Towards estimating shade response of bermudagrass (*Cynodon* spp.) using field-based photosynthetic properties

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Abstract

Shade tolerance is a highly desirable trait when breeding new bermudagrass (*Cynodon* spp.) lines, but current screening methods can take many years to complete. There is a clear need for large-scale turfgrass breeding programs to reliably, accurately, and quickly predict shade tolerance in their germplasm. The objectives of this research were to: (i) build custom chambers to reproducibly estimate photosynthetic characteristics from turfgrass canopies at different light intensities and (ii) determine which photosynthetic characteristics are indicative of past shade performance. A custom-built chamber was constructed to determine average photosynthetic characteristics for the whole plant by studying the turfgrass canopy at natural leaf angles for light interception. Shade tolerant (11-T-56) and shade sensitive (Tifway) bermudagrass cultivars were used to examine the effectiveness of the chamber within an array of photosynthetic characteristics when the grasses were grown in full-sun and 73% shade environments. Light compensation point, chlorophyll content, quantum yield, dark respiration rate, and maximum quantum yield of photosystem II were evaluated in this trial. Based on the results of this study, the authors recommend that light compensation point or maximum quantum yield be further evaluated as an accurate indicator of shade tolerance when performed in the field on spring days with grasses grown in full sun or 73% shade environments. Lower R_d rates and ambient temperatures on spring days appear to minimize unexplained variance in the data, which would allow researchers to better detect genotypic differences during this season.

INTRODUCTION

The characterization of shade tolerance for warm season turfgrasses can be challenging as they experience additional stress when grown under shaded conditions. Reduced light intensity translates to reduced photosynthesis and consequently grass growth and health. Shaded microenvironments tend to have higher humidity and slower air movement than open areas which creates a higher risk for disease incidence that can reduce the vigor of plants[1,2]. Turfgrasses growing near or under trees are forced to compete for soil moisture and nutrients. In some cases, allelopathic interactions are found between species in these microenvironments[3].

When the aforementioned challenges are coupled with the perennial nature of warm-season perennial turfgrasses, it is not surprising that the characterization of shade tolerance can take many years. For example, Fox[4] compared commercial cultivars of bermudagrass (*Cynodon* spp.) to several experimental genotypes in a reduced light environment beneath a 73% shade cloth in a field-based variety trial. Though the author ultimately determined that experimental 11-T-56 maintained greater ground cover than the standard 'Tifway' (40% vs. 12%), it took over four years to reach this conclusion. Likewise, Barrios et al.[5] and Beard[2] reported significant leaf canopy reduction in zoysiagrass (*Zoysia* spp.), St. Augustinegrass (*Stenotaphrum secundatum*), and centipedegrass (*Eremochloa ophiuroides*)

when managed under low light conditions for three and two years respectively. Clearly large-scale turfgrass breeding programs need predictable and time-efficient methods for identifying shade tolerance in their germplasm.

The light compensation point (LCP) is defined as the amount of light needed to reach the balance point of the rate of carbon exchange within the plant or the point where the rate of photosynthesis equals the rate of respiration. This point can be estimated by generating a light response curve where photosynthetic rate is regressed against light (i.e., photosynthetic photon flux density)[6]. Grasses that are inherently more adapted to low light conditions tend to have lower LCPs when compared to species or cultivars adapted to higher light intensity (full sun) environments. In a tropical forage grass study, Bernardino Dias-Filho[7] found both *Brachiaria brizantha* and *B. humidicola* grass species displayed lower LCP's after each was exposed to a shaded environment compared to the full sun treatment. They also noted that apparent quantum yield was unaffected by the treatments while the dark respiration rates and chlorophyll a:b ratio were greatly reduced by the shade treatment. Van Huylenbroeck et al.[8] concluded that red fescues (*Festuca rubra*) generally had lower LCPs than perennial ryegrasses (*Lolium perenne*), which corresponded to better adaptation to the lower light intensities. When multiple genotypes of four species of cool-season grasses were evaluated, Van Huylenbroeck & Van Bockstaele[9] determined that individual genotypes differed in

their LCP within their respective species.

