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Irradiance Response of Tall Fescue Genotypes with Contrasting Levels of Photosynthesis and Yield

W. W. Wilhelm and C. J. Nelson

ABSTRACT

The purpose of this study was to determine if genotype by irradiance interactions or genetic variation in diurnal trends of CO₂ exchange rate (CER) influenced the CER-yield relationship in tall fescue (Festuca arundinacea Schreb.). Genotypes were selected in the field for high CER-high yield, high CER-low yield, low CER-high yield, and low CER-low yield. Responses of CER to photosynthetic photon flux density (PPFD) of these genotypes were determined using both growth chamber- and field-grown material. The shapes of the PPFD response curves were similar for all genotypes, and saturation occurred at approximately 1,200 µE m⁻² s⁻¹ (400 to 700 nm) under both growth conditions. In a growth chamber at 23/20 °C (light/dark), all genotypes achieved near maximal CER and photosynthesis within 1 hour of the beginning of the photoperiod and maintained these rates throughout the rest of the photoperiod, with high CER genotypes exhibiting about 30% higher rates than low CER genotypes. Photosynthesis rates were significantly correlated (r = 0.80) with CER. Leaf diffusive resistance was similar for all genotypes throughout the photoperiod.

Genotypic differences did not occur in PPFD-response curves or diurnal patterns of CER. This suggests that differences in these two factors among genotypes are not the underlying cause of the poor relationship reported between short term measurements of leaf photosynthesis on recently collared leaves and forage yield. Other factors must be limiting genetic expression for CER in terms of yield.

Additional index words: Leaf diffusive resistance, Photosynthesis, Diurnal trends, Festuca arundinacea Schreb., Photosynthetic photon flux density.

GENETIC variability has been reported in tall fescue (Festuca arundinacea Schreb.) for both CO₂ exchange rate (CER) of single leaves and yield (Nelson et al., 1975a). Similar findings have been reported for other cool-season perennial forage grasses (Wilson and Cooper, 1970; Carlson et al., 1971; Rhodes, 1972; Borrill et al., 1974). Although genetic variability has been found, a positive relationship between CER of single leaves and yield has not been well documented. Increased forage yield and decreased CER were associated with selection for small mesophyll cells when compared to selections made for large mesophyll cells in perennial ryegrass (Lolium perenne L.) (Wilson and Cooper, 1970). Nelson et al. (1975a) reported an inconsistent relationship between CER and yield in clonal lines of tall fescue. Individual harvest period correlation coefficients between CER and yield ranged from -0.60 to +0.60 in three field studies, but the overall correlation coefficient was nonsignificant and negative.

Canopy shading and development (Rhodes, 1973) and dry matter distribution (Treharne and Eagles, 1970) have been suggested as factors influencing the relationship between leaf photosynthesis and yield. Nelson et al. (1975a) also suggested that genotype by irradiance interactions may influence the CER-yield relationship. In addition, genetic variation in diurnal trends in CER could affect this relationship (Pallas, 1978).

We hypothesized that different yields exhibited by tall fescue genotypes having similar photosynthetic photon flux density (PPFD) — saturated CER as determined by short term, midday measurements may result from genotypic variation in the diurnal pattern of CER or the photosynthetic PPFD response curve. The rates of carbon exchange during the early and late parts of a photoperiod may not be similar as suggested by PPFD-saturated midday measurements. Therefore, the total amount of CO₂ fixed throughout a photoperiod may not be equivalent for the two types of genotypes and yields would logically differ. Yield differences among genotypes with similar PPFD-saturated CER may also be explained by differences in the shape of their photosynthetic PPFD response curve. The objectives of this research were to determine whether variation in the diurnal pattern of CER or variation in PPFD response curve could be influencing the leaf photosynthesis-yield relationship among selected genotypes of tall fescue.

MATERIALS AND METHODS

Four genotypes of tall fescue were selected from field evaluations to represent high and low CER on a leaf area basis, in combination with high and low forage yield (Table 1). Forage yield and CER (Nelson et al., 1974) were measured on three replications of 67 genotypes during 1972. Genotypes were grown as solid stands in 1.7 x 3.7 m field plots as described by Nelson et al. (1975a). Cumulative yield of the first two cuttings and mean of two CER measurements during early and late June were used to select the genotypes used in the study. Differences between the high and low categories (Table 1) were significant and large enough to make meaningful comparisons. In later studies reported herein, CER's of the genotypes in the high CER category were more comparable than those presented for the field measurements in Table 1.

Table 1. Mean CO₂ exchange rate (CER) for two measurement dates and forage yield of four selected genotypes of tall fescue, 1972.

