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Comparative Performance of Three Tropical Turfgrasses *Digitaria longiflora*, *Axonopus compressus* and St. Augustinegrass under Simulated Shade Conditions

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ABSTRACT. Shade affects turf quality by reducing light for photosynthesis. The shade tolerance of the tropical grasses, *Digitaria longiflora* and *Axonopus compressus* were evaluated against *Stenotaphrum secundatum* (St. Augustinegrass). The grasses were established under shade structures that provide 0%, 50%, 75% or 90% shade level for 30 days. A suite of leaf traits, recorded from similar leaf developmental stage, displayed distinct responses to shade conditions. Leaf length, relative to control, increased in all three species as shade level increased. The mean leaf extension rate was lowest in St. Augustinegrass (80.42%) followed by *A. compressus* (84.62%) and *D. longiflora* (90.78%). The higher leaf extension rate in *D. longiflora* implied its poor shade tolerance. Specific leaf area (SLA) increased in all species with highest mean SLA increase in *D. longiflora* (348.55 cm² mg⁻¹) followed by *A. compressus* (286.88 cm² mg⁻¹) and St. Augustinegrass (276.28 cm² mg⁻¹). The highest SLA increase in *D. longiflora* suggested its lowest performance under shade. The percent green cover, as estimated by digital image analysis, was lowest in *D. longiflora* (53%) under 90% shade level compared to both species. The relative shade tolerance of the three turfgrasses could be ranked as St. Augustinegrass > *A. compressus* > *D. longiflora*.

Key words: Leaf extension, Leaf senescence, Percent green cover, Specific leaf area, Shade tolerance

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Introduction

Responses of turfgrass under shade have been well characterized in many tropical turfgrass species e.g. *Zoysia* (Qian and Engelke, 1999); seashore paspalum (Jiang et al., 2004) and *Stenotaphrum secundatum* (Walt.) Kuntze [St. Augustinegrass] (Trenholm and Nagata, 2005). Of the tropical turfgrasses examined, St. Augustinegrass is generally considered one of the most shade-tolerant (Beard, 1973).

Turf quality declines under prolonged severe shade conditions (Jiang et al., 2004). This decline of turf quality has been attributed to the reduction of photosynthesis that led to a reduction of tiller growth (Wu et al., 1985). Previous studies have identified common morphological and physiological adaptive leaf traits in turfgrass when they were subjected to increasing levels of shade, either under natural or simulated shade conditions. The distinct morphological changes include

increased leaf length (Peterson et al., 2014), shoot elongation (Tegg and Lane, 2004), and increased leaf area (Beard, 1973). The significant physiological shade responses of turf largely involve reduction of clipping weight (Tegg and Lane, 2004) and increased in chlorophyll content (Beard, 1973). In addition, leaf senescence was induced under severe shade conditions when plants were experiencing a net negative carbon balance i.e. increased respiration over photosynthesis (Brouwer et al., 2012).

The grass *Digitaria longiflora* (Retz.) Pers. is naturally occurring in Singapore. It grows in various soil types and often growing among the locally abundant turfgrass, *Axonopus compressus* (Sw.) Beauv. or locally known as 'cowgrass'. The desirable vegetative turf characteristics of *D. longiflora* such as low vertical increase accompanied with vigorous lateral growth were described by Chin (2015). Until then, there was no useful information on *D. longiflora* with regards to its

utility as turf except its commonly reported occurrence as a turf weed (Kim et al., 2002). Prior to introducing *D. longiflora* as a suitable turf in Singapore, there is a need to characterize its response and suitability under shade—a pervasive microenvironment generated by the shadows of urban buildings and trees.

This study was conceived to evaluate the performance of *D. longiflora* and *A. compressus* under four shade levels (including a control). Their shade performance will be compared to St. Augustinegrass, a highly shade-tolerant turfgrass. No comparative studies between St. Augustinegrass and *A. compressus* have been performed previously; though *A. compressus* has been noted to be a shade-tolerant grass under plantation canopies (Wong, 1990). The primary objective of the study was to rank the relative shade tolerance of the three tropical species based on a suite of leaf morphological responses.