The majority of research conducted to determine LCPs of turfgrasses has been performed under the controlled environments of growth chambers and greenhouses. Plants that are grown in the natural field environment could perform differently and need to be compared to these other studies. In order for a turfgrass program to efficiently measure LCP in the field, the breeder needs to utilize a portable photosynthesis system. In many crops, single leaf analysis of photosynthetic gas exchange is possible, but not in turfgrass where leaves are much smaller and cannot properly be studied with the available equipment. Also, the density of these small leaves causes some leaves to be more shaded out than others, therefore studying single leaves would not accurately depict the overall shade tolerance of that genotype. A custom-built chamber is needed to determine an accurate average for an area of the turf canopy at natural leaf angles for light interception. Using the proposed chamber, it may be possible to predict shade tolerance from light response curves of bermudagrasses grown in the field under real-world environmental conditions.

Therefore, the objectives of this research were to: (i) build custom chambers to reproducibly estimate photosynthetic characteristics from turfgrass canopies at different light intensities and (ii) determine which photosynthetic characteristics are indicative of past shade performance.

RESULTS AND DISCUSSION

Light compensation point

No significant sources of variation were identified for LCP of the genotypes in the pilot study, likely due to unexplained variation between dates of measurement for this trait as indicated by higher CV's in this analysis. The full sun trial was conducted in order to alleviate the daily variation and we found that LCP was affected by genotype x month interactions ($P <$ 0.0001; Tables 1 & 2). The LCP of 11-T-56 was lower than Tifway at the May sampling event, but no differences were seen in the following months (Table 2). Likewise, the LCP was 95% lower for 11-T-56 than Tifway when the genotypes were evaluated under shaded conditions at the May sampling event ($P \leq 0.01$; Table 3). There were no differences found after this sampling date (Table 3). Bermudagrass cover in both genotypes was similar in both the full sun and the shaded studies except in August of the shaded study where Tifway tended to decline quicker in the fall.

The LCPs of two other bermudagrass cultivars ('FloraDwarf' and 'Tifdwarf') were determined in growth chambers by Miller et al.[10]. They found genotypic differences between the two cultivars when the plants were exposed to 12 h of artificial light at 1,540 µmol m^{-2} s^{-1}, a comparable light intensity as the full-sun exposure in this study. The authors were unable to identify cultivar differences when the plants were grown under shaded conditions[10]. Other studies have found that plants exposed to shade will have lower LCPs[7,11], but research comparing genotypic differences for LCPs in sun-acclimated or shade-acclimated plants measured in the field is often inconclusive. Many previous attempts to determine LCPs of turfgrass that were grown in full sun[12,13] using clear chambers with ambient light were largely unsuccessful because of intermittent daily and seasonal cloud cover, and the time needed for CO_2 assimilation rates to stabilize. The chamber design used in this study

Table 1. Mean light compensation point, quantum yield, dark respiration rate, chlorophyll content, and chlorophyll fluorescence of two bermudagrass genotypes grown in full-sun during 2016 and 2017 in Tifton, GA, USA. Data are pooled across replications.

Response	LCP†	ϕCO_2	R_d	CC	F_v/F_m
	(µmol m^{-2} s^{-1})			(mg m^{-2})	
Month					
Aug. 2016	248.6	0.0114	1.7a‡	407.9	0.7885
Oct. 2016	211.4	0.0094	1.3b	469.4	0.7613
Apr. 2017	141.2	0.0086	1.4b	421.3	0.7513
May 2017	110.1	0.0120	1.1b	505.0	0.6993
Jun. 2017	114.7	0.0147	1.1b	447.9	0.7310
Sep. 2017	72.7	0.0093	0.7c	449.9	0.7082
Genotype					
11-T-56	138.7	0.0711	1.3	438.0b	0.7510
Tifway	160.8	0.1578	1.7	467.7a	0.7370
CV§	19.7	41.9	23.8	7.9	5.7

† LCP: light compensation point, ϕCO_2: quantum yield, R_d: dark respiration rate, CC: chlorophyll content, F_v/F_m: chlorophyll fluorescence
‡ Least square means within each canopy characteristic and response followed by different letters differ according to Fisher's LSD test ($P \leq 0.05$)
§ CV: Coefficient of Variation

Table 2. Mean light compensation point, chlorophyll content, and chlorophyll fluorescence of two bermudagrass genotypes grown in full-sun during 2018 in Tifton, GA, USA. Data are pooled across replications.

