, CS-8, CS-9, CS-10 and CS-11, was evaluated. All these mulberry genotypes, including control genotypes (M-5, Sahana and V-1) grown under open and shade conditions, exhibit varied responses and are accordingly categorized as shade-tolerant (CS-3, CS-6, CS-7 and Sahana), shade-avoidant (CS-1, CS-4, CS-5, CS-9, CS-10, CS-11, M-5 and V-1) and shade-intolerant (CS-2 and CS-8).

**Shade Tolerance**

The shade tolerance exhibited by the mulberry genotypes CS-3, CS-6, CS-7 and Sahana with stability in morphology, growth and productivity explicit that these have evolved with specific adaptations to thrive under shade stress. Notably, as there was no variability in leaf color, leaf surface or growth habit when grown under partial shade compared to full sunlight, it depicts these plants did not undergo significant changes in their structure or growth patterns due to reduced light. However, the ability of these genotypes to maintain consistent performance in low light conditions is largely due to several key anatomical and physiological traits (Valladares and Niinemets, 2008). For instance, these shade-tolerant genotypes display more leaf thickness with thicker cuticles and spongy parenchyma tissues, which are likely to contribute to enhanced light absorption and water retention (Beck, 2010 and Ni *et al.,* 2015). The higher number of chloroplasts in the stomata suggests that these plants are better equipped for photosynthesis in lower light conditions, while the lower number of trichomes on the leaf surface may help reduce water loss and light reflection. These anatomical features are consistent with findings by Babu *et al.* (2006), who also identified similar adaptive traits for shade tolerance in mulberry genotypes. Furthermore, to adapt to the low irradiance in shaded environments, shade-tolerant genotypes like CS-3, CS-6, CS-7 and Sahana have been shown to increase their net photosynthetic rate. This is achieved by higher levels of chlorophyll, which enhances light absorption, as well as stronger antioxidant activities that help mitigate oxidative stress under reduced light (Ganguly *et al.,* 2020). These anatomical and physiological modifications collectively make these genotypes highly efficient in utilizing available light and resources to ensure success under partial shade.

However, the mechanisms underlying high-yielding ability under shade can vary significantly between different mulberry varieties or genotypes (Balakrishna *et al.,* 2000 and Babu *et al.,* 2006). This suggests that while some genotypes are well-adapted to shaded environments, the degree of adaptation and the specific mechanisms that confer shade tolerance may differ across genotypes. In line with this, shade-tolerant mulberry genotypes such as CS-3, CS-6, CS-7 and Sahana have been found to exhibit a lower reduction in leaf biochemical parameters such as proteins, carbohydrates and phenols under coconut shade conditions compared to shade-susceptible genotypes. These biochemical parameters are critical for maintaining plant growth and productivity and their relative stability under shaded conditions (Luigi *et al.,* 2022).

One such important biochemical factor is the level of phenolic compounds in the leaves. Phenolics play a key role in plant defence mechanisms, but they also impact photosynthetic performance. Under shade, an imbalance between the supply and demand for photosynthetic electrons can trigger the accumulation of phenolic compounds as a stress response. According to Zhang *et al.* (2018), this imbalance in the electron transport chain can lead to an increase in phenolic production, potentially reducing the efficiency of photosynthesis if the levels become too high. However, in shade-tolerant genotypes like CS-3, CS-6, CS-7 and Sahana, the relatively lower reduction in biochemical parameters, including phenols, suggests that these genotypes are better equipped to maintain metabolic balance and photosynthetic efficiency under reduced light conditions. This could be an important factor contributing to their higher overall productivity under shade, as they can maintain critical physiological functions even in less-than-ideal light environments. Therefore, understanding how different mulberry genotypes manage biochemical compounds like phenolic accumulation under shade can provide valuable insights for selecting cultivars that are both productive and resilient under varying light conditions (Zhang *et al.*, 2018).