Materials and Methods

Experimental site

This study was conducted in open field conditions at CUGE Research Station, HortPark (Singapore) from July - October 2015. The temperature and relative humidity over the study period ranged between 26°C to 30°C and 80 to 90%, respectively.

Plant material and establishment

Vegetative shoots of St. Augustinegrass & *A. compressus* were collected from turf lawns at HortPark (Singapore) while *D. longiflora* shoots were collected from Mt Faber Park (Singapore). The shoots were transplanted into planting flats (53×35×9 cm) filled with green waste compost (composted leaves and branches). Compound fertilizers (15:15:15) were applied at the time of planting and also bi-monthly at a rate of 5 g Nm⁻². Irrigation was supplied daily using a watering can until field capacity. The grasses were grown to uniform coverage under full sunlight for 3 months. The established grasses were cut to a uniform height of 5 cm to promote lateral growth prior to shade treatments.

Shade treatments

The different shade levels were obtained by varying number of black shade cloth sheets mounted over a polyvinyl chloride (PVC) frame of 110×110×100 cm. The four sides of the structure were fully covered to reduce light transmitting during morning and evening. The photosynthetic active radiation (PAR) within the shade structure was collected at hourly interval with a Photosynthetic light sensor-HOBO Micro Station datalogger unit (model S-LIA-M003, Onset Computer Corp., Bourne, MA). The control treatment was placed in full sunlight (100% photosynthetic photon flux,

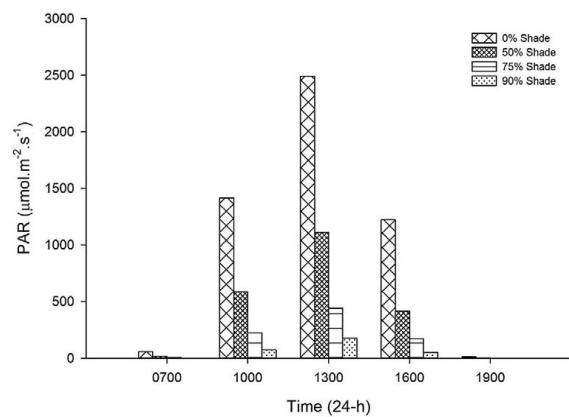


Fig. 1. Mean light intensity of light treatments taken over 10 days in October 2015.

PPF). The different density of shade cloth (one to 3 layers) provided shade levels of 50%, 75% and 90% (Fig. 1). The shade level was determined from percent reduction in light intensity from mid-day light condition (1300-1400 hr, light intensity ranging from 500-2500 mol m⁻² s⁻¹).

Leaf measurements

All the leaf measurements (length & width) were determined from first fully expanded leaf (5 from each replicate). Leaf length was measured from the tip to base of the leaf (above leaf sheath). The width of the leaf was determined by measuring across the midpoint. Young fully expanded leaves (5 from each replicate) were destructively harvested at end of treatments to determine leaf area (via Adobe Photoshop) and dry mass. Dry mass of each labeled leaf (same leaf as determined leaf area) was oven dried at 70°C for 48 hr. Specific leaf area of each leaf was determined by the acquired weight and leaf area.

Chlorophyll estimation

The chlorophyll level in the fully expanded leaf was determined using a hand-held chlorophyll meter (model SPAD-502, Minolta Corp., Ramsey, NJ).

Digital image analysis

Digital image analysis to determine percent green cover was conducted based on photographs (in JPEG format) taken with a tripod-mounted digital camera for an area covering 0.5×0.4 m. A light box that covered the entire measuring area was used to provide a uniform light source to prevent any changes in external lighting condition due to passing cloud shadows or cloudy weather. Percent green coverage was determined using SigmaScan Pro 5 (Systat Software Inc., San Jose, CA) following the macros and methods described by Karcher and Richardson (2003).

Experimental design & statistical analysis

Each species tray was placed under each shade level. The species were arranged in a randomized design of 4 (shade) x3 (turf) factorial arrangement with four replicates. All data were subjected to analysis of variance (ANOVA) procedure conducted using SPSS (version 23.0, IBM Corp., Armonk, NY). Means separation was determined using Tukey test at $P<0.05$.