Genotype	May	July	August	CV†
	Light compensation point (µmol m^{-2} s^{-1})			
11-T-56	63.1b‡	211.2	273.9	5.6
Tifway	76.9a	248.9	267.7	
	Chlorophyll content (mg m^{-2})			
11-T-56	553.5a	390.0	374.8	9.6
Tifway	383.5b	397.5	379.5	
	Chlorophyll fluorescence			
11-T-56	0.7436a	0.7301	0.6358	5.4
Tifway	0.5490b	0.7625	0.6290	

† CV: Coefficient of Variation
‡ Least square means within each response and month followed by different letters differ according to Fisher's LSD test ($P \leq 0.05$)

Table 3. Mean light compensation point of two bermudagrass genotypes grown under 73% shade during 2018 in Tifton, GA, USA. Data are pooled across replications.

Genotype	May	July	August	CV†
	Light compensation point (µmol m^{-2} s^{-1})			
11-T-56	2.6b‡	20.8	64.8	14.8
Tifway	57.6a	72.2	65.8	

† CV: Coefficient of Variation
‡ Least square means within each month followed by different letters differ according to Fisher's LSD test ($P \leq 0.05$)

allowed for the accurate production of light response curves using a controlled light source, which allows the user to accommodate for unpredictable cloud cover and weather conditions observed in the Southeast USA.

Quantum yield (ϕCO_2)

There were no differences in genotype or sampling month when the analysis of variance for quantum yield were analyzed for the grasses grown in the pilot study, under full sun, or under 73% shade (Tables 1, 4 & 5). Several published research studies also report similar quantum yields between genotypes within C_4 species[7,14]. This is not surprising since plants with similar

Table 4. Mean quantum yield and dark respiration rate recorded on bermudagrass grown in full-sun during three sampling dates in 2018 in Tifton, GA, USA. Data are pooled across replications and two bermudagrass genotypes, Tifway and experimental number 11-T-56.

Response	May	July	August	CV[†]
Quantum yield, (μmol m^{-2} s^{-1})	0.0096	0.0095	0.0118	8.3
Dark respiration rate, (μmol m^{-2} s^{-1})	0.8b[‡]	2.4a	2.7a	10.9

[†] CV: Coefficient of Variation
[‡] Least square means within each response followed by different letters differ according to Fisher's LSD test ($P \leq 0.05$)

Table 5. Mean quantum yield, dark respiration rate, chlorophyll content, and chlorophyll fluorescence of two bermudagrass genotypes grown under 73% shade during 2018 in Tifton, GA, USA. Data are pooled across replications and month.

Response	Genotype		CV[†]
	11-T-56	Tifway	
Quantum yield, (μmol m^{-2} s^{-1})	0.0185	0.0167	14.6
Dark respiration rate, (μmol m^{-2} s^{-1})	0.6	0.4	18.1
Chlorophyll content, (mg m^{-2})	404.1	396.6	8.0
Chlorophyll fluorescence[‡]	0.7376a[§]	0.6779b	2.1

[†] CV: Coefficient of Variation
[‡] Chlorophyll fluorescence could only be measured on one day (May) out of the growing season because of the lack of ground cover
[§] Least square means within each response followed by different letters differ according to Fisher's LSD test ($P \leq 0.05$)

photosynthetic pathways should possess similar quantum yields[15]. Plants will only deviate from their population mean when exposed to stressful environments[15]. Although quantum yield is a critical component of calculating overall light response curves, it does not appear to be predictive of shade tolerance in bermudagrass.

Dark respiration rate (R_d)

The R_d rate of the turfgrass was affected by month in the pilot study ($P \leq 0.01$; Table 1). The greatest R_d rate was recorded in August 2016 and the lowest rate in September 2017. All other months were intermediate to these two, yet not different to each other. Month was also significant in the full sun study where the lowest R_d rate was recorded in May (Table 4). Neither month nor genotype affected R_d rate of grasses grown under 73% shade (Table 5).