<table>
<thead>
<tr>
<th>Genotype</th>
<th>Source</th>
<th>CER</th>
<th>Yield</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(CER/yield)</td>
<td>mg CO₂ dm⁻² hour⁻¹</td>
<td>metric tons/ha</td>
</tr>
<tr>
<td>H-H</td>
<td>'Alta'</td>
<td>29.30</td>
<td>10.30</td>
</tr>
<tr>
<td>H-L</td>
<td>Missouri pasture</td>
<td>25.03</td>
<td>7.41</td>
</tr>
<tr>
<td>L-H</td>
<td>'Demeter'</td>
<td>20.64</td>
<td>9.32</td>
</tr>
<tr>
<td>L-L</td>
<td>'Kenwell'</td>
<td>21.27</td>
<td>7.45</td>
</tr>
<tr>
<td>L.S.D. (0.05)</td>
<td>3.45</td>
<td>1.43</td>
<td></td>
</tr>
</tbody>
</table>
Three vegetative tillers of each genotype were established in 10 \times 15 \text{ cm} plastic pots filled with Mexico silt loam soil in four replications. Plants were allowed to grow in the greenhouse at 25 \pm 3 \text{ C} for approximately 2 months before being transferred to a controlled environment chamber with 25/20 \text{ C} (light/dark) temperature and greater than 50\% relative humidity. A 14-hour photoperiod of 500 \mu \text{E m}^{-2} \text{sec}^{-1} PPFD was provided by cool-white fluorescent tubes and incandescent bulbs. Plants were maintained in a well watered condition and supplemented with 50 ml of a complete nutrient solution (Einstein, 1972) each week. Plants were cut to 6 cm to start the experiments after a 2-week acclimatization period in the growth chamber. Pots of each genotype had about 40 tillers.

### Laboratory PPFD Response

The four genotypes, grown under growth chamber conditions described above, were used to measure CER response to varying PPFD in the laboratory. Radiation was provided by 16 150-W floodlights, filtered through 15 cm of running tap water, and regulated using a rheostat. A Lambda Instruments LI-170 quantum sensor was used to measure PPFD at the leaf surface. Rate of CO$_2$ exchange was measured as described above, starting at a PPFD of 1,800 \mu \text{E m}^{-2} \text{sec}^{-1}. Leaves reached new CER equilibrium in about 10 min, after which PPFD was reduced by increments of 290 \mu \text{E m}^{-2} \text{sec}^{-1}. Leaf temperatures were maintained at 29 \pm 2 \text{ C}.

### Field PPFD Response

Four replications of each genotype were vegetatively established in field plots (0.5 \times 1.5 \text{ m}) during September 1973 on imperceptibly drained Mexico silt loam soil at the Agronomy Research Center, Columbia, Mo. Pots had developed into a sward and were fertilized with 26, 12, and 22 kg/ha of elemental N, P, and K, respectively, on 16 Mar., 13 May, 21 June, and 12 Aug. 1975. Pots were cut on 21 August and plants had regrown to 25 to 30 cm in height when measurements were made.

Simultaneous measurements of CER (Nelson et al., 1974) and PPFD were made on six recently collared leaves/replication from 1000 to 1500 hours on 1 Oct. 1975 when intermittent cumulus clouds occurred. Assembling points allowed a response curve to be constructed for each genotype. Response curves of CER to PPFD of the four genotypes were also generated on a clear day (3 Oct. 1975) by placing multiple layers of cheesecloth and fiber glass screens over the air-sealed chambers during PPFD and CER measurements. Leaf temperatures varied from 20 to 29 \text{ C} on the days of CER measurements. The degrees to which variation in temperatures affected PPFD response was probably negligible, because within one replication maximum range in leaf temperature was 3 \text{ C}.

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### RESULTS AND DISCUSSION

#### Diurnal Trends

When regrowth was 20 to 25 cm tall, measurements of diffusive resistance and CER in 21 and 2\% O$_2$ were made each hour from 1 hour before the beginning of the photoperiod until 1 hour after the end of the photoperiod. The CER was measured on two newly collared leaves from each pot using infrared gas analysis and air-sealed chambers as described by Nelson et al. (1974). Leaves were placed in the air-sealed chambers only during the time CER measurements were made (approximately 10 min/hour). Photorespiration (PR) was estimated by the increase in CER in 2\% O$_2$ over that in 21\% O$_2$ (Canvin, 1968). Photosynthetic photon flux density inside the leaf chamber was 460 \mu \text{E m}^{-2} \text{sec}^{-1}. Leaf temperature was 26 \pm 1 \text{ C} during the light period and 20 \pm 2 \text{ C} during the dark period.

Leaf diffusive resistance was measured using a Lambda Instruments, Model LI-60 diffusion porometer (Kanemasu et al., 1969) on the same leaf tissue after each CER measurement. Following the last daily measurements, leaves were detached from the plant and leaf area measured.

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hhibited high PR rates throughout the day, while low CER genotypes exhibited low rates. Differences between high and low CER genotypes were not as well defined for PR as for CER measurements, but a significantly positive correlation was found \( r = 0.80 \) between PR and CER over the entire day. This direct relationship between CER and PR supports the conclusion of Nelson et al. (1975b) and Laing et al. (1974) that these two processes are closely related metabolically, and selection for high CER will probably also select for high PR.