**Shade Avoidance**

Often, plants exhibit shade avoidance syndrome, a strategy where they grow taller or increase photosynthetic efficiency to escape shade and capture more light (Mousset *et al.,* 2021). The shade-avoidant genotypes of mulberry (CS-1, CS-4, CS-5, CS-9, CS-10, CS-11, M-5 and V-1) exhibit a higher degree of phenotypic plasticity by altering their morphological and physiological traits in response to varying light conditions (Alpert and Simms, 2002). These include increased shoot length due to inter-node elongation, enhanced petiole growth, increased apical dominance, reduced branching and a higher leaf area to biomass ratio. These traits allow the plant to grow taller and spread its leaves more effectively, improving its chances of reaching light above the canopy in shaded environments (Niinemets, 2010 and Van Kleunen *et al.,* 2011). The mechanisms behind these alterations are complex and involve various photoreceptors and phytohormones, which regulate the plant's response to light. The photoreceptors - phytochromes and cryptochromes - detect the quality and intensity of light, which in turn triggers hormonal signals. These signals, involving key hormones like auxins and gibberellins, coordinate the changes in growth patterns such as elongation and leaf expansion (Ballare and Pierik, 2017).

In response to shade, many plants, including mulberry, typically develop smaller and thinner leaves, but in these genotypes, the increased leaf area and changes in stomatal density reflect anatomical plasticity, allowing better gas exchange and light capture under reduced light conditions (Terashima *et al.,* 2001 and Kumara *et al.,* 2021). Additionally, these shade-avoidant genotypes show improved leaf color, which correlates with a higher number of chloroplasts and chlorophyll concentration, indicating enhanced photosynthetic capacity. In shaded environments, chlorophyll-b accumulates more preferentially than chlorophyll-a, helping the plant adjust its light-harvesting mechanisms (Koike *et al.,* 2001). Chlorophyll b is a crucial component of the light-harvesting complex (LHC), which aids in capturing and transmitting light energy to the photosystem II (PSII) reaction center, optimizing photosynthesis even in low light (Lam *et al.,* 1984). Studies, such as those by Huang *et al.* (2011), have shown that shaded leaves can enhance their photosynthetic efficiency by utilizing LHC II to capture more light energy, making shade-avoidant genotypes more adaptable and efficient in light-limited environments. Through these combined physiological and developmental mechanisms, mulberries exhibiting shade avoidance are able to optimize their growth in response to shading, ensuring better light capture and maximizing their photosynthetic efficiency under low-light conditions (Mousset *et al.,* 2021).

**Shade Intolerance**

The shade-intolerant mulberry genotypes CS-2 and CS-8 exhibit significant reductions in growth and development when exposed to low light, reflecting their inability to deploy effective tolerance or avoidance mechanisms under shade conditions. These genotypes fail to adapt to low-light environments, leading to a decrease in their net carbon gain and overall growth (Lambers *et al.,* 1998). As a result, photosynthesis is severely affected, contributing to a stress response that impacts various physiological processes. Low light levels hinder the rates of anticlinal cell expansion, which affects leaf thickness, with leaves becoming thinner due to a reduction in both cell growth and cell division. In particular, the number of palisade cells, a layer of cells responsible for light absorption and photosynthesis, decreases because of the impaired cell division (Kalve *et al.,* 2014). This reduction in cell layers further contributes to the structural limitations of the leaf. Thinner leaves, as observed in CS-2 and CS-8, tend to have lower leaf dry mass per unit area (Terashima *et al.,* 2011). However, this trait is not beneficial for these genotypes under shade stress. The thinner leaves of CS-2 and CS-8 contain fewer chloroplasts and have thinner palisade tissue, which limits their ability to conduct efficient photosynthesis and $CO_2$ transport (Terashima *et al.,* 2011). These structural limitations reduce the capacity of the leaves to accumulate biomass, resulting in poor overall plant growth. Additionally, the reduced leaf thickness impacts carbon fixation and the ability to store energy, further compound the negative effects of low light. Moreover, carbohydrate concentrations in leaves can influence leaf structure. Research has shown that higher sucrose levels in leaves can lead to an increase in the number of palisade cell layers, which may help improve light capture and photosynthetic efficiency (Terashima *et al.,* 2006). However, in shade-intolerant genotypes, the lower light availability combined with reductions in soluble carbohydrates results in a lower specific leaf area (SLA) and poor leaf structure (Lambers and Poorter, 2004). When light deprivation exceeds 50 per cent, a significant reduction in soluble protein concentrations is also observed in shaded leaves. This reduction in soluble proteins is associated with decreased activity in enzymes critical for nitrogen metabolism, such as nitrate reductase, glutamine synthetase and glutamate synthetase, all of which are essential for the plant's ability to synthesize amino acids and support growth (Wang *et al.,* 2020).