Previous studies found that plants will have lower dark respiration rates when grown under shade compared to a plant grown in full sun[7,16]. Wilkinson & Beard[17] reported a lower R_d rate for 'Pennlawn' red fescue when exposed to shade compared to similar plants grown in full sun. Conversely, the R_d rate for 'Merion' Kentucky bluegrass (*Poa pratensis*) did not change when exposed to shade in the same study. This indicates that some species may not acclimate to shade as well as others. Soil respiration studies have found that soil respiration is lower in the spring when the soil temperatures are cooler, since the methods of our study depend highly upon soil respiration this could explain why R_d was lower during spring months[18]. If there is less soil respiration to conflict with the R_d measurements, that could explain why these months are more accurate.

The experimental design of the current study did not allow for statistical comparison of the full sun and shaded trials, but the two trial locations were geographically similar. Tables 4 & 5 show that the R_d rates were numerically lower on the grasses

grown under shade compared to the same genotypes grown in full sun.

There is limited research investigating if R_d rates are indicative of higher or lower shade tolerance within the same species. In a study using growth chambers to measure photosynthetic characteristics Miller et al.[10] found no significant differences in R_d rates of Floradwarf and Tifdwarf when exposed to six different light regimes. Based on the results of this trial, R_d rate was unable to illustrate the greater shade tolerance of 11-T-56 and its ability to maintain higher turfgrass quality under the shade than Tifway.

Chlorophyll content (CC)

In the pilot study, 11-T-56 had a lower CC than Tifway when data were pooled across all months ($P \leq 0.05$; Table 1). The full sun study yielded a genotype by month interaction ($P \leq 0.01$), however, 11-T-56 only possessed a greater CC in May when data were analyzed by month ($P \leq 0.05$; Table 2). The two genotypes were similar at the other sampling dates in the full sun study and when exposed to 73% shade in the shade trial there were no differences found. ($P > 0.05$; Tables 2 & 5)

Some researchers have reported that CC will increase when a plant is exposed to shade to maximize the light-harvesting capacity under low-light conditions although these responses are not always consistent[19,20]. High CC often corresponds to a darker green plant and may be related to shade tolerance in many plant species[16,21]. Jiang et al.[12] examined shade responses of eight seashore paspalum (*Paspalum vaginatum*) and two bermudagrass genotypes by comparing plants grown under full sun to those managed under light conditions that were reduced by 70 and 90%. From this work, 'TifSport' bermudagrass displayed the highest CC when grown in full sun, but had lower levels when grown under both shade treatments. TifSport did not adapt after exposure to the shade, implying that chlorophyll content in the full sun may not be a direct indicator of true shade tolerance in bermudagrass. More research is needed to understand how CC corresponds to shade tolerance, what drives certain genotypes to acclimate their CC under different light conditions, and the importance of early season differences in CC.

Chlorophyll fluorescence (F_v/F_m)

Neither month nor genotype affected F_v/F_m in the pilot study (Table 1). Genotype and month interacted to affect F_v/F_m for the grasses when grown under full sun ($P \leq 0.01$). When the data were analyzed within month, 11-T-56 had a greater F_v/F_m than Tifway in May ($P \leq 0.05$; Table 2). There were no differences found in the other sampling events for the full sun study. Likewise, 11-T-56 had a greater F_v/F_m than Tifway when grown under 73% shade ($P \leq 0.05$; Table 5). Unfortunately, F_v/F_m could only be measured one day in this study (May) because there was insufficient leaf material present at subsequent sampling events. The thin, etiolated leaves on both genotypes did not give a strong enough signal strength for the fluorometer to perform the measurement.

The value of F_v/F_m has been studied in the past to understand the effects of shade on different plant species. Dąbrowski et al.[22] reported a steady upward trend in F_v/F_m when three perennial ryegrass genotypes were grown in full sun, half shade, and shade from May through September. Though we were only able to obtain one measurement in our shaded study, we saw similar results with Tifway displaying a higher

photochemical efficiency in the shade compared to the full sun in May while 11-T-56 had similar readings. Jiang et al.[23] also measured F_v/F_m of Sea Isle 1 seashore paspalum to TifSport bermudagrass under high (500–900 μmol m^{-2} s^{-1}) and low (60–100 μmol m^{-2} s^{-1}) light conditions. Despite using artificial supplemental lights, the F_v/F_m in these grasses were generally not affected by shade.