Results & Discussion

Shade had induced significant morphological changes for all species in this study. The leaf length and area generally increased in all species with increasing shade (Table 1). St. Augustinegrass displayed the lowest relative leaf extension rate at 50% shade level while *Digitaria longiflora* manifested the highest relative leaf extension rate at 90% shade level (Table 2). The mean relative leaf extension rate was highest in *D. longiflora* (90.78%) followed by *Axonopus compressus* (84.62%) and St. Augustinegrass (80.42%), Table 2. Relative leaf greenness, based on SPAD measurements, generally peaked at 75% shade level in all species (Table 1). This can be visually seen as darker green leaf color at 75% shade level. SPAD measurements decreased in *D. longiflora* and *A. compressus* at 90% shade level but remained stable in St. Augustinegrass (Table 1). Most of the leaves in *D. longiflora* appeared chlorotic and severe leaf senescence was observed under the 90% shade level. Leaves of St. Augustinegrass still remained dark green at 90% shade level while the leaves in *A. compressus* became less green and comparable with control plants (0% shade level).

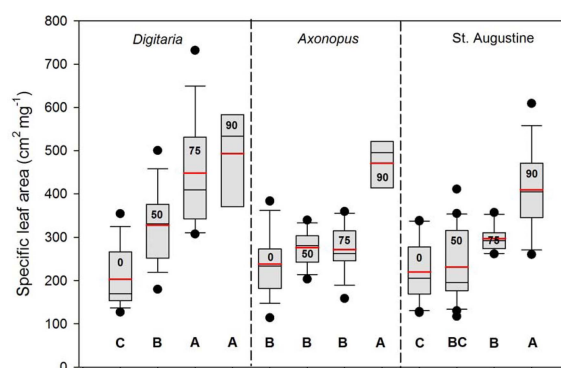


Fig. 2. Box plots displaying the range of specific leaf area ($\text{cm}^2 \text{mg}^{-1}$) in three species (*Digitaria longiflora*, *Axonopus compressus* and St. Augustinegrass) under four shade levels (indicated as 0, 50, 75 & 90%). Shade box indicates central 50% quantile, vertical lines the total variation in each treatment ($n=40$ observations) and horizontal lines within the box (black and red) as the median and mean value respectively. Means with same letters (intraspecific shade comparison) are not significantly different by Tukey test ($P<0.05$).

Specific leaf area (SLA) increased with increased shade levels in all species (Fig. 2 & Table 2). SLA increase in *D. longiflora* was mostly linear as the shade level increased from 0-90%. In contrast, the SLA increase was generally not responsive from 0-75% shade level in St. Augustinegrass and *A. compressus*; the increase in SLA was only significant at 90% shade level. Mean SLA (0-90% shade level) was highest in *D. longiflora* ($348.55 \text{ cm}^2 \text{mg}^{-1}$) followed by *A. compressus* ($286.88 \text{ cm}^2 \text{mg}^{-1}$) and St. Augustinegrass ($276.28 \text{ cm}^2 \text{mg}^{-1}$), Table 2.

Table 1. Plant characteristics (leaf length, leaf width, leaf area, dry weight and chlorophyll) of St. Augustinegrass (St. Augu.), *Axonopus compressus* (Ax. comp.) and *Digitaria longiflora* (Di. longi.) under different shade levels (0-90%) at 30 DAT (days after treatment). Means with same letter are not significantly different by Tukey test ($P<0.05$).

Sp.	Leaf length/cm				Leaf width/cm				Leaf area/ cm^2				Dry weight/mg				Chlorophyll (SPAD)			
	Shade, %	0	50	75	90	0	50	75	90	0	50	75	90	0	50	75	90	0	50	75
St. Augu.	3.2c	3.6c	6.2b	6.9a	0.7a	0.7a	0.7a	0.7a	1.9c	1.9c	4.4c	3.7b	8.9c	7.0c	16.3a	9.6b	39.4b	35.7b	40.6a	41.6a
Ax. comp.	6.6c	8.3b	8.3b	11.0a	0.9a	1.0a	1.0a	0.8a	4.2c	6.5a	6.5a	6.0b	18.6a	22.9a	23.6a	13.4b	28.3b	27.3b	34.0a	29.4b
Di. longi.	2.5d	3.6c	5.1b	7.5a	0.5a	0.6a	0.5a	0.4b	1.1c	1.8a	2.2a	1.7b	5.5a	5.3a	4.6c	3.4b	29.3b	29.7b	33.2a	23.2c

