

DIFFERENTIAL SHADE TOLERANCE OF SEVEN WARM-SEASON TURFGRASS SPECIES: GROWTH, TURF PERFORMANCE, CHLOROPHYLL CONTENT AND NET PHOTOSYNTHESIS UNDER GRADED SHADE

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ABSTRACT

Shade from trees and built structures is a major constraint to turf establishment and persistence in landscapes. Seven warm-season turfgrasses viz., St. Augustine grass, bermudagrass, Manila zoysiagrass, bahiagrass, seashore paspalum, centipedegrass and carpet grass were evaluated under four nominal shade levels (0, 25, 50 and 75%) in a completely randomised design (CRD) with a 7 × 4 factorial arrangement and three replications (84 plots). Shoot and root biomass, root:shoot ratio, turf quality (1-9), turf density (1-5), total chlorophyll, chlorophyll a:b ratio and net photosynthetic rate (Pn) were recorded. Species, shade and the species × shade interaction were significant ($P < 0.001$) for all traits. Measured photosynthetically active radiation (PAR) was reduced by 31.5, 53.8 and 71.9% under the nominal 25, 50 and 75% shade levels, respectively. Across species, shoot dry weight declined from 11.74 g 100 cm⁻² in full sun to 5.08 g 100 cm⁻² at 75% shade, and Pn from 7.61 to 4.25 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. At 75% shade, St. Augustine grass retained 75% of its full-sun shoot dry weight, 91% of root dry weight and 101% of turf quality, and bahiagrass retained 55%, 85% and 95%, respectively, and recorded the highest Pn (10.49 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). Bermudagrass was the most shade-sensitive showing retention of 62% turf quality and density (and 41% of full-sun values retained), whereas centipedegrass and carpet grass lost more than 75% of shoot biomass while largely retaining visual quality ratings (87-98%). Manila zoysiagrass showed an atypical peak in growth at 25% shade. St. Augustine grass and bahiagrass were the most shade-adapted species under the conditions tested, and bermudagrass the least.

KEYWORDS: shade tolerance; turfgrass; completely randomised design; factorial ANOVA; turf quality; chlorophyll; photosynthesis; root:shoot ratio

1. INTRODUCTION

Turfgrasses grown beneath tree canopies, buildings and other structures receive both a lower quantity of light and an altered light quality, and shade is among the most common causes of turf decline in landscapes (Beard, 1973; Dudeck and Peacock, 1992). Shaded turf typically shows reduced tillering and density, etiolated leaf growth and reduced root development, so that selecting an appropriate species is the principal management option where shade cannot be removed. Warm-season turfgrasses are generally adapted to high irradiance, but they differ widely in the degree to which growth and turf quality are sustained as light declines (Dudeck and Peacock, 1992; Jiang et al., 2004). Quantifying this variation requires that shade be imposed at defined, measured levels and that both morphological and physiological responses be recorded. Turf quality ratings describe the visual product, whereas biomass, root:shoot allocation, chlorophyll and photosynthesis describe the underlying acclimation of the plant; the two do not always move together. The objectives of this study were (i) to quantify the effect of graded shade (0-75%) on shoot and root growth, turf quality, density, chlorophyll content and net photosynthesis of seven warm-season turfgrass species, (ii) to test whether species respond differently to shade (species × shade interaction), and (iii) to rank the species for shade tolerance.

2. MATERIALS AND METHODS

2.1 Experimental site and design

The experiment was conducted at Dholi, Muzaffarpur, Bihar in a humid subtropical climate, sandy loam soil in a completely randomised design (CRD) with a 7 × 4 factorial arrangement of treatments (seven species × four shade levels) replicated three times, giving 28 treatment combinations and 84 experimental units (plots). Treatments were assigned at random to plots, and plots were treated as independent experimental units. Although a block number was recorded on the data sheet, blocking was not part of the design and was not included in the statistical model.

2.2 Treatments

The species were St. Augustine grass (*Stenotaphrum secundatum*), bermudagrass (*Cynodon dactylon*, Selection 1), Manila zoysiagrass (*Zoysia matrella*), bahiagrass (*Paspalum notatum*), seashore paspalum (*Paspalum vaginatum*), centipedegrass (*Eremochloa ophiuroides*) and carpet grass (*Axonopus compressus*). Turf was established by sprigging in the year 2020 and shade was imposed in the summer month of year 2021 at nominal levels of 0, 25, 50 and 75% using green shade net. Photosynthetically active radiation (PAR) was recorded at the time of each photosynthesis measurement; the measured PAR under each net is given in Table 1, and nominal shade levels are used throughout to label treatments.

2.3 Observations

Shoot and root fresh weights (FW) and dry weights (DW) were expressed per 100 cm² of sampled area (g 100 cm⁻²), and the root:shoot ratio was calculated as root DW divided by shoot DW. Turf quality was scored visually on a 1-9 scale (9 = best) and turf density on a 1-5 scale (5 = densest). Total chlorophyll was expressed as mg g⁻¹ FW and the chlorophyll a:b ratio was calculated from the individual pigment values. Net photosynthetic rate (Pn, $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) was measured together with the ambient PAR under each shade level (Table 1), so Pn values represent the realised rate under the prevailing light rather than photosynthetic capacity at a fixed PAR. Methodological details for chlorophyll extraction (e.g. Arnon, 1949), the gas-exchange instrument, sampling date(s) and drying conditions are to be inserted here.