Maximum quantum yield could be an accurate indicator of shade tolerance when performed in the field on spring days with grasses grown in sun or shade environments. More research is needed to determine the minimum amount of canopy (ground) coverage required to obtain these measurements. Regardless, there should be further investigation of using F_v/F_m to determine and compare shade tolerance among turfgrass genotypes.

CONCLUSIONS

Based on the results of this study, the authors recommend that LCP or maximum quantum yield be further evaluated as an accurate indicator of shade tolerance when performed in the field on spring days with grasses grown in full sun or 73% shade environments. Chlorophyll content may also be a potential indicator, but would only be applicable in full sun environments on spring days. These measures were selected since they could quantitatively portray the improved shade tolerance of 11-T-56 over Tifway as previously determined in other trials[4]. Although quantum yield and R_d rate are critical components of calculating overall light response curves, they do not appear to be predictive of shade tolerance in bermudagrass. Lower R_d rates and ambient temperatures on spring days appear to minimize unexplained variance in the data, which would allow researchers to better detect genotypic differences during this season. More research is needed to understand the importance of early season measures on season long shade tolerance and performance, as well as the minimum amount of canopy (ground) coverage required to obtain accurate and reliable measurements.

The chamber design used in this experiment should be implemented in future trials, although it would be ideal to have additional chambers so that measurements could be taken on the same day for all genotypes. Unfortunately, limited equipment prevented this for the full-sun and shaded studies. Future consideration of investment in more chambers and a larger power supply will be needed if this technique will be deployed in our breeding program to evaluate many genotypes at the same time.

MATERIALS AND METHODS

Pilot study

In 2014 the grasses for the initial experiment were vegetatively propagated in the greenhouse and planted in the field on Tifton loamy sand to establish into 10.7 m × 4.6 m plots located in Tifton, GA, USA (31°28'36.5"N 83°31'38.4"W). The plots were mowed at 12.7 mm once per week and fertilized and irrigated as needed for proper plant health.

The research began in 2016 and tested the assimilation rates of CO_2 on two bermudagrass genotypes (Tifway and 11-T-56) grown in full sun. The experimental design was a randomized complete block design that was replicated in time. Measure-

ments were collected from both genotypes on the same day for a total of four sampling days per month and were collected in August and October 2016 and April, May, June, and September in 2017 using the procedure described below. Each measurement day within a month was defined as a rep since an entire day was needed to build the light response curves.

It was previously established that 11-T-56 was more shade tolerant than Tifway[4]. Consequently, the methods proposed in this research are only valid proxies for assessing shade tolerance if they can accurately and repeatedly predict that 11-T-56 is more shade tolerant than Tifway. Unfortunately, the large day to day variation did not allow the summarization of data over each month and determination of shade tolerance Therefore, two subsequent experiments with a randomized complete block design were established to minimize day-to-day variation and improve the repeatability of the genotypic comparisons.

Full-sun study

Two subsequent experiments with a randomized complete block design were established to minimize day-to-day variation and improve the repeatability of the genotypic comparisons. The first of these studies was established on 2 May 2017 with 5.1 cm plugs planted on 1.8 m centers and grown into a total area of 1.8 m × 1.8 m. There were four replications of 11-T-56 and Tifway bermudagrass and the plots were grown under full sun. Similar methods to those described for the pilot study were used during 2018 to build light response curves and determine photosynthetic characteristics of the turfgrasses at three different dates. Measurements were collected from all replications of one genotype on the same day. Data from the second genotype was measured on the following day.

Shaded study

The second experiment was established under a 73% shade cloth on August 2016 with 5.1 cm plugs planted on 0.9 m centers and grown into a total area of 0.9 m × 0.9 m. There were three replications of 11-T-56 and Tifway bermudagrass under the shade cloth area. Similar methods to those described above in the pilot study were used during 2018 to build light response curves and determine photosynthetic characteristics of the turfgrasses at three different dates. Again, all replications of one genotype were measured on the same day and the second genotype on the following day. The sampling dates occurred within the same week of sampling dates for the full-sun experiment.