Table 2. Relative leaf extension rate (with respect to control) and Specific leaf area at 30 DAT (days after treatment) of three turfgrass species under different shade levels. Mean relative leaf extension rate was determined from 50-90% shade level. Mean specific leaf area was determined from 0-90% shade level. Means with same letter are not significantly different by Tukey test ($P<0.05$): between species comparison (lowercase); within species comparison (uppercase).

Species	Relative leaf extension rate (%)				Specific leaf area ($\text{cm}^2 \text{mg}^{-1}$)											
	Shade, %	50	75	90	Mean	0	50	75	90	Mean						
St. Augustinegrass	10.93	c C	98.74	a B	121.17	b A	80.42	220.31	a C	231.04	b BC	297.34	b B	409.33	a A	276.28
<i>Axonopus compressus</i>	55.09	a B	55.05	b B	144.48	bc A	84.62	237.79	a B	275.97	b B	272.08	b B	470.68	a A	286.88
<i>Digitaria longiflora</i>	35.16	b C	85.40	a B	167.04	ac A	90.78	202.98	a C	327.94	a B	448.08	a A	493.09	a A	348.55

Relative leaf extension growth

Shade-intolerant plants growing under low light extend their leaves as a shade avoidance mechanism to compete for more light (Smith and Whitelam, 1997; Tegg and Lane, 2004). This has been observed in several tropical turfgrass species and genotypes that were subjected to various shade treatments e.g., St. Augustinegrass (Wherley et al., 2013); zoysiagrass (Peterson et al., 2014); bermudagrass (Tegg and Lane, 2004) and seashore paspalum (Jiang et al., 2004). The leaf extension rate has been effectively used as an inference of shade tolerance in turfgrass—a lower increase in leaf extension rate was postulated to display better shade tolerance than a higher rate (Qian et al., 1998; Tegg and Lane, 2004; Wherley et al., 2013). The mean leaf extension rate across the three species can be ranked as *D. longiflora* (90.78%) > *A. compressus* (84.62%) > St. Augustinegrass (80.42%). Thus, it can be inferred that St. Augustinegrass has the highest shade tolerance followed by *A. compressus* and *D. longiflora*.

Leaf chlorophyll

Increased chlorophyll under low light (70-90% shade level) has been perceived as another adaptive mechanism to improve light harvesting capacity over photochemistry (Baij et al., 2005). This mechanism has been reported in many turfgrass species e.g. St. Augustinegrass (Wherley et al., 2013), tall fescue (Wherley et al., 2005) and, seashore paspalum (Jiang et al., 2004). The peak chlorophyll content at 75% shade level for all species in this study suggested the employment of similar mechanism in adapting to the low light conditions. Furthermore, the increased surface area via leaf extension at 75% shade level also coupled this increased chlorophyll content for more efficient light harvesting. However, under 90% shade level, the low light condition has triggered leaf senescence in *D. longiflora* (as seen in the reduction of chlorophyll). Shade-induced leaf senescence has been suggested to be triggered by a negative carbon balance (respiration rate higher than photosynthetic rate) when the light intensity was lower than the photosynthetic light compensation point (Veierskov, 1987; Brouwer et al., 2012). On the other hand, no shade-induced senescence events were observed in St. Augustinegrass or *A. compressus* at 90% shade level. However, the peaked chlorophyll content at 75% shade level was sustained in St. Augustinegrass at 90% shade level but showed a decrease in *A. compressus* (Table 1). Therefore, it can be conjectured that *D. longiflora* has a lower shade tolerance on the basis that it has a higher light compensation point than St. Augustinegrass or *A. compressus* due to the observable shade-induced leaf senescence events at 90% shade level.