2.4 Statistical analysis

Data were analysed as a two-factor fixed-effects factorial in a CRD with the model $y_{ijk} = \mu + \alpha_i + \beta_j + (\alpha\beta)_{ij} + \varepsilon_{ijk}$, where α_i is the effect of species ($i = 1 \dots 7$), β_j is the effect of shade level ($j = 1 \dots 4$), $(\alpha\beta)_{ij}$ is their interaction and ε_{ijk} is the random error ($k = 1 \dots 3$), giving 56 error degrees of freedom. Effects were tested against the residual mean square. Partial eta-squared ($\eta^2_p = \text{SS}_{\text{effect}} / [\text{SS}_{\text{effect}} + \text{SS}_{\text{error}}]$) and the coefficient of variation ($\text{CV} = \sqrt{\text{MSE}} / \text{grand mean} \times 100$) were calculated for each trait. Normality of residuals was checked with the Shapiro-Wilk test (Shapiro and Wilk, 1965) and homogeneity of variance among the 28 treatment combinations with Levene's test (Levene, 1960). Chlorophyll a:b ratio departed from normality and was analysed after natural-log transformation; means are reported on the original scale. Means were separated with Tukey's honestly significant difference (HSD) test at $P \leq 0.05$ (Tukey, 1949) using the pooled error mean square: marginal means were compared across species and across shade levels, and, because the interaction was significant, species were compared within each shade level and shade levels within each species. Shade tolerance was expressed as the value at 75% shade as a percentage of the value in full sun (0% shade), and a tolerance index was calculated as the mean of these percentages for shoot DW, root DW, turf quality and Pn. Turf quality and density are ordinal scores; they were analysed by ANOVA, as is conventional for turf ratings, after confirming that residual assumptions were met. Analyses were performed in Python (statsmodels and SciPy). General procedures follow Gomez and Gomez (1984).

3. RESULTS

3.1 Light environment

Measured PAR decreased with increasing shade, but the reductions were greater than the nominal values for each level (Table 1): full sun averaged 1890 $\mu\text{mol m}^{-2} \text{ s}^{-1}$, and the nominal 25, 50 and 75% shade levels transmitted 1294, 872 and 532 $\mu\text{mol m}^{-2} \text{ s}^{-1}$, corresponding to measured reductions of 31.5, 53.8 and 71.9%.

Table 1. Photosynthetically active radiation (PAR) recorded at the time of Pn measurement under the four shade levels.

Nominal shade (%)	Mean PAR ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)	SD (n = 3)	Measured PAR reduction (%)
0	1890	52	0.0
25	1294	49	31.5
50	872	81	53.8
75	532	53	71.9

PAR was recorded once per replicate set at each shade level (n = 3).

3.2 Analysis of variance

Species, shade and their interaction were highly significant ($P < 0.001$) for every trait (Table 2; full ANOVA tables in Appendix Table A1). Model R^2 ranged from 0.82 (chlorophyll a:b) to 0.998 (root fresh weight), and CV ranged from 3.1 to 11.3%. The interaction accounted for a large share of the variation in biomass and Pn (partial $\eta^2 = 0.94$ -0.98 for the four biomass traits and 0.94 for Pn), showing that species differed markedly in how they responded to shade; the main effects are therefore interpreted together with the interaction means (Tables 5-11). Residuals were normally distributed for nine of the ten traits (Shapiro-Wilk $P = 0.11$ -0.92) and variances were homogeneous for all traits (Levene $P = 0.14$ -0.998). Chlorophyll a:b departed from normality on the original scale ($P < 0.001$) but not after ln transformation ($P = 0.17$).

Table 2. Summary of ANOVA F-values for species, shade and their interaction (CRD, 7 × 4 factorial, n = 3).

Trait	Species F _(6,56)	Shade F _(3,56)	Species Shade F _(18,56)	CV (%)	R ²
Shoot fresh weight	371.4***	976.0***	132.1***	4.9	0.99
Shoot dry weight	148.9***	422.5***	56.8***	7.3	0.98
Root fresh weight	4552.1***	1180.6***	147.9***	3.1	1.00
Root dry weight	1429.4***	361.2***	52.2***	5.5	0.99
Root:shoot ratio (DW)	584.4***	14.8***	16.6***	8.6	0.99
Turf quality (1-9)	32.6***	39.3***	6.7***	4.8	0.89
Density (1-5)	43.0***	53.9***	14.5***	6.7	0.92
Total chlorophyll	92.8***	152.4***	23.5***	6.3	0.96
Chlorophyll a:b ratio†	32.4***	8.6***	4.4***	11.3	0.84
Net photosynthesis (Pn)	910.7***	590.9***	48.7***	4.7	0.99

* $P < 0.001$. Error d.f. = 56. †F-values from ln-transformed data (residual normality); CV and R² from the untransformed model (R² of the ln model = 0.84)

3.3 Main effects of species and shade

Shade reduced growth progressively (Table 3). Averaged over species, shoot DW fell from 11.74 g 100 cm⁻² in full sun to 5.08 g 100 cm⁻² at 75% shade (-57%) and root DW from 15.10 to 8.77 g 100 cm⁻² (-42%); shoot and root FW showed the same pattern (35.78 to 15.34 and 45.56 to 26.15 g 100 cm⁻², respectively). Among species, St. Augustine grass and bahiagrass had the greatest root DW (22.25 g 100 cm⁻² each) and root:shoot ratios (2.11 and 2.69, respectively), while carpet grass had the lowest shoot DW (4.14 g 100 cm⁻²), root DW (2.26 g 100 cm⁻²) and root:shoot ratio (0.46). Manila zoysiagrass, St. Augustine grass and seashore paspalum had the highest mean shoot DW (10.96, 10.78 and 10.42 g 100 cm⁻², respectively).

Turf quality declined from 7.71 in full sun to 6.64 at 75% shade (-14%) and density from 4.13 to 3.31 (-20%) (Table 4). Pn declined from 7.61 to 4.25 μmol CO₂ m⁻² s⁻¹ (-44%), and bahiagrass had the highest mean Pn (10.49), followed by St. Augustine grass (8.02). In contrast to the other traits, total chlorophyll was lowest in full sun (2.36 mg g⁻¹ FW) and highest at 25% shade (3.51). Bermudagrass had the highest mean chlorophyll content (4.12 mg g⁻¹ FW).

Table 3. Main effects of species and shade on shoot and root growth traits.

