

FIELD STUDIES OF PHOTOSYNTHETIC AND GROWTH RESPONSES TO IRRADIANCE IN THREE FOREST UNDERSTORY SPECIES OF THE C₄ GRASS GENUS MUHLENBERGIA¹

MARIAN SMITH² AND CRAIG E. MARTIN

Department of Botany, University of Kansas, Lawrence, Kansas 66045

Three species of the C₄ grass genus *Muhlenbergia* from the forest understory—*M. frondosa*, *M. sobolifera*, and *M. schreberi*—and one species from an open prairie, *M. cuspidata*, were transplanted to a sunny common garden and to a forest understory. After 4 mo of growth, all species in the common garden produced more biomass and greater leaf area and number than those in the understory. *Muhlenbergia cuspidata* died in the understory. Chlorophyll (chl) concentrations were higher, and a/b ratios were lower, in plants from the understory. All species were grown in the laboratory under two PPFD regimes: (1) 15 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for 9 h plus two 10-min periods of 500 $\mu\text{mol m}^{-2} \text{s}^{-1}$; and (2) 15 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for 20 h. Total integrated PPFD, not peak photon flux density, appeared to determine all aspects of the photosynthetic responses of these plants. Characteristics of photosynthetic gas exchange in situ for *M. frondosa* and *M. sobolifera* were similar to laboratory findings. Although results indicated that the three understory species adjusted their chl characteristics and survived when grown under low levels of PPFD, they grew optimally under the higher PPFD.

Introduction

Since the discovery of the C₄ metabolic pathway (KORTSCHAK et al. 1965), many studies have shown that C₄ plants, as a result of their higher ATP requirement, are adapted to sunny environments (BJÖRKMAN and BERRY 1973; HATCH and OSMOND 1976). The distribution of C₄ species generally supports this conclusion, with most C₄ plants restricted to warm, sunny habitats (TEERI and STOWE 1976; DOLINER and JOLLIFFE 1979; TIESZEN et al. 1979; TEERI et al. 1980). However, the discovery of several C₄ species growing in forest understories (BROWN 1977; WINTER et al. 1982; PEARCY 1983; PEARCY and CALKIN 1983; WARD and WOOLHOUSE 1986) challenged the dogma that the distribution of these plants is determined primarily by their photosynthetic pathway (PEARCY and EHRLINGER 1984).

Three species of the C₄ grass genus *Muhlenbergia*—*M. frondosa*, *M. sobolifera*, and *M. schreberi*—occur in the understory of deciduous forests in eastern Kansas (GREAT PLAINS FLORA ASSOCIATION 1986). Although the understory PPFD levels are often as low as 15 $\mu\text{mol m}^{-2} \text{s}^{-1}$, transient sun flecks that vary from 100 to 1,700 $\mu\text{mol m}^{-2} \text{s}^{-1}$ periodically illuminate the plants through breaks in the canopy throughout the day. These sun flecks

can vary in duration from 30 s to 20 min (personal observation).

In laboratory studies (SMITH and MARTIN 1987a, 1987b), the three understory species, when compared with *M. cuspidata*, which is restricted to open prairie, exhibited characteristics of shade tolerance: (1) substantial biomass production at low PPFD; (2) an increase in chl content and a decrease in chl a/b ratios with decreasing PPFD; (3) photosynthetic CO₂ exchange and photosystem I electron transport saturation at low levels of PPFD; and (4) high quantum yields in plants grown at low PPFD. The four species of *Muhlenbergia* produced more biomass under higher PPFD than existed in their natural habitats (SMITH and MARTIN 1987a).

For a better understanding of this paradoxical finding, field studies were conducted in which growth and chl responses of plants grown in a forest understory were compared with those of plants grown in a sunny common garden, and photosynthetic gas exchange was measured in situ for *M. frondosa* and *M. sobolifera*. In addition, to assess the potential ability of these species to capitalize on transient sun flecks, a laboratory study was conducted to determine their chl and photosynthetic responses to brief periods of high PPFD.