Leaf diffusive resistance among the four genotypes varied greatly early and late in the photoperiod when stomata were opening and closing (Fig. 1c). However, they were similar during the remaining 11 hours of the photoperiod and did not account for the observed differences in CER. A slight increase in diffusive resistance of all genotypes was noted after 7 hours into the photoperiod, but this was not related to a change in CER. The L-H genotype had resistances of 3.3 sec/cm between 8 and 9 hours into the photoperiod, which was significantly higher than the other genotypes. This was not related to a significant change in CER. In agreement with the present study, Frank and Barker (1976) indicated that calculated stomatal resistances ranging from 0.8 to 4.6 sec/cm in several grass species were not controlling CER under conditions which allowed stomata to be fully open. Misken et al. (1972) reported that stomatal resistance of flag leaves of barley \((Hordeum vulgare \ L.)\) increased from 1.27 to 1.92 sec/cm with decreasing stomatal frequency, but photosynthetic rates did not vary.

Pallas (1973) reported that several dicotyledonous species exhibited midday depressions and characteristic diurnal trends in CER, but in agreement with our study on the monocolyledon, tall fescue, the only monocotyledonous species in his study, bermudagrass \((Cynodon dactylon \ L.)\), maintained a constant CER throughout the photoperiod. He also indicated that changes in stomatal diffusive resistance were not solely responsible for fluctuations in CER.

**PPFD Response**

Response of CER to PPFD for the four genotypes is presented as percent of maximum (Fig. 2). Genotype PPFD response curves were not significantly different \((p<0.05)\) by any of the three methods of determination (Fig. 2a, b, c). Therefore, differences in photosynthetic rates between genotypes were due to inherent CER rather than differential PPFD saturation. Absolute values for the high CER genotypes were not as high in the field as in the growth chamber, but were significantly greater \((p<0.05)\) than the low CER genotypes. The field study reported here was conducted during early October and the lower air temperatures during this part of the season may have contributed to the relatively low CER.

The PPFD saturation \((90\% \text{ of maximum CER})\) of tall fescue leaves for each measurement (Fig. 2d) occurred at approximately 1,200 \(\mu\text{E m}^{-2}\text{sec}^{-1}\) suggesting that PPFD response was independent of previous irradiance history. This result was not expected because plants were grown under both field \((\text{up to} \ 2,000 \ \mu\text{E m}^{-2}\text{sec}^{-1})\) and growth chamber \((500 \ \mu\text{E M}^{-2}\text{sec}^{-1})\) conditions. Woledge (1971) reported tall fescue plants grown at high irradiance were capable of higher photosynthetic rates/unit leaf area and saturated at higher flux densities than similar plants grown at lower irradiance. However, similar CER responses to increasing illumination were reported by Singh et al. (1974) for leaves of orchardgrass \((Dactylis glomerata \ L.)\) plants grown under full sun and screens which reduced natural illumination by 30, 50, and 70%.

Wilson and Cooper (1969) also reported a nonsignificant genotype by light intensity interaction for photosynthesis in a
growth chamber study of 10 ryegrass genotypes. Similar PPFD response curves have recently been reported for Paniceum maximum Jacq., grown under controlled environment chamber, greenhouse, and field conditions by Ludlow and Ng (1976).

Photosynthetic fixation of CO₂ contributes the majority of the total dry matter produced by a plant. A positive association between leaf photosynthesis and dry matter production would seem necessary if present methods of measuring photosynthesis are accurately estimating a plant's total CO₂ fixation potential, and if other processes involved in deposition of dry matter are occurring with equal efficiency across genotypes. Results of this study indicated that genotypes selected for different maximum CER maintained those differences throughout the photoperiod. Some changes in leaf diffusive resistance were noted in the later part of the photoperiod, but were not associated with decreased CER.

The results of the studies reported here indicate that variation in the relationship between CER and yield in tall fescue can not be explained by the two hypotheses stated in the beginning of this paper. The four genotypes used in these experiments displayed similar CER responses to PPFD and similar PPFD saturation points when grown in two distinctly different environments and similar diurnal patterns of CER when measured on growth chamber grown plant material. Although these responses were similar, the genotypes consistently displayed rates of CO₂ exchange that were consistent with their respective selection criteria. It does not appear that low CER, high yield genotypes have an advantage in total amount of CO₂ fixed/unit leaf area under reduced PPFD conditions or at various times during the photoperiod which would explain how they are able to achieve their high yield characteristic. These experiments do, however, suggest that comparative CER of genotypes of tall fescue can be accurately estimated over a wide range of light conditions. Other factors are apparently expressing a dominating influence on the yield potential of the selected genotypes. Some of these factors might be dark respiration, dry matter distribution, and canopy architecture and development.

REFERENCES