Treatment	Shoot fresh weight (g 100 cm ⁻²)	Shoot dry weight (g 100 cm ⁻²)	Root fresh weight (g 100 cm ⁻²)	Root dry weight (g 100 cm ⁻²)	Root:shoot ratio (DW)
<i>Species (marginal means over shade levels, n = 12)</i>					
St. Augustine	31.42 ± 0.96 b	10.78 ± 0.49 a	65.27 ± 1.04 b	22.25 ± 0.30 a	2.11 ± 0.09 b
Bermuda	29.29 ± 4.06 c	9.55 ± 1.25 b	34.66 ± 5.35 d	11.82 ± 1.84 c	1.18 ± 0.05 c
Manila zoysia	33.20 ± 4.43 a	10.96 ± 1.45 a	39.41 ± 4.07 c	13.01 ± 1.41 b	1.24 ± 0.06 c
Bahia	25.76 ± 1.55 d	8.57 ± 0.54 c	69.00 ± 1.40 a	22.25 ± 0.48 a	2.69 ± 0.14 a
Seashore paspalum	31.89 ± 2.64 ab	10.42 ± 0.91 a	29.91 ± 2.15 e	9.84 ± 0.72 d	0.96 ± 0.03 d
Centipede	28.31 ± 4.70 c	9.43 ± 1.55 b	19.32 ± 3.15 f	6.12 ± 0.98 e	0.65 ± 0.04 e
Carpet grass	11.29 ± 2.25 e	4.14 ± 0.73 d	6.43 ± 1.56 g	2.26 ± 0.64 f	0.46 ± 0.06 f
<i>Nominal shade (marginal means over species, n = 21)</i>					
0%	35.78 ± 2.26 a	11.74 ± 0.75 a	45.56 ± 4.36 a	15.10 ± 1.42 a	1.35 ± 0.13 b
25%	33.03 ± 2.89 b	11.01 ± 0.91 b	43.42 ± 5.09 b	14.39 ± 1.67 b	1.26 ± 0.14 bc
50%	25.08 ± 2.13 c	8.65 ± 0.72 c	35.72 ± 5.25 c	11.76 ± 1.77 c	1.25 ± 0.17 c
75%	15.34 ± 1.44 d	5.08 ± 0.44 d	26.15 ± 5.09 d	8.77 ± 1.74 d	1.46 ± 0.23 a

Values are mean ± SE. Within each column and block (species or shade), means followed by the same letter do not differ significantly (Tukey HSD, $P \leq 0.05$, pooled error mean square).

Table 4. Main effects of species and shade on turf performance and physiological traits.

Treatment	Turf quality (1–9)	Density (1–5)	Total chlorophyll (mg g ⁻¹ FW)	Chlorophyll a:b ratio	Net photosynthesis (Pn) (μmol CO ₂ m ⁻² s ⁻¹)
<i>Species (marginal means over shade levels, n = 12)</i>					
St. Augustine	7.77 ± 0.14 a	4.18 ± 0.11 a	2.98 ± 0.28 b	1.87 ± 0.05 b	8.02 ± 0.38 b
Bermuda	6.80 ± 0.36 b	3.06 ± 0.31 c	4.12 ± 0.16 a	2.34 ± 0.12 a	3.89 ± 0.30 e
Manila zoysia	6.61 ± 0.25 b	3.93 ± 0.21 a	2.99 ± 0.10 b	1.70 ± 0.05 b	3.72 ± 0.33 e
Bahia	7.70 ± 0.11 a	3.19 ± 0.22 bc	2.73 ± 0.06 c	2.55 ± 0.19 a	10.49 ± 0.40 a
Seashore paspalum	6.62 ± 0.14 b	3.91 ± 0.12 a	2.49 ± 0.18 d	1.70 ± 0.05 b	4.97 ± 0.28 d
Centipede	7.75 ± 0.14 a	3.43 ± 0.07 b	2.80 ± 0.13 bc	2.27 ± 0.06 a	4.95 ± 0.56 d
Carpet grass	7.78 ± 0.10 a	4.20 ± 0.07 a	2.87 ± 0.29 bc	1.86 ± 0.04 b	5.78 ± 0.86 c
<i>Nominal shade (marginal means over species, n = 21)</i>					
0%	7.71 ± 0.13 a	4.13 ± 0.09 a	2.36 ± 0.17 d	1.88 ± 0.05 c	7.61 ± 0.67 a
25%	7.58 ± 0.13 a	3.94 ± 0.12 a	3.51 ± 0.14 a	1.97 ± 0.07 bc	6.74 ± 0.51 b
50%	7.22 ± 0.18 b	3.42 ± 0.15 b	3.28 ± 0.14 b	2.19 ± 0.11 a	5.30 ± 0.46 c
75%	6.64 ± 0.21 c	3.31 ± 0.20 b	2.85 ± 0.14 c	2.13 ± 0.13 ab	4.25 ± 0.53 d

Values are mean ± SE. Letters as in Table 3. Letters for chlorophyll a:b are from untransformed means.

3.4 Species × shade interaction: biomass and allocation

The species × shade interaction was the dominant source of variation for biomass (Tables 5 and 6; Fig. 1a,b). St. Augustine grass-maintained shoot DW (11.08–12.27 g 100 cm⁻²) and root DW (22.35–23.16 g 100 cm⁻²) across 0–50% shade and declined only at 75% shade, where it retained 75% and 91% of full-sun shoot and root DW. Bahiagrass likewise kept its root DW (23.52 to 20.08 g 100 cm⁻²; 85% retained) although its shoot DW fell to 55% of full sun. Seashore paspalum declined steadily (shoot DW 13.32 to 5.96 g 100 cm⁻²; root DW 12.70 to 6.40 g 100 cm⁻²). Bermudagrass and centipedegrass were the most affected among the higher-yielding species: bermudagrass shoot DW fell from 14.38 to 4.64 g 100 cm⁻² and root DW from 18.98 to 4.28 g 100 cm⁻² (32% and 23% retained), and centipedegrass shoot DW dropped from 17.47 to 8.47 g 100 cm⁻² already at 25% shade and to 3.29 g 100 cm⁻² at 75%. Carpet grass, which had the lowest biomass overall, lost most of its root DW (5.78 to 0.66 g 100 cm⁻²; 11% retained). Manila zoysiagrass did not follow a monotonic pattern: shoot DW (7.32 to 17.62 g 100 cm⁻²) and root DW (10.79 to 19.50 g 100 cm⁻²) were highest at 25% shade and then declined to 5.69 and 6.98 g 100 cm⁻² at 75% shade (see Section 4.1).