The molecular mechanisms underlying shade tolerance, shade avoidance and shade intolerance in mulberry genotypes involve distinct pathways regulating light perception, growth and metabolic processes (Martinez-Garcia and Rodriguez-Concepcion, 2023). Shade-tolerant genotypes, like CS-3, CS-6, CS-7 and Sahana, exhibit upregulated genes involved in chlorophyll biosynthesis, antioxidant defense and stress-responsive pathways, which help maintain photosynthetic efficiency and metabolic stability under low light (Hay *et al.,* 2014; Molina-Contreras *et al.,* 2019 and Eghbal *et al.,* 2024). Shade-avoidant genotypes, such as CS-1, CS-4, CS-5, CS-9, CS-10, CS-11, M-5 and V-1, rely on light perception genes and growth regulators to promote elongation and optimize photosynthesis by enhancing chlorophyll production and leaf area (Hay *et al.,* 2014; Molina-Contreras *et al.,* 2019 and Eghbal *et al.,* 2024). In contrast, shade-intolerant genotypes, like CS-2 and CS-8, show reduced expression of photosynthesis-related genes, impaired cell division and decreased carbohydrate metabolism, leading to lower photosynthetic capacity and poor growth under shade (Zhang *et al.,* 2020). These molecular pathways determine each genotype's ability to adapt to varying light conditions.

**Powdery Mildew Resistance**

The powdery mildew (*Phyllactinia corylea*), a major foliar disease affecting mulberry plants, thrives well under low light intensity and high relative humidity common in shade environments (Austin *et al.,* 2011). This fungal disease disrupts the host plant's metabolic processes, leading to a reduced moisture content in infected leaves. These changes decrease the nutritional value and yield of the leaves and in severe cases, the disease can cause loss up to 20 per cent of the mulberry foliage (Gupta, 2001). More importantly, the disease significantly impacts the quality of the leaves (Manimegalai and Chandramohan, 2007). Powdery mildew incidence is most prevalent during the cooler months, particularly from September to March with peak infections occurring between January and February (Krishna Prasad and Siddaramaiah, 1979 and Biswas *et al.,* 1992). In the study, powdery mildew infection was observed throughout the year in mulberry genotypes grown under shade, indicating that the disease can persist even in conditions where light is limited. However, the disease resistance varied significantly across genotypes. Among the genotypes tested, CS-6 exhibited strong resistance to powdery mildew, while CS-3, CS-7 and Sahana showed moderate resistance. On the other hand, genotypes such as CS-2, CS-4, CS-5, CS-8, CS-9, CS-10, CS-11, M-5 and V-1 were highly susceptible to the disease. Interestingly, the leaf and cuticular thickness in certain genotypes, particularly the shade-tolerant ones like CS-3, CS-6, CS-7 and Sahana, were linked to increased resistance to powdery mildew. Thicker leaf cuticles are believed to act as a physical barrier against fungal infection, as they can limit the attachment and spread of spores (Commenil *et al.,* 1997). The resistance observed in CS-6 is particularly notable because it represents a genetic resistance, which is often considered the most sustainable and cost-effective method of controlling diseases like powdery mildew (Chattopadhyay *et al.,* 2011). By relying on genetic resistance, mulberry cultivation can reduce the need for chemical treatments, making it a more environmentally friendly and economically viable strategy in the long term.

Recognizing the availability of land in coconut plantations, although root distribution is confined to a 2-meter radius around the base or about 25 per cent of the total area and leaves 75-80 per cent of the land area for farming, the limiting factor is light and the need for a shade-tolerant mulberry variety with high yield and quality of leaves under reduced light. Among three promising shade-tolerant genotypes, CS-6 emerged as the highest-performing genotype with the highest leaf yield of 405.43 g/harvest and good leaf quality under up to 51 per cent shade. In addition, CS-6 exhibited resistance to powdery mildew, making it particularly valuable for cultivation in shaded environments. Having these significances, CS-6 shall be a potential mulberry variety for commercial exploitation and use as a genetic resource in breeding programmes to evolve greater shade-tolerant mulberry cultivars towards sustainable mulberry production even in an environment with less-than-ideal light conditions. The ability to cultivate CS-6 in these conditions opens the door for sustainable fodder production, as its leaves can serve as high-quality feed for livestock (Reshma and Asha, 2018).

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