Material and methods

TRANSPLANT EXPERIMENT

Muhlenbergia frondosa (Poir.) Fern. and *M. sobolifera* (Muhl.) Trin. were collected from the understory of an oak-hickory forest (WELLS and MORLEY 1964) 14 km S of Lawrence, Kansas (Douglas Co.). Rhizomes of *M. frondosa* were collected along a 200-m transect of an abandoned railway bed. Levels of PPFD varied from less than 150 $\mu\text{mol m}^{-2} \text{s}^{-1}$ under the canopy to full sunlight in open areas. Rhizomes of *M. sobolifera* were col-

¹Abbreviations: A, assimilation; ANCOVA, analysis of covariance; ANOVA, analysis of variance; chl, chlorophyll; c_i, intercellular CO₂ concentration; g_c, conductance to CO₂; LA, leaf area; LDW, leaf dry weight; LN, leaf number; LSD, least significant difference; PPFD, photosynthetic photon flux density; RDW, root dry weight; SDW, stem dry weight; TDW, total dry weight.

²Current address and address for correspondence and reprints: Department of Biological Sciences, Southern Illinois University, Edwardsville, Illinois 62026.

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lected from a site ca. 100 m from the railway bed on a steep, moist bank above a stream. The PPFD levels at the site were ca. 10–25 $\mu\text{mol m}^{-2} \text{s}^{-1}$ except during transitory sun flecks.

Muhlenbergia schreberi Gmel. was collected beneath a canopy of *Juniperus virginiana* along a small creek near an unpaved road 0.5 km NW of Alma, Kansas (Wabaunsee Co.). The PPFD levels below the canopy were 300–1,500 $\mu\text{mol m}^{-2} \text{s}^{-1}$. *Muhlenbergia cuspidata* (Torre.) Rydb. was collected from an open prairie 1.6 km E of Hiattville, Kansas (Linn Co.), in dense clumps in cracks and at the edges of limestone outcrops.

Plants were transplanted to an open, sunny common garden in the Nelson Environmental Study Area of the University of Kansas, 18 km NE of Lawrence in Jefferson County, 0.5 km E of County Road 9. The upper 10 cm of soil were tilled in four 1 × 1-m plots, and 30 plants of each species were placed ca. 15 cm apart in rows and covered with 10 cm of soil. Stems were clipped at ground level. The immediate area was cleared of other vegetation, and the plots were weeded regularly, but not watered, during the study. Levels of PPFD at the site, determined at 1500 hours (no. = 3) on a clear day, ranged from 1,700 to 2,000 $\mu\text{mol m}^{-2} \text{s}^{-1}$.

A second group of plants was transplanted in an identical fashion to a forest understory ca. 2 km from the common garden site. The canopy was composed of *Ulmus rubra*, *Carya ovata*, and *Celtis occidentalis* and saplings of *Cercis canadensis* and *Toxicodendron radicans*. Levels of PPFD on the day of planting, when the trees had not fully leafed out, varied from ca. 700 to 1,000 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Two weeks later, PPFD (no. = 5) varied from 25 to 300 $\mu\text{mol m}^{-2} \text{s}^{-1}$ under the full canopy.

Plants from both transplant areas were harvested after 4 mo of growth. The LA was determined with a LI-COR (Lincoln, Neb.) LI-3000 leaf area meter for five samples randomly chosen from each species and each treatment. The chl content and chl a/b ratios were determined (SMITH and MARTIN 1987b). All chl data were statistically analyzed by ANOVA, and means were compared for LSD (SOKAL and ROHLF 1981). Statistical difference was inferred when $P < .05$.

The remaining plants were oven-dried at 80 °C for 4 days for biomass determinations. All biomass data were analyzed by ANCOVA. Rhizome dry weight, closely correlated with initial rhizome fresh weight (determined previously), was the covariate in all biomass analyses. Means were compared for LSD.

LIGHT FLECK EXPERIMENT

Rhizomes of all species were collected, potted, and grown for 28–35 days in the laboratory (SMITH and MARTIN 1987a). Twenty plants of each species were placed under two PPFD regimes: (1) 15 μmol

$\text{m}^{-2} \text{s}^{-1}$ for 20 h, and (2) 15 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for 9 h plus two 10-min periods of 500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (integrated daily irradiance = 1.08 mol m^{-2} for both sets of plants).

Photosynthetic gas exchange from each PPFD regime was measured on three attached leaves of each species. The gas exchange system was as described by SMITH and MARTIN (1987b) except that (1) air temperature varied from 27 to 31 °C; (2) vapor pressure deficit varied from 1.75 to 2.70 kPa; and (3) mean CO₂ concentration was 346 $\mu\text{L L}^{-1}$ (SD = 8, no. = 54).

After gas exchange measurements, LA and chl concentrations were determined. CO₂ and H₂O exchange rates were measured (SĚSTÁK et al. 1971), and A, g_c, and c_i were calculated (FARQUHAR and VON CAEMMERER 1982).

All gas exchange data were analyzed by a two-way ANOVA (SPSS^x, Chicago, Ill.), and means were compared for LSD (SOKAL and ROHLF 1981). Statistical difference was inferred when $P < .05$.

FIELD PHOTOSYNTHESIS

On 2 clear days in August 1984, photosynthetic measurements were determined in situ on 18–20 plants of *M. frondosa* and *M. sobolifera*. Measurements were made on a single attached leaf of each plant and included plants both in and out of transient sun flecks. Leaf temperatures were 17–31 °C; chamber relative humidity, 7%–35%; and light levels, 5–1,700 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD. All data were calculated with a LI-COR LI-6000 portable photosynthesis system (0.25 L chamber) calibrated every 2 h.

Results and discussion

TRANSPLANT EXPERIMENT

The failure of *Muhlenbergia cuspidata*, a prairie plant, to survive in the understory is consistent with results obtained for plants grown in the laboratory at low PPFD (SMITH and MARTIN 1987a) and further emphasizes that this species is an obligate sun plant.

Although *M. frondosa*, *M. sobolifera*, and *M. schreberi* survived when transplanted to the understory, exhibiting some degree of shade tolerance, all three species produced significantly greater biomass (TDW, SDW, LDW, and RDW) when grown in a common garden (table 1). In addition, LA and LN were greater for these three species grown in the common garden (table 2). Although growth conditions are not identical with those in the laboratory growth experiments (SMITH and MARTIN 1987a), the field data corroborate results obtained under laboratory high and low PPFD regimes. Both experiments indicate that, although the species survive at reduced PPFD, they are able to exploit higher levels of light when available during

TABLE 1

EFFECTS OF PPFD LEVEL ON PLANT, STEM, LEAF, AND ROOT
(INCLUDING RHIZOME) BIOMASS (TDW, SDW, LDW, RDW) (g)
IN THREE UNDERSTORY AND ONE PRAIRIE SPECIES OF MUHLENBERGIA

SPECIES	GROWTH ENVIRONMENT	
	Common garden $\bar{X} \pm SE$	Understory $\bar{X} \pm SE$
<i>M. frondosa</i> :	(No. = 28)	(No. = 22)
TDW	3.82 \pm .37a	.30 \pm .03b
SDW	1.30 \pm .09a	.09 \pm .01b
LDW70 \pm .07a	.06 \pm .01b
RDW	1.83 \pm .20	.16 \pm .02
<i>M. sobolifera</i> :	(No. = 23)	(No. = 27)
TDW	1.76 \pm .24a	.40 \pm .05b
SDW54 \pm .08a	.09 \pm .01b
LDW41 \pm .06a	.09 \pm .01b
RDW71 \pm .11	.23 \pm .03
<i>M. schreberi</i> :	(No. = 23)	(No. = 16)
TDW	1.65 \pm .21a	.07 \pm .01b
SDW87 \pm .11a	.02 \pm <.01b
LDW33 \pm .04a	.01 \pm .01b
RDW46 \pm .06	.04 \pm .01
<i>M. cuspidata</i> :	(No. = 23)	
TDW45 \pm .05	a
SDW19 \pm .02	a
LDW10 \pm .01	a
RDW12 \pm .02	a

NOTE.—Probabilities were calculated from ANCOVA. Only means with different letters differ significantly ($P < .05$, LSD).

^a No plants survived.

TABLE 2

EFFECTS OF PPFD ON LA (cm²) AND LN IN THREE UNDERSTORY
AND ONE PRAIRIE SPECIES OF MUHLENBERGIA

SPECIES	GROWTH ENVIRONMENT	
	Common garden $\bar{X} \pm SE$	Understory $\bar{X} \pm SE$
<i>M. frondosa</i> :		
LA (5, 10) ^a	221.67 \pm 42.72a	21.85 \pm 2.12b
LN (28, 22) ^a	99.79 \pm 8.61a	13.45 \pm 1.17b
<i>M. sobolifera</i> :		
LA (4, 11)	128.28 \pm 55.00 ^b	27.54 \pm 4.36
LN (23, 27)	79.09 \pm 12.81 ^b	12.44 \pm 1.07
<i>M. schreberi</i> :		
LA (5, 6)	75.13 \pm 14.27 ^b	2.60 \pm .25
LN (23, 16)	109.61 \pm 14.62a	7.31 \pm .65b
<i>M. cuspidata</i> :		
LA (5)	16.90 \pm 6.91	c
LN (23)	24.74 \pm 2.35	c

NOTE.—Probabilities were calculated from ANCOVA. Only means with different letters differ significantly ($P < .05$, LSD).

^a Nos. in parentheses are sample sizes for common garden and understory, respectively.

^b The slopes of the regression lines for the different light levels were not parallel; therefore, no further testing of the means was attempted.

^c No plants survived.

growth. Similar results were observed in *Microstegium vimineum* (WINTER et al. 1982) and *Paspalum conjugatum* (WARD and WOOLHOUSE 1986), other shade-adapted C₄ plants. The greatest degree of shade tolerance in the present transplant study is observed in *M. sobolifera*, which is the only species to produce larger leaves in the understory. Also, these plants suffer less reduction in TDW (ca. 78%) than *M. frondosa* (ca. 92%) or *M. schreberi* (ca. 96%).

Chl concentrations were lower, and chl a/b ratios higher, in plants of *M. frondosa*, *M. sobolifera* and *M. schreberi* grown in the garden than in those grown in the understory (table 3). All three species apparently adjusted chl concentrations and ratios in response to lower levels of PPFD during growth under natural conditions. Greater chl concentrations in the understory plants should result in an increase in light-harvesting ability and constitutes a physiological adjustment to shade (BJÖRKMAN 1981). This is also consistent with results obtained under laboratory conditions for these three species (SMITH and MARTIN 1987b) and with field studies of other species (GRANT and RYUGO 1984; MASAROVICOVÁ and MINARČIC 1985). Lower chl a/b ratios, observed in plants transplanted to the understory, are an indication of an increase in size of the light-harvesting complex, a response demonstrated by other shade-adjusted plants in field and laboratory experiments (BJÖRKMAN et al. 1972; BOARDMAN 1977; WINTER et al. 1982) and again are consistent with results obtained in our laboratory (SMITH and MARTIN 1987b).

TABLE 3

EFFECT OF PPFD ON chl CONCENTRATION (mg g⁻¹ DW) AND chl
a/b RATIOS IN THREE UNDERSTORY SPECIES AND ONE PRAIRIE
SPECIES OF MUHLENBERGIA

SPECIES	GROWTH ENVIRONMENT	
	Common garden $\bar{X} \pm SE$	Understory $\bar{X} \pm SE$
<i>M. frondosa</i> :	(No. = 10)	(No. = 10)
Chl concentration....	4.42 \pm .38a	12.02 \pm 1.00b
Chl a/b ratio	3.37 \pm .13a	2.54 \pm .03b
<i>M. sobolifera</i> :	(No. = 10)	(No. = 7)
Chl concentration....	2.20 \pm .22a	11.28 \pm .73b
Chl a/b ratio	2.95 \pm .06a	2.63 \pm .09b
<i>M. schreberi</i> :	(No. = 10)	(No. = 6)
Chl concentration....	4.97 \pm .35a	15.37 \pm .99b
Chl a/b ratio	3.30 \pm .08a	2.54 \pm .04b
<i>M. cuspidata</i> :	(No. = 10)	
Chl concentration....	3.80 \pm .13	a
Chl a/b ratio	3.60 \pm .03	a

NOTE.—Only means with different letters differ significantly ($P < .05$, LSD).

^a No plants survived.

TABLE 4

EFFECT OF DIFFERENT PEAK PHOTON FLUX DENSITIES (SAME DAILY TOTAL) ON chl CONCENTRATION (mg g^{-1} DW) AND chl a/b RATIOS IN THREE UNDERSTORY SPECIES AND ONE PRAIRIE SPECIES OF MUHLENBERGIA

SPECIES	GROWTH LIGHT REGIME	
	Light fleck $\bar{X} \pm \text{SE}$	Low light $\bar{X} \pm \text{SE}$
<i>M. frondosa</i> :		
Chl concentration	21.28 ± 1.89	24.62 ± 2.89
Chl a/b ratio	$2.71 \pm .08$	$2.76 \pm .09$
<i>M. sobolifera</i> :		
Chl concentration	28.79 ± 2.13	20.54 ± 7.52
Chl a/b ratio	$2.43 \pm .14$	$2.39 \pm .20$
<i>M. schreberi</i> :		
Chl concentration	$6.41 \pm .72a$	$16.86 \pm .20b$
Chl a/b ratio	$2.99 \pm .09$	$2.97 \pm .10$

NOTE.—Light fleck = $15 \mu\text{mol m}^{-2} \text{s}^{-1}$ for 9 h and $500 \mu\text{mol m}^{-2} \text{s}^{-1}$ for two 10-min periods. Low light = $15 \mu\text{mol m}^{-2} \text{s}^{-1}$ for 20 h day⁻¹. Only means with different letters differ significantly ($P < .05$, LSD). No. = 3 for all species. *Muhlenbergia cuspidata* did not survive under either regime.

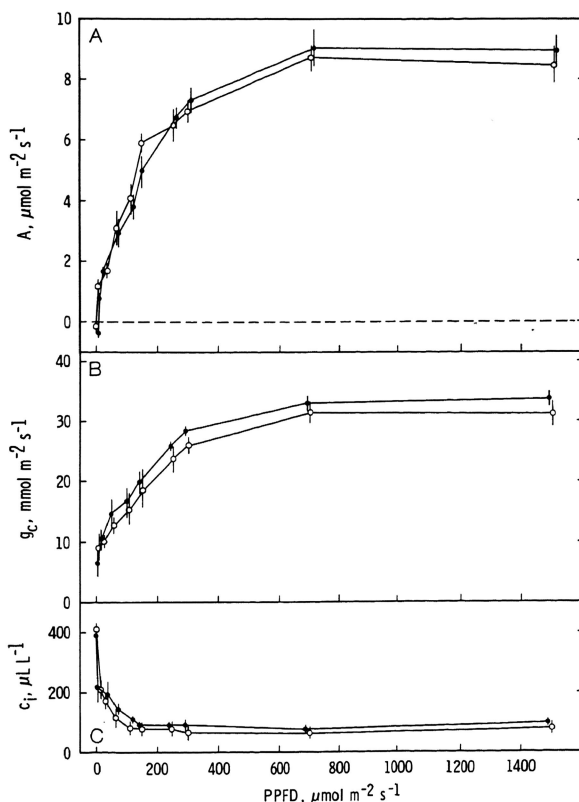


FIG. 1.—*Muhlenbergia frondosa*. A, Assimilation rate (A); B, leaf conductance (g_c); and C, intercellular CO_2 concentration (c_i) as functions of light. Plants were grown for 28–35 days at the following light levels (same daily fluence rate): \circ , light fleck = $15 \mu\text{mol m}^{-2} \text{s}^{-1}$ for 9 h plus two 10-min periods of $500 \mu\text{mol m}^{-2} \text{s}^{-1}$. \bullet , low light = $15 \mu\text{mol m}^{-2} \text{s}^{-1}$ for 20 h. Data are means and SE of three plants.

LIGHT FLECK EXPERIMENT

Plants of *M. cuspidata* failed to survive under both PPFD regimes. Brief increases in PPFD had no effect on chl (table 4) or photosynthetic responses (figs. 1–3) in *M. frondosa*, *M. sobolifera*, and *M. schreberi* relative to plants grown at constant low PPFD. One exception was the chl content of *M. schreberi*, which decreased under the light regime with two periods of high PPFD.

The similarity in photosynthetic responses to PPFD of plants of *M. frondosa*, *M. sobolifera*, and *M. schreberi* from both PPFD regimes to increasing instantaneous PPFD indicates that the integrated amount of PPFD received during growth was the limiting factor, not the peak photon flux density. Similar results, in terms of growth as well as photosynthesis, were demonstrated by HURD and THORNLEY (1974), NOBEL (1976), and CHABOT et al. (1979). Shade-adapted species of the C₄ genus *Euphorbia* in Hawaiian forests, however, respond to sun flecks uniquely and maintain higher CO_2 assimilation rates than expected, given the integrated daily PPFD (PEARCY and CALKIN 1983; PEARCY et al. 1985).

For the three understory species in the present study, A curves were nearly identical with those

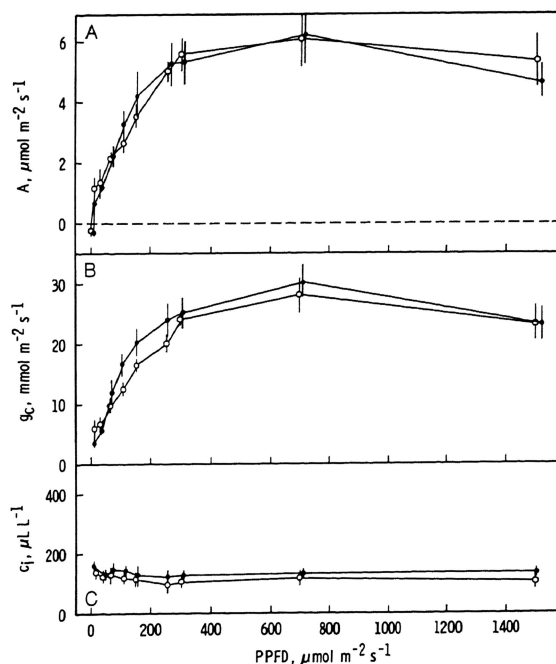


FIG. 2.—*Muhlenbergia sobolifera*. A, Assimilation rate (A); B, leaf conductance (g_c); and C, intercellular CO_2 concentration (c_i) as functions of light. Plants were grown for 28–35 days at the following light levels (same daily fluence rate): \circ , light fleck = $15 \mu\text{mol m}^{-2} \text{s}^{-1}$ for 9 h plus two 10-min periods of $500 \mu\text{mol m}^{-2} \text{s}^{-1}$. \bullet , low light = $15 \mu\text{mol m}^{-2} \text{s}^{-1}$ for 20 h. Data are means and SE of three plants.

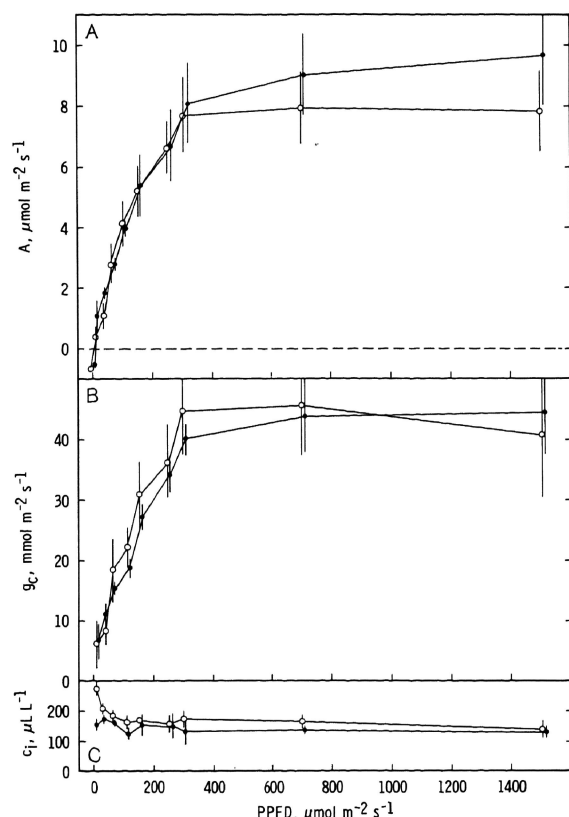


FIG. 3.—*Muhlenbergia schreberi*. A, Assimilation rate (A); B, leaf conductance (g_c); and C, intercellular CO_2 concentration (c_i) as functions of light. Plants were grown for 28–35 days at the following light levels (same daily fluence rate): O, light fleck = $15 \mu\text{mol m}^{-2} \text{s}^{-1}$ for 9 h plus two 10-min periods of $500 \mu\text{mol m}^{-2} \text{s}^{-1}$. ●, low light = $15 \mu\text{mol m}^{-2} \text{s}^{-1}$ for 20 h. Data are means and SE of three plants.

obtained for the same species grown in the laboratory at $15\text{--}25 \mu\text{mol m}^{-2} \text{s}^{-1}$ under a 12-h photoperiod (SMITH and MARTIN 1987b). Photosynthetic saturation below $400 \mu\text{mol m}^{-2} \text{s}^{-1}$ indicates that the plants are unable to utilize high PPFD fully. Equal photosynthetic rates of plants receiving short periods of high PPFD and those receiving a constant low level of PPFD indicate that higher PPFD levels, while not being utilized, do not cause any damage to the photosynthetic system. This is further emphasized by the c_i values, which decrease with increasing instantaneous PPFD and were in the range for C_4 plants (ca. $100 \mu\text{L L}^{-1}$) (WONG et al. 1985; WARD and WOOLHOUSE 1986).

Results of the light fleck experiment, when combined with those of laboratory plants grown at high, medium, and low PPFD (SMITH and MARTIN 1987b), emphasize that *M. frondosa* and *M. sobolifera* can adjust to the total quanta available in a variety of light environments and that their chl is not damaged by brief periods of high PPFD. It is

unclear whether the greater chl concentration observed in *M. schreberi* under low PPFD reflects chl damage by short periods of high PPFD or chl synthesis under constant low PPFD.

FIELD PHOTOSYNTHESIS

The pattern of photosynthetic responses to PPFD (figs. 4, 5) of *M. frondosa* and *M. sobolifera* in the field was similar to that observed in the laboratory (SMITH and MARTIN 1987b): (1) A increased in conjunction with g_c , resulting in a relatively constant c_i ; (2) saturation of A with respect to instantaneous PPFD occurred at ca. $200\text{--}400 \mu\text{mol m}^{-2} \text{s}^{-1}$; and (3) maximum rates of A for *M. frondosa* were higher than for *M. sobolifera*. *Muhlenbergia sobolifera*, however, exhibited substantially higher

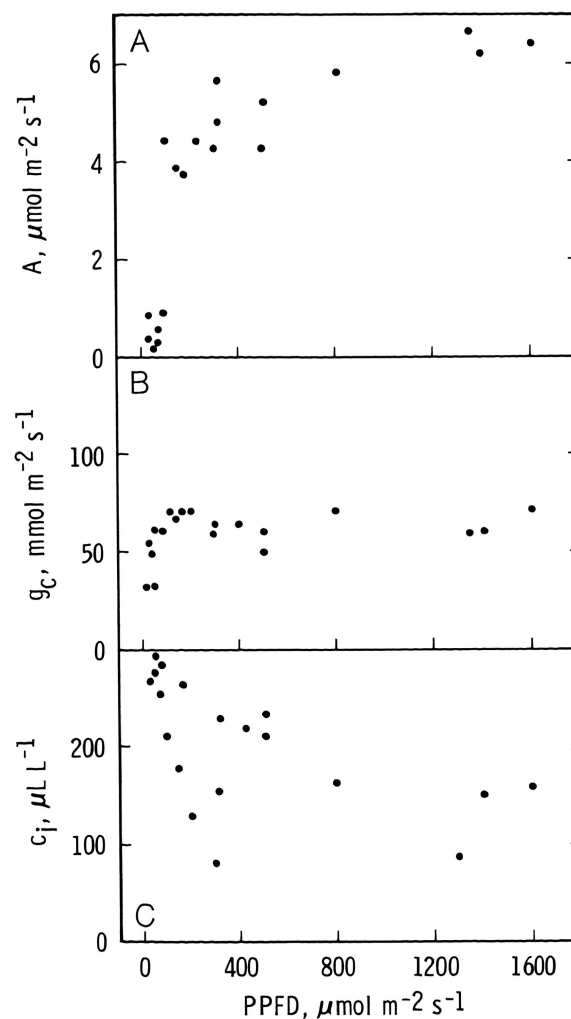


FIG. 4.—*Muhlenbergia frondosa*. A, Assimilation rate (A); B, leaf conductance (g_c); and C, intercellular CO_2 concentration (c_i) as functions of light. Each data point represents a measurement in the field on a single attached leaf.

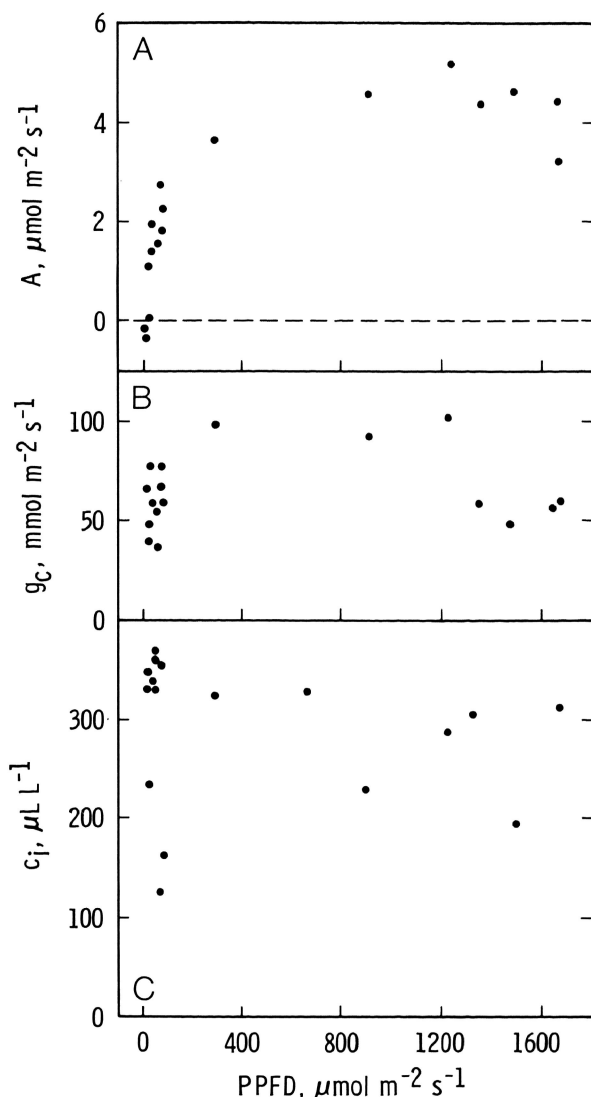


FIG. 5.—*Muhlenbergia sobolifera*. A, Assimilation rate (A); B, leaf conductance (g_c); and C, intercellular CO_2 concentration (c_i) as functions of light. Each data point represents a measurement in the field on a single attached leaf.

g_c in the field than in the laboratory, resulting in higher values for c_i than normal for C₄ plants. The high g_c observed in situ may reflect the relatively cool temperatures and high soil moisture prevalent at the study site during measurements, in addition to the late time of measurement (late summer). Both *M. frondosa* and *M. sobolifera* have positive carbon exchange at ca. $10 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD, indicating very low rates of respiration. This can be considered an adaptation to growth under shaded conditions and may be crucial to the survival of these species in understory habitats.

Apparently, the C₄ syndrome in these species of *Muhlenbergia*, as well as in *Microstegium vimineum* (WINTER et al. 1982), *Paspalum conjugatum* (WARD and WOOLHOUSE 1986), and several species of *Euphorbia* (PEARCY et al. 1982; PEARCY and CALKIN 1983), does not impose an inherent limitation on the ability to adjust to shaded habitats. From this transplant study, which corroborates our laboratory study (SMITH and MARTIN 1987a), it is clear that, although these understory species of *Muhlenbergia* survive at low levels of PPFD, they produce significantly more biomass when grown at higher levels of PPFD. They are not, therefore, operating at their physiological optimum in the habitats in which they occur. We hypothesize that ecological factors play a crucial role in determining the presence of these grasses and perhaps other shade-tolerant C₄ species in forest understories.

Acknowledgments

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