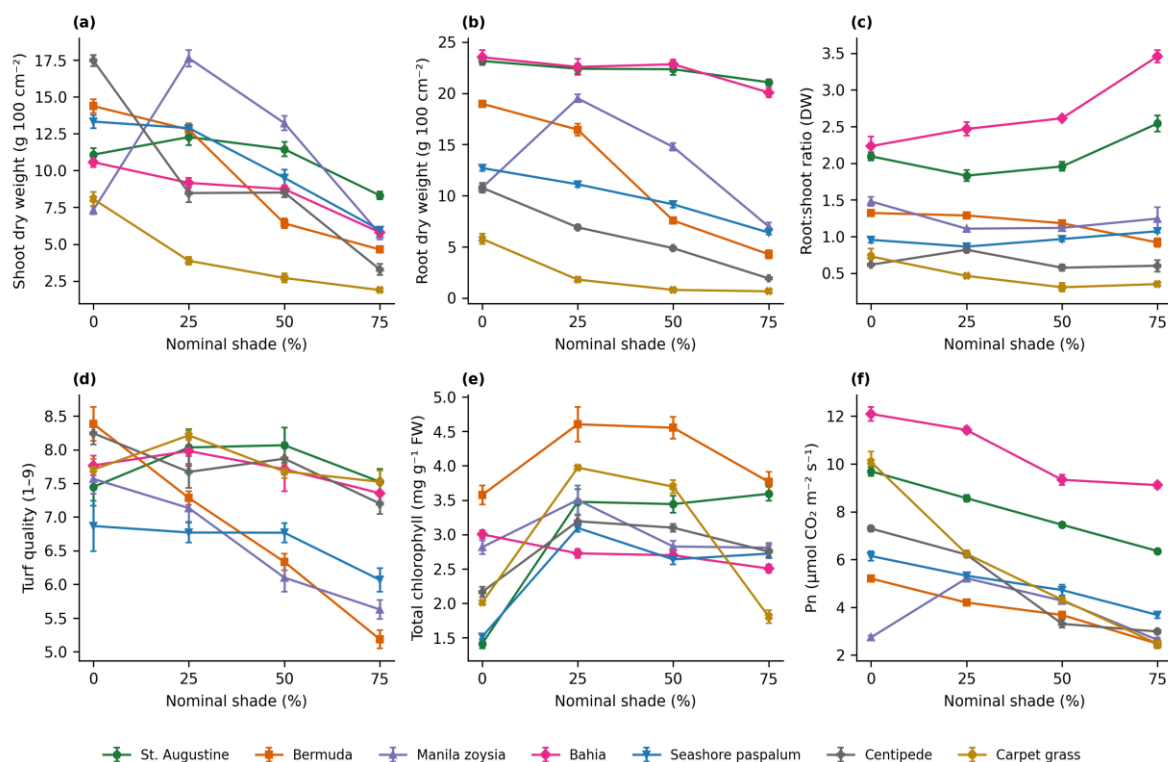


Fig. 1. Response of seven turfgrass species to nominal shade (0–75%): (a) shoot dry weight, (b) root dry weight, (c) root:shoot ratio, (d) turf quality, (e) total chlorophyll and (f) net photosynthesis (Pn). Points are means ± SE (n = 3).

Table 5. Shoot dry weight (g 100 cm⁻²) as affected by species and shade.

Species	0% shade	25% shade	50% shade	75% shade	Species mean
St. Augustine	11.08 ± 0.45 cA	12.27 ± 0.55 bA	11.45 ± 0.49 bA	8.31 ± 0.26 aB	10.78 a
Bermuda	14.38 ± 0.46 bA	12.78 ± 0.43 bB	6.41 ± 0.33 dC	4.64 ± 0.19 bcD	9.55 b
Manila zoysia	7.32 ± 0.29 dC	17.62 ± 0.56 aA	13.22 ± 0.49 aB	5.69 ± 0.36 bD	10.96 a
Bahia	10.57 ± 0.33 cA	9.16 ± 0.34 cAB	8.74 ± 0.25 cB	5.81 ± 0.12 bC	8.57 c
Seashore paspalum	13.32 ± 0.45 bA	12.88 ± 0.20 bA	9.51 ± 0.56 cB	5.96 ± 0.09 bC	10.42 a
Centipede	17.47 ± 0.38 aA	8.47 ± 0.62 cB	8.51 ± 0.31 cB	3.29 ± 0.38 cdC	9.43 b
Carpet grass	8.07 ± 0.49 dA	3.88 ± 0.27 dB	2.71 ± 0.31 eBC	1.89 ± 0.11 dC	4.14 d
Mean	11.74 a	11.01 b	8.65 c	5.08 d	—

Values are mean ± SE (n = 3). Within a shade level (column), means sharing a lowercase letter do not differ (Tukey HSD = 1.67); within a species (row), means sharing an uppercase letter do not differ (Tukey HSD = 1.44; P ≤ 0.05). Marginal means (last row and column) are compared with lowercase letters (Tukey HSD = 0.55 for shade, 0.83 for species).

Table 6. Root dry weight (g 100 cm⁻²) as affected by species and shade.

Species	0% shade	25% shade	50% shade	75% shade	Species mean
St. Augustine	23.16 ± 0.41 aA	22.40 ± 0.49 aAB	22.35 ± 0.56 aAB	21.07 ± 0.29 aB	22.25 a
Bermuda	18.98 ± 0.29 bA	16.45 ± 0.59 cB	7.57 ± 0.29 cC	4.28 ± 0.40 cD	11.82 c
Manila zoysia	10.79 ± 0.27 dC	19.50 ± 0.39 bA	14.76 ± 0.36 bB	6.98 ± 0.42 bD	13.01 b
Bahia	23.52 ± 0.71 aA	22.58 ± 0.80 aA	22.83 ± 0.47 aA	20.08 ± 0.47 aB	22.25 a
Seashore paspalum	12.70 ± 0.25 cA	11.11 ± 0.27 dB	9.15 ± 0.31 cC	6.40 ± 0.21 bD	9.84 d
Centipede	10.77 ± 0.49 dA	6.91 ± 0.21 eB	4.87 ± 0.19 dC	1.92 ± 0.08 dD	6.12 e
Carpet grass	5.78 ± 0.52 eA	1.80 ± 0.15 fB	0.80 ± 0.06 eB	0.66 ± 0.03 dB	2.26 f
Mean	15.10 a	14.39 b	11.76 c	8.77 d	—

Values are mean ± SE (n = 3). Within a shade level (column), means sharing a lowercase letter do not differ (Tukey HSD = 1.73); within a species (row), means sharing an uppercase letter do not differ (Tukey HSD = 1.50; P ≤ 0.05). Marginal means (last row and column) are compared with lowercase letters (Tukey HSD = 0.57 for shade, 0.87 for species).