Specific leaf area & Green cover

Specific leaf area (SLA) is directly related to light

interception. Shade-intolerant plants growing in low light have a tendency to increase SLA via increasing their leaf area to harvest more light (Reich et al., 1998a). Interestingly, this study observed a maximal increase in area (~2 fold, relative to control) at 75% shade level across all three species (Table 1). The increase in leaf area was accompanied by an increase of biomass in St. Augustinegrass and *A. compressus* except for *D. longiflora*; which concomitantly led to lower SLA in St. Augustinegrass and *A. compressus* compared to *D. longiflora*. The reduction of leaf biomass in *D. longiflora* reflects a decline of photosynthesis, plausibly attributed to shade-induced leaf senescence as discussed above. Nonetheless, the SLA increase was not responsive in St. Augustinegrass or *A. compressus* at 50-75% shade level; suggesting their ability to sustain or increase their biomass under these low light conditions. If the ability to sustain biomass production under shade determines its success in shade, it became apparent that *D. longiflora* is a poorer shade performer compared to the other two species. Moreover, it has been generally defined that species that are better adapted to shade show lower SLA than poorly adapted species (Reich et al., 1998b; Modrzyński et al., 2015). Since the mean SLA was highest in *D. longiflora* (348.55 cm² mg⁻¹) compared to St. Augustinegrass (276.28 cm² mg⁻¹) or *A. compressus* (286.88 cm² mg⁻¹), it can be supported that *D. longiflora* has a lower shade tolerance than the other grasses.

The percent green cover as determined by digital image analysis (Karcher and Richardson, 2003) indicated a significantly lower green cover of 53% in *D. longiflora* at 90% shade level compared to 76-78% green cover in *A. compressus* and St. Augustinegrass respectively. The lower percent green cover in *D. longiflora* was translated visually as an abundance of senesced and chlorotic shoots than the other two species. This loss of green cover was most likely a result of prolonged photosynthetic recession and shade-induced senescence events. Hence, this further supported the relatively poor shade performance of *D. longiflora*.

Shade performance & Turf Comparison

St. Augustinegrass has been consistently reported to have superior shade tolerance over other tropical species (Beard, 1973; Trenholm & Nagata, 2005). This study supported a higher shade tolerance of St. Augustinegrass over *A. compressus* and *D. longiflora* in terms of lower leaf extension rate, lower mean specific leaf area and higher light compensation point. No similar studies have been performed to compare shade performance between St. Augustinegrass and *A. compressus* or *D. longiflora* even though *A. compressus* was determined to display good shade tolerance under plantation crop canopies (Wong, 1990). Thus, this study has demonstrated that St. Augustinegrass outperformed *A. compressus* and *D. longiflora* under shade due to its ability to sustain higher biomass production under a deep shade

condition e.g. 90% shade level.

The duration and level of light intensity depict the degree of turf decline over time (Jiang et al., 2004). The period of this study was albeit shorter than several previous shade studies (Jiang et al., 2004; Sladek et al., 2009; Wherley et al., 2013). But, the shade responses reported in this study e.g. leaf elongation, and SLA increase were similar to all previous studies. Quality of seashore paspalum cultivars and TifEagle bermudagrass was shown to decline after a period of two weeks exposure to continuous 70 and 90% shade levels; with further deterioration of turf quality observed at 42 DAT (Jiang et al., 2004). This two weeks period of shade treatment was defined by them as a critical time to evaluate responses of turfgrasses to shade. Hence, the experimental period (4 weeks) in this study would therefore be sufficient to evaluate the relative shade tolerance between species based on their discernible morphological responses under shade. Nonetheless, the limitation of this study lies in its lack of capacity to determine the persistence of each species under prolonged shade.

Conclusions

This study of leaf morphological responses to shade has further corroborated St. Augustinegrass as a highly shade tolerant turfgrass. The ability of St. Augustinegrass to sustain high leaf biomass production under deep shade condition due to its superior shade adaptive mechanisms has certainly outperformed *A. compressus* and *D. longiflora*. Therefore, the relative shade tolerance of the three turfgrasses could be ranked as St. Augustinegrass > *A. compressus* > *D. longiflora*. Hence, the utility of *D. longiflora* under close canopy tree shade or within the deep shadow of buildings will not be encouraged over the other two turfgrasses.

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