Chamber installation

Detailed information on the construction of the chambers utilized in these experiments may be found in the Supplementary Information File associated with this manuscript.

Prior to each sampling event, a 10.2-cm PVC pipe was hammered into the ground and removed to prepare the area needed to insert the actual chamber. The chamber was inserted 25 mm deep into the turfgrass canopy to ensure stability and to form a seal on the bottom of the chamber[12]. Each chamber was covered with a small shade structure that measured 61 cm × 61 cm and 30 cm above the turf canopy to insure no ambient light could reach the chamber. The structures were assembled with 1.27 cm PVC pipe and covered with black faux stretch leather fabric (Hobby Lobby Stores, Inc.; Oklahoma City, OK, USA) across the top and down two sides with the other two sides open for air flow and measurement capability. By facing

the two shaded sides in the east and west direction to account for the movement of the sun, we were able to prevent most ambient light penetration and allow for complete control of light intensity.

Response variables

Assimilation rates of CO_2 were measured using an infrared gas analyzer (LI-6400, LI-COR Biosciences; Lincoln, NE, USA) attached to the custom chamber. The first CO_2 assimilation rates were collected pre-dawn to measure a true dark respiration rate (R_d) at 0 μmol m^{-2} s^{-1} photosynthetically active radiation (PAR). Light intensity inside of the chambers was measured at each increased increment in PAR using a light meter (Extech, LT45 Color LED Light Meter; Wilmington, NC, USA). The meter's sensor was fixed onto a 10.2-cm PVC cap that fitted onto the top of the chamber so light intensity was recorded at equal distances from the LED.

The light level was then incrementally increased throughout the day while recording CO_2 assimilation rates to create the light response curve. The turfgrass was allowed a 15 to 20-minute acclimation period after each light intensity increase before CO_2 assimilation rates were measured and recorded as net photosynthesis. An additional five minutes was required to accommodate for the chamber's size and reach a steady state at each intensity before CO_2 exchange rates were recorded.

Chlorophyll content (CC) was measured outside of the chamber area using a chlorophyll content meter (OPTI- SCIENCES CCM-300; Hudson, NH, USA) with a signal gain of four. Three leaves were sampled from each plot and the average CC was recorded[24]. Chlorophyll fluorescence (F_v/F_m) was measured to determine the light harvesting capabilities of grasses. A portable chlorophyll fluorometer (OPTI-SCIENCES Multimode Chlorophyll Fluorometer; Hudson, NH) was used to measure five locations in each plot and the average F_v/F_m was recorded. The fluorometer probe was placed in direct contact with the turfgrass surface, exposing the sample to a low-intensity, modulation light to determine F_0 followed by a saturating flash of light for ~0.8 s to determine F_m. The value for F_v/F_m was calculated by the device as $[(F_m - F_0)/F_m]$[25].

After each data collection event, the photosynthetic rates were first graphed with the corresponding PPFD reading to create a light response curve. It is generally observed that at low light levels (< 200 μmol par) photosynthesis increases in a linear manner. Points within this initial linear phase were selected for linear regression, the slope of which was then used to determine quantum yield of CO_2 assimilation[26,27].

The LCP for each genotype was determined by solving the linear regression formula $Y = a + bX$ and solving for "a" which in this case is the LCP[28].

Statistical analysis

Prior to analysis, data were transformed to ensure normality of the dataset and thus validity of the F-statistic. The distribution of data for each characteristic was assessed for normality using a histogram and Shapiro-Wilks test for normality. Square root transformations were used on LCP, ϕCO_2, and R_d datasets since conditions of normality were not met. Two outliers were detected for LCP data in the full sun study so they were removed before a reciprocal (1/x) transformation was applied to accommodate the wide distribution of values. No transformations were used for CC and F_v/F_m.

An analysis of variance (ANOVA) was then performed for each response variable using the PROC GLM procedure in SAS 9.4 (SAS Institute, Cary, NC, USA). Month and genotype were delineated as fixed effects while season and replication were set as random. Where genotype × month interactions were significant, data were analyzed by month where applicable (ANOVA not shown). Differences were examined using a Fisher's LSD test and were considered significant at $\alpha = 0.05$.

Conflict of interest

The authors declare that they have no conflict of interest.

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