Root:shoot ratio responded differently among species (Table 7; Fig. 1c). It increased under shade in bahiagrass (2.23 to 3.46) and St. Augustine grass (2.09 to 2.54), because shoot DW declined proportionally more than root DW, and decreased in bermudagrass (1.32 to 0.92) and carpet grass (0.73 to 0.35), in which roots declined faster than shoots. Although the shade main effect was significant, marginal shade means differed little (1.25–1.46) because these opposing responses partly cancelled.

Table 7. Root:shoot ratio (DW basis) as affected by species and shade.

Species	0% shade	25% shade	50% shade	75% shade	Species mean
St. Augustine	2.09 ± 0.05 aB	1.83 ± 0.07 bC	1.96 ± 0.06 bBC	2.54 ± 0.11 bA	2.11 b
Bermuda	1.32 ± 0.03 bA	1.29 ± 0.03 cA	1.18 ± 0.02 cA	0.92 ± 0.06 dB	1.18 c
Manila zoysia	1.48 ± 0.06 bA	1.11 ± 0.01 cdB	1.12 ± 0.04 cB	1.25 ± 0.15 cAB	1.24 c
Bahia	2.23 ± 0.13 aC	2.47 ± 0.09 aBC	2.61 ± 0.02 aB	3.46 ± 0.09 aA	2.69 a
Seashore paspalum	0.96 ± 0.04 cA	0.86 ± 0.02 deA	0.97 ± 0.03 cA	1.07 ± 0.02 cdA	0.96 d
Centipede	0.62 ± 0.02 dA	0.82 ± 0.04 eA	0.58 ± 0.04 dA	0.60 ± 0.08 eA	0.65 e
Carpet grass	0.73 ± 0.11 cdA	0.46 ± 0.01 fB	0.31 ± 0.06 dB	0.35 ± 0.03 eB	0.46 f
Mean	1.35 b	1.26 bc	1.25 c	1.46 a	—

Values are mean ± SE (n = 3). Within a shade level (column), means sharing a lowercase letter do not differ (Tukey HSD = 0.29); within a species (row), means sharing an uppercase letter do not differ (Tukey HSD = 0.25; P ≤ 0.05). Marginal means (last row and column) are compared with lowercase letters (Tukey HSD = 0.09 for shade, 0.14 for species).

3.5 Turf quality and density

Visual quality and density separated the species more sharply than biomass did (Tables 8 and 9; Fig. 1d). Turf quality of St. Augustine grass (7.45 to 7.52), bahiagrass (7.77 to 7.35), carpet grass (7.70 to 7.52) and centipedegrass (8.24 to 7.20) remained at or above about 7 at all shade levels, whereas bermudagrass declined from 8.38 to 5.18 (62% retained) and Manila zoysiagrass from 7.57 to 5.63 (74%). Bermudagrass density fell from 4.57 to 1.89 (41% retained), and bahiagrass density from 3.93 to 2.53 even though its turf quality rating was maintained. St. Augustine grass density increased from 3.77 in full sun to 4.63 at 75% shade.

Table 8. Turf quality (1–9 scale) as affected by species and shade.

Species	0% shade	25% shade	50% shade	75% shade	Species mean
St. Augustine	7.45 ± 0.28 bcA	8.03 ± 0.27 abA	8.07 ± 0.26 aA	7.52 ± 0.19 aA	7.77 a
Bermuda	8.38 ± 0.25 aA	7.28 ± 0.10 bcdB	6.33 ± 0.12 bC	5.18 ± 0.14 cD	6.80 b
Manila zoysia	7.57 ± 0.22 abcA	7.13 ± 0.20 cdA	6.10 ± 0.21 bB	5.63 ± 0.14 bcB	6.61 b
Bahia	7.77 ± 0.15 abA	7.98 ± 0.19 abcA	7.71 ± 0.33 aA	7.35 ± 0.13 aA	7.70 a
Seashore paspalum	6.87 ± 0.38 cA	6.77 ± 0.15 dAB	6.77 ± 0.15 bAB	6.07 ± 0.18 bB	6.62 b
Centipede	8.24 ± 0.17 abA	7.67 ± 0.24 abcAB	7.87 ± 0.24 aAB	7.20 ± 0.15 aB	7.75 a
Carpet grass	7.70 ± 0.16 abcA	8.21 ± 0.07 aA	7.68 ± 0.10 aA	7.52 ± 0.17 aA	7.78 a
Mean	7.71 a	7.58 a	7.22 b	6.64 c	—

Values are mean ± SE (n = 3). Within a shade level (column), means sharing a lowercase letter do not differ (Tukey HSD = 0.88); within a species (row), means sharing an uppercase letter do not differ (Tukey HSD = 0.76; $P \leq 0.05$). Marginal means (last row and column) are compared with lowercase letters (Tukey HSD = 0.29 for shade, 0.44 for species).

Table 9. Turf density (1–5 scale) as affected by species and shade.

Species	0% shade	25% shade	50% shade	75% shade	Species mean
St. Augustine	3.77 ± 0.15 bcB	4.24 ± 0.14 abAB	4.07 ± 0.15 abB	4.63 ± 0.09 aA	4.18 a
Bermuda	4.57 ± 0.15 aA	3.31 ± 0.12 cB	2.47 ± 0.09 dC	1.89 ± 0.07 eD	3.06 c
Manila zoysia	4.63 ± 0.20 aA	4.55 ± 0.16 aA	3.48 ± 0.07 bcB	3.07 ± 0.18 cdB	3.93 a
Bahia	3.93 ± 0.23 bcA	3.71 ± 0.20 bcA	2.58 ± 0.14 dB	2.53 ± 0.32 dB	3.19 bc
Seashore paspalum	4.28 ± 0.04 abA	4.30 ± 0.11 abA	3.58 ± 0.07 bcB	3.48 ± 0.08 bcB	3.91 a
Centipede	3.62 ± 0.10 cA	3.20 ± 0.12 cA	3.34 ± 0.11 cA	3.56 ± 0.15 bcA	3.43 b
Carpet grass	4.14 ± 0.09 abcA	4.24 ± 0.14 abA	4.44 ± 0.11 aA	3.99 ± 0.12 bA	4.20 a
Mean	4.13 a	3.94 a	3.42 b	3.31 b	—

Values are mean ± SE (n = 3). Within a shade level (column), means sharing a lowercase letter do not differ (Tukey HSD = 0.62); within a species (row), means sharing an uppercase letter do not differ (Tukey HSD = 0.54; $P \leq 0.05$). Marginal means (last row and column) are compared with lowercase letters (Tukey HSD = 0.20 for shade, 0.31 for species).

3.6 Chlorophyll and net photosynthesis

Total chlorophyll generally rose between full sun and 25% shade (Table 10; Fig. 1e): St. Augustine grass 1.41 to 3.48, seashore paspalum 1.52 to 3.10, carpet grass 2.01 to 3.97 and bermudagrass 3.58 to 4.60 mg g⁻¹ FW. At 75% shade chlorophyll remained above the full-sun level in four of the seven species but fell sharply in carpet grass (3.97 to 1.81 mg g⁻¹ FW). The chlorophyll a:b ratio increased with shade in bermudagrass (1.84 to 2.75) and bahiagrass (1.99 to 3.01) but changed little or declined in the other species (Table 4; Appendix Table A1).

Table 10. Total chlorophyll (mg g⁻¹ FW) as affected by species and shade.

Species	0% shade	25% shade	50% shade	75% shade	Species mean
St. Augustine	1.41 ± 0.07 dB	3.48 ± 0.19 cA	3.44 ± 0.12 bcA	3.59 ± 0.10 aA	2.98 b
Bermuda	3.58 ± 0.14 aB	4.60 ± 0.25 aA	4.55 ± 0.16 aA	3.77 ± 0.15 aB	4.12 a
Manila zoysia	2.82 ± 0.10 bB	3.50 ± 0.21 bcA	2.83 ± 0.08 dB	2.81 ± 0.07 bB	2.99 b
Bahia	3.00 ± 0.06 bA	2.73 ± 0.06 dAB	2.70 ± 0.06 dAB	2.51 ± 0.06 bB	2.73 c
Seashore paspalum	1.52 ± 0.04 dC	3.10 ± 0.05 cdA	2.64 ± 0.07 dB	2.72 ± 0.04 bAB	2.49 d
Centipede	2.17 ± 0.07 cC	3.19 ± 0.09 cdA	3.10 ± 0.06 cdAB	2.75 ± 0.10 bB	2.80 bc
Carpet grass	2.01 ± 0.02 cB	3.97 ± 0.04 bA	3.70 ± 0.10 bA	1.81 ± 0.09 cB	2.87 bc
Mean	2.36 d	3.51 a	3.28 b	2.85 c	—

Values are mean ± SE (n = 3). Within a shade level (column), means sharing a lowercase letter do not differ (Tukey HSD = 0.47); within a species (row), means sharing an uppercase letter do not differ (Tukey HSD = 0.41; $P \leq 0.05$). Marginal means (last row and column) are compared with lowercase letters (Tukey HSD = 0.15 for shade, 0.24 for species).

Pn decreased with shade in every species except Manila zoysiagrass (Table 11; Fig. 1f). Bahiagrass maintained the highest Pn at every shade level (12.09 to 9.11 μmol CO₂ m⁻² s⁻¹; 75% retained), followed by St. Augustine

grass (9.69 to 6.36; 66% retained). Carpet grass had a full-sun Pn similar to St. Augustine grass (10.08) but lost 75% of it at 75% shade (2.47). Pn was measured under ambient PAR beneath each net (Table 1), so the decline partly reflects the lower instantaneous irradiance and cannot be separated from acclimation; Pn was positively related to PAR within every species except Manila zoysiagrass (Fig. 2).

Table 11. Net photosynthesis, Pn ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), as affected by species and shade.

Species	0% shade	25% shade	50% shade	75% shade	Species mean
St. Augustine	9.69 $\pm$ 0.19 bA	8.57 $\pm$ 0.14 bB	7.46 $\pm$ 0.08 bC	6.36 $\pm$ 0.06 bD	8.02 b
Bermuda	5.20 $\pm$ 0.10 eA	4.20 $\pm$ 0.06 eB	3.68 $\pm$ 0.10 deB	2.48 $\pm$ 0.08 dC	3.89 e
Manila zoysia	2.74 $\pm$ 0.07 fC	5.22 $\pm$ 0.06 dA	4.28 $\pm$ 0.07 cdB	2.64 $\pm$ 0.09 dC	3.72 e
Bahia	12.09 $\pm$ 0.29 aA	11.42 $\pm$ 0.14 aB	9.34 $\pm$ 0.22 aC	9.11 $\pm$ 0.13 aC	10.49 a
Seashore paspalum	6.15 $\pm$ 0.20 dA	5.32 $\pm$ 0.12 dB	4.72 $\pm$ 0.23 cB	3.68 $\pm$ 0.13 cC	4.97 d
Centipede	7.30 $\pm$ 0.11 cA	6.21 $\pm$ 0.11 cB	3.31 $\pm$ 0.16 eC	2.99 $\pm$ 0.09 cdC	4.95 d
Carpet grass	10.08 $\pm$ 0.44 bA	6.24 $\pm$ 0.15 cB	4.32 $\pm$ 0.12 cdC	2.47 $\pm$ 0.20 dD	5.78 c
Mean	7.61 a	6.74 b	5.30 c	4.25 d	—

Values are mean $\pm$ SE (n = 3). Within a shade level (column), means sharing a lowercase letter do not differ (Tukey HSD = 0.70); within a species (row), means sharing an uppercase letter do not differ (Tukey HSD = 0.61; $P \leq 0.05$). Marginal means (last row and column) are compared with lowercase letters (Tukey HSD = 0.23 for shade, 0.35 for species).

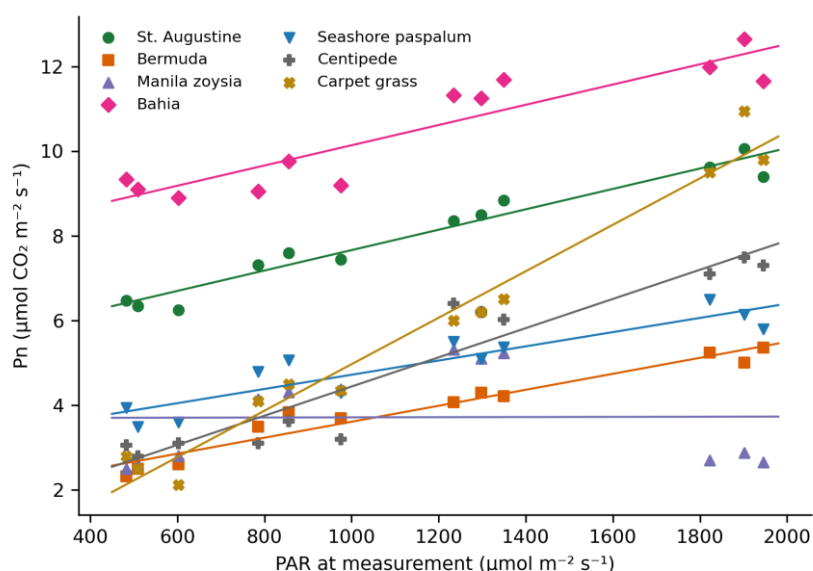


Fig. 2. Relationship between Pn and ambient PAR at measurement for each species (points are individual plots; lines are species-wise linear fits). PAR differed among plots only through the shade level.

3.7 Shade tolerance

Expressing the 75% shade value as a percentage of the full-sun value (Table 12; Fig. 3) ranked St. Augustine grass (tolerance index 83.1), Manila zoysiagrass (78.2) and bahiagrass (77.6) highest, followed by seashore paspalum (60.8), and then centipedegrass (41.2), bermudagrass (41.1) and carpet grass (39.3). The ranking of Manila zoysiagrass is inflated by its unusually low full-sun values and should be treated with caution (Section 4.1). The lowest-ranked species lost shoot biomass for different reasons and with different consequences for visual quality: bermudagrass lost both biomass and quality, whereas centipedegrass and carpet grass lost biomass but retained turf quality ratings (87% and 98% of full sun) and density (98% and 97%).

Table 12. Values at 75% shade as a percentage of the full-sun (0% shade) value, and shade tolerance index.

Species	Shoot DW	Root DW	Turf quality	Density	Total chl	Pn	Tolerance index‡
St. Augustine	75	91	101	123	254	66	83.1
Manila zoysia	78	65	74	66	100	96	78.2
Bahia	55	85	95	64	83	75	77.6
Seashore paspalum	45	50	88	81	180	60	60.8
Centipede	19	18	87	98	127	41	41.2
Bermuda	32	23	62	41	105	48	41.1
Carpet grass	23	11	98	97	90	25	39.3

‡Mean of the percentages for shoot DW, root DW, turf quality and Pn. Species are listed in descending order of the index.

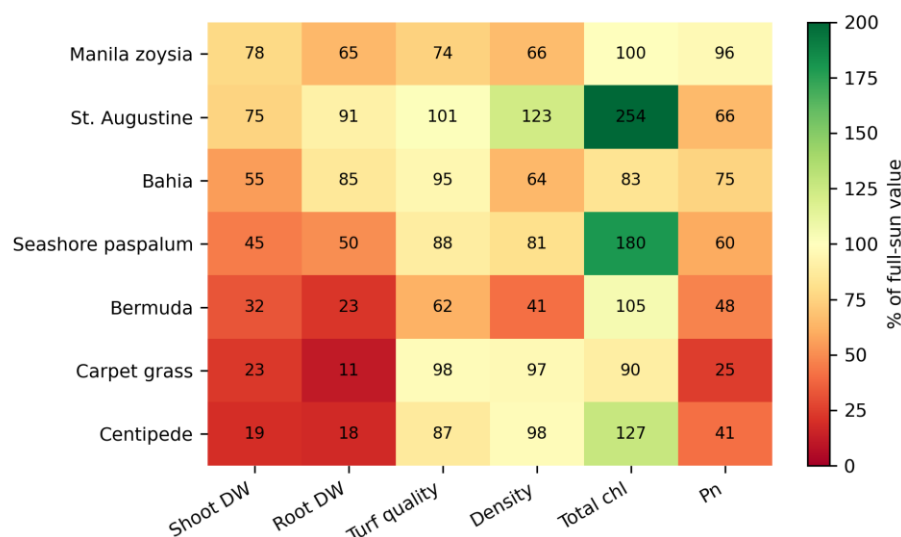


Fig. 3. Heat map of trait values at 75% shade as a percentage of full-sun values (100 = no change), species ordered by shoot DW retention.

4. DISCUSSION

4.1 Data considerations

Two features of the data sheet should be checked before the results are submitted for publication. First, in replicate 1 the shoot DM% is 33.3% in all 28 plots and the root DM% is 33.3% in 26 of 28 plots, whereas DM% varies among plots in replicates 2 and 3. This pattern suggests that replicate 1 dry weights may have been calculated from fresh weight ($DW \approx FW/3$) rather than weighed. As a sensitivity check, the ANOVA for shoot DW, root DW and root:shoot ratio was repeated using replicates 2 and 3 only (28 error d.f.); species, shade and interaction effects all remained significant ($P < 0.001$, except the shade effect on root:shoot ratio, $P = 0.0003$), so the conclusions do not depend on replicate 1, but the original weights should be confirmed. Second, Manila zoysiagrass at 0% shade had markedly lower shoot DW ($7.32 \text{ g } 100 \text{ cm}^{-2}$), root DW ($10.79 \text{ g } 100 \text{ cm}^{-2}$) and Pn ($2.74 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) than at 25% shade (17.62, 19.50 and 5.22, respectively), and the replicates within each treatment are consistent. A strong increase in growth under moderate shade is biologically unusual, and the full-sun plots of this species should be checked for a labelling or treatment error before this result is interpreted physiologically.

4.2 Species differ in shade adaptation

The highly significant species $\times$ shade interaction for all traits confirms that the ranking of species depends on the shade level, which is the central result of this study. Two broad response types were evident. St. Augustine grass and bahiagrass sustained root mass, turf quality and photosynthetic activity under shade while shoot biomass declined, and both increased root:shoot ratio at 75% shade. This contrasts with the lower root allocation under shade that is commonly reported for turfgrasses (Beard, 1973; Dudeck and Peacock, 1992), and may reflect the sampling method for roots, which should be described in the Methods. St. Augustine grass also increased density at 75% shade, consistent with its reputation as a comparatively shade-adapted warm-season species.

Bermudagrass showed the steepest combined loss of biomass (68% shoot DW, 77% root DW), turf quality (38%) and density (59%), which agrees with its recognised requirement for high light (Beard, 1973). Seashore paspalum was intermediate, retaining 45% of shoot DW and 88% of turf quality at 75% shade, which is consistent with reports that it tolerates low light better than bermudagrass (Jiang et al., 2004). Centipedegrass and carpet grass form a third group: biomass collapsed (shoot DW retained 19% and 23%; root DW 18% and 11%), yet visual quality and density changed little. These species may therefore be scored as acceptable in short-term ratings while root systems and shoot reserves decline, and longer-term persistence should be evaluated before they are recommended for heavy shade.

4.3 Chlorophyll and photosynthesis

Chlorophyll concentration increased between full sun and 25% shade in most species, a response consistent with pigment accumulation as an acclimation to reduced light, and with low pigment content per unit fresh weight in strongly illuminated tissue. The increase in chlorophyll a:b ratio under shade in bermudagrass and bahiagrass is opposite to the decline usually expected in shade-acclimated leaves, and pigment-specific data (chlorophyll a and b separately) together with the extraction method should be reported before drawing conclusions from this trait. Because Pn was measured under ambient light beneath each net, its decline with shade combines lower instantaneous irradiance with acclimation; measurements at a fixed saturating PAR would be needed to separate photosynthetic capacity from the light response. The high Pn of bahiagrass at all shade levels corresponded with its maintained root mass and turf quality, although density declined.

5. CONCLUSIONS

Shade reduced growth, turf density, quality and photosynthesis of warm-season turfgrasses, but the magnitude of the response differed significantly among species at every level of shade. Under the conditions of this experiment, St. Augustine grass and bahiagrass were the most shade-adapted species, retaining root mass, turf quality and the highest photosynthetic rates at 75% shade; seashore paspalum was intermediate; bermudagrass was the most shade-sensitive for turf quality and density; and centipedegrass and carpet grass lost most of their biomass while retaining visual quality in the short term. Turf quality ratings alone do not adequately describe shade tolerance and should be interpreted together with biomass, root and physiological measurements.

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9. Appendix

Table A1. Analysis of variance for all traits (CRD, 7 × 4 factorial, n = 3; error d.f. = 56).

Source	df	SS	MS	F	P	Partial η^2
Shoot fresh weight — CV = 4.9%						
Species	6	4037.4	672.9	371.35	<0.001	0.98
Shade	3	5305.4	1768.5	975.98	<0.001	0.98
Species × Shade	18	4308.7	239.4	132.10	<0.001	0.98
Error	56	101.5	1.81			
Shoot dry weight — CV = 7.3%						
Species	6	399.1	66.52	148.94	<0.001	0.94
Shade	3	566.0	188.7	422.45	<0.001	0.96
Species × Shade	18	456.6	25.37	56.81	<0.001	0.95
Error	56	25.01	0.4466			
Root fresh weight — CV = 3.1%						
Species	6	37539.7	6256.6	4552.06	<0.001	1.00
Shade	3	4868.2	1622.7	1180.63	<0.001	0.98
Species × Shade	18	3658.4	203.2	147.87	<0.001	0.98
Error	56	76.97	1.37			
Root dry weight — CV = 5.5%						
Species	6	4121.7	687.0	1429.41	<0.001	0.99
Shade	3	520.8	173.6	361.21	<0.001	0.95
Species × Shade	18	451.1	25.06	52.15	<0.001	0.94
Error	56	26.91	0.4806			
Root:shoot ratio (DW) — CV = 8.6%						
Species	6	46.04	7.67	584.38	<0.001	0.98
Shade	3	0.5835	0.1945	14.81	<0.001	0.44
Species × Shade	18	3.92	0.2176	16.57	<0.001	0.84
Error	56	0.7353	0.0131			
Turf quality (1–9) — CV = 4.8%						
Species	6	24.09	4.02	32.62	<0.001	0.78
Shade	3	14.52	4.84	39.33	<0.001	0.68
Species × Shade	18	14.76	0.8199	6.66	<0.001	0.68
Error	56	6.89	0.1231			
Density (1–5) — CV = 6.7%						
Species	6	15.92	2.65	43.01	<0.001	0.82
Shade	3	9.97	3.32	53.87	<0.001	0.74
Species × Shade	18	16.15	0.8972	14.54	<0.001	0.82

Error	56	3.45	0.0617			
Total chlorophyll — CV = 6.3%						
Species	6	19.77	3.30	92.81	<0.001	0.91
Shade	3	16.24	5.41	152.43	<0.001	0.89
Species × Shade	18	15.02	0.8342	23.50	<0.001	0.88
Error	56	1.99	0.0355			
Chlorophyll a:b ratio (ln-transformed) — CV = 11.3%						
Species	6	1.77	0.2942	32.45	<0.001	0.78
Shade	3	0.2338	0.0779	8.60	<0.001	0.32
Species × Shade	18	0.7238	0.0402	4.44	<0.001	0.59
Error	56	0.5077	0.0091			
Net photosynthesis (Pn) CV = 4.7%						
Species	6	433.3	72.21	910.65	<0.001	0.99
Shade	3	140.6	46.86	590.88	<0.001	0.97
Species × Shade	18	69.51	3.86	48.70	<0.001	0.94
Error	56	4.44	0.0793			

SS = sum of squares; MS = mean square; partial $\eta^2 = SS_{\text{effect}} / (SS_{\text{effect}} + SS_{\text{error}})$. Chlorophyll a:b ratio was analysed after ln transformation; CV shown is for the untransformed model.