

RELATIONSHIP BETWEEN EVOLUTIONARY ADAPTATION AND GAS EXCHANGE CHARACTERISTICS OF DIVERSE *SORGHUM* TAXA

By R. W. DOWNES*

[Manuscript received March 31, 1971]

Abstract

Ten species and varieties of *Sorghum* were conditioned to either full or part sunlight. Gas exchange parameters of attached leaves were determined under a range of levels of photosynthetically active radiation and leaf temperature. *S. arundinaceum* which originated in the low light environment of equatorial forests was capable of higher rates of photosynthesis and greater stomatal opening if it was conditioned to low rather than high radiation conditions. In this respect it differed from the other species though all have the characteristics of plants with the C₄ pathway of photosynthesis. Generally species from high radiation environments were capable of the highest rates of photosynthesis though some exceptions were noted. Genetic implications are briefly discussed.

I. INTRODUCTION

The net photosynthetic rate (P) and transpiration rate (T) of leaves of *Sorghum sudanense* vary, depending on the light intensity to which leaves are adapted (Downes 1971). However, various *Sorghum* species and races have evolved under, or become adapted to, diverse light intensity conditions from equatorial forests (*S. arundinaceum*) to subequatorial deserts (*S. virgatum*) (De Wet, Harlan, and Price 1970).

In the genus *Triticum*, Evans and Dunstone (1970) and Khan and Tsunoda (1970) have demonstrated that P is greatest per unit leaf area in wild diploid species and that P has decreased with increase in chromosome number and modification and cultivation by man. In *Sorghum*, chromosome number varies between $2n = 10$ and $2n = 40$ with most species having $2n = 20$ (Celarier 1958). Within cytologically homologous groups both wild and cultivated forms occur (Doggett 1970).

Thus the genus *Sorghum* contains species and races of diverse evolutionary adaptation and ploidy among which genetic relationships, anatomical features, and physiological responses may be expected to vary. In this context, the rates of gas exchange and leaf characteristics were examined in 10 *Sorghum* races selected for study because of diversity of habitat, ploidy, degree of modification by man, and taxonomic relationships.

* Division of Plant Industry, CSIRO, P.O. Box 109, Canberra City, A.C.T. 2601.

II. MATERIALS AND METHODS

(a) *Plants*

Seeds of the accessions shown in Table 1 were sown in 15-cm diameter pots containing equal proportions of vermiculite and perlite to which water and modified Hoagland's nutrient solution were applied daily. Plants were raised at a day/night temperature of 27/22°C under a 16-hr photoperiod consisting of the Canberra summer day length extended by light of 25 f.c. from incandescent sources. The sky was mostly clear during the course of these experiments.

TABLE 1

SORGHUM ACCESSIONS STUDIED: THEIR ORIGIN, CHROMOSOME NUMBERS, AND LEAF THICKNESS

Accession*	Origin	Chromo- some No. (2n)	Leaf Thick- ness (μ m)
EU-SORGHUM—WILD RACES:			
<i>S. arundinaceum</i> (Desv.) Stapf. (51660)	Sierra Leone	20	110
<i>S. verticilliflorum</i> (Steud.) Stapf. (51664)	Transvaal	20	100
<i>S. aethiopicum</i> (Hack.) Rupr ex Stapf. (51658)	Sudan	20	70
<i>S. virgatum</i> (Hack.) Stapf. (51666)	Egypt	20	110
<i>S. propinquum</i> (Kunth) Hitchc. (43907)	Borneo	20	80
<i>S. halepense</i> (L.) Pers. (local)	Mediterranean type, ex United States of America	40	70
CULTIVATED STRAINS OF HYBRID ORIGIN:			
<i>S. sudanense</i> (Piper) Stapf. cv. Greenleaf	United States of America	20	100
<i>S. bicolor</i> (L.) Moench. cv. Texas 610	United States of America	20	120
STIPOSORGHUM—WILD RACES:			
<i>S. intrans</i> F. Muell.	Northern Territory, Australia	10	140
<i>S. stipoides</i> Gardner & Hubbard	Northern Territory, Australia	10	90

* The number shown is that of the CSIRO plant introduction service. The species are named in the common form. However, De Wet and Huckabay (1967) have proposed a revised terminology, demoting many species to variety status.

When approximately six leaves had expanded, three plants of each of the 10 accessions were shaded by nylon netting which excluded about half of the incident radiation at noon, as measured by a photometer calibrated against a Kipp solarimeter. After 12–20 days of shading, during which time the plants should have become biochemically adapted to the conditions (Hatch, Slack, and Bull 1969), plants were removed for gas analysis studies. At least three other plants remained under high radiation conditions until leaf-chamber studies were conducted.

(b) *Gas Analysis*

Plants were removed from glasshouses in the afternoon and maintained in a constant-temperature room (22°C) overnight with portion of an attached fully expanded leaf (the third youngest) enclosed in a leaf chamber. Next day, the leaf was automatically exposed to a series of programmed temperature and light conditions each of 60 min duration. When leaf temperature

was held constant at 30°C, the photosynthetically active radiation was varied within the range 0.08, 0.24, and 0.40 cal cm⁻² min⁻¹. Radiation was measured by silicon solar cells (with BG38 and GG19 filters) which had been calibrated with an RG8 filter against a Kipp solarimeter. At the high radiation level, leaf temperature was changed in the range 20, 25, 30, and 35°C.

Air was passed over the leaf in open circuit, with net photosynthetic rate (P) and transpiration rate (T) being measured simultaneously by an infrared gas analyser and differential psychrometers respectively. A more detailed description of equipment has been published previously (Downes 1970a).

Data were analysed according to the equations of Gaastra (1959) and used by Downes (1970a):

$$P = (C_a - C_i)/(r_a + r_s)_{\text{CO}_2}, \quad (1)$$

$$T = (W_i - W_a)/(r_a + r_s)_{\text{water}}, \quad (2)$$

where C_a and C_i represent the CO₂ concentration in the external air and in the intercellular spaces respectively; W_i and W_a the water vapour concentrations in the intercellular spaces and air respectively; and r_a and r_s represent the resistances attributed to the boundary layer and stomata + intercellular spaces of the leaf, respectively, to CO₂ and water vapour, as defined by subscripts. Relationships between $(r)_{\text{CO}_2}$ and $(r)_{\text{water}}$ used were those suggested by Gale and Poljakoff-Mayber (1968), $(r_a + r_s)_{\text{CO}_2}$ being calculated from values of $(r_a + r_s)_{\text{water}}$ obtained from equation (2).

(c) Leaf Anatomy

Portions of young expanded leaves were removed in the afternoon of a clear day and fixed in formalin-acetic acid-alcohol. Transverse sections were stained by the method of Sharman (1943).

III. RESULTS

(a) Response to Light Intensity

While leaf temperature was constant at 30°C, incident radiation was varied. In all species, plants adapted to full sunlight exhibited higher values of P as light intensity was increased. This is shown for three species in Figure 1. In all cases, the rise in P was associated with a decrease in $(r_a + r_s)_{\text{CO}_2}$. However, despite the general trends, differences among species were apparent in their response to light. Highest P values, which were associated with low resistance values, were detected in *S. virgatum*, *S. halepense*, *S. sudanense*, and *S. bicolor*. Rates were lower in *S. stipoides*, *S. propinquum*, and *S. arundinaceum* (Appendix I).

In plants which had been exposed to half sunlight conditions before testing, P also increased with light intensity (Fig. 1). In this case highest P values were detected in *S. arundinaceum* and *S. virgatum* while *S. verticilliflorum* was least responsive (Appendix I).

In several species the response of P to light intensity was lower in plants which had been conditioned to half sunlight than to full sunlight, e.g. *S. verticilliflorum*, *S. sudanense*, and *S. bicolor*. Others, like *S. propinquum* and *S. stipoides*, were apparently not differentially affected by light intensity pretreatment. In contrast to all others, *S. arundinaceum* exhibited higher P values if conditioned to half rather than full sunlight conditions. The responses of three species illustrating these differing effects are shown in Figure 1. It is also worth noting that *S. virgatum* had high P values relative to those of other entries, irrespective of light adaptation (Appendix I).

(b) *Response to Leaf Temperature*

With incident photosynthetically active radiation constant at $0.4 \text{ cal cm}^{-2} \text{ min}^{-1}$, leaf temperature was varied between 20 and 35°C . When plants had been previously grown under full sunlight conditions, P increased as leaf temperature increased

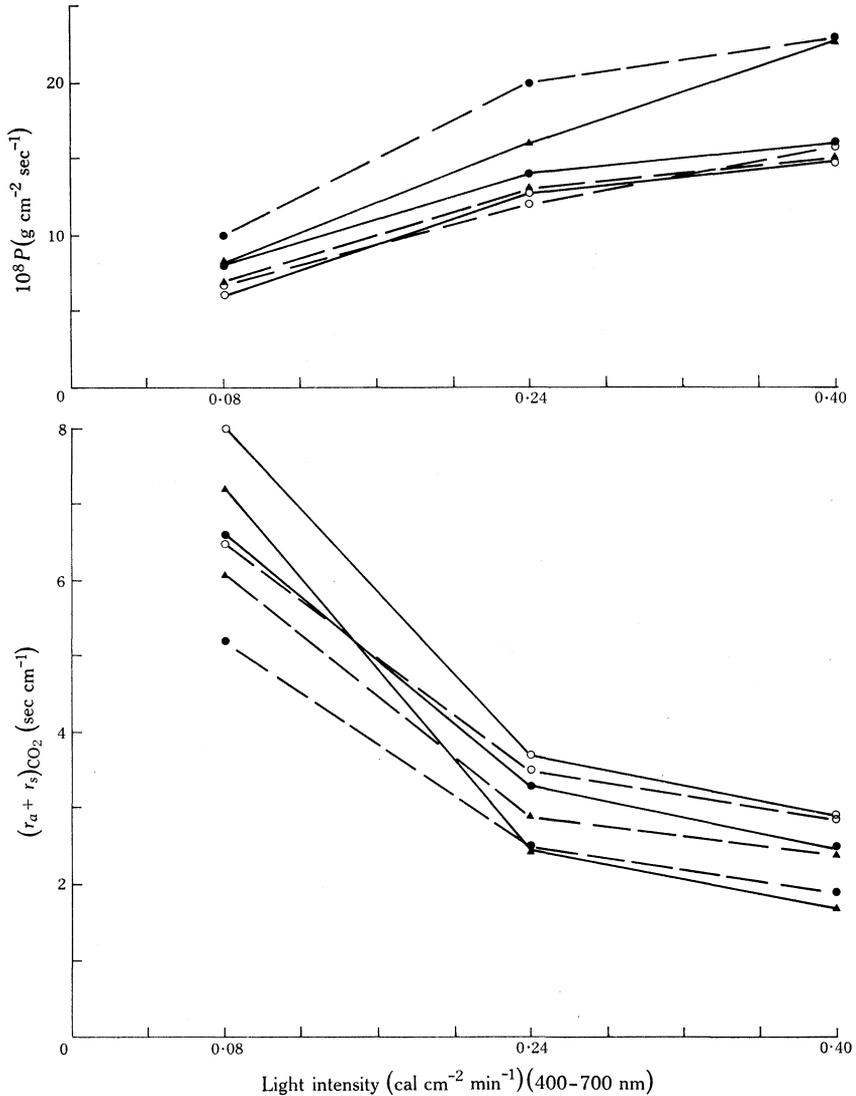


Fig. 1.—Photosynthetic rate and resistance of three sorghum species which respond differently to three levels of radiation at 30°C depending on their light intensity adaptation. (Data for all 10 species are included in Appendix I.) ● *S. arundinaceum*. ○ *S. stipoides*. ▲ *S. bicolor*. ——— Adapted to full sunlight. - - - Adapted to half sunlight.

(Fig. 2). In this case, change in P was related to changes in $C_a - C_i$ and inversely associated with changes in $(r_a + r_s)\text{CO}_2$ in most species (Appendix II). Similar trends were

apparent in plants conditioned to half sunlight but values of P were lower, unchanged, or higher than in the high radiation plants depending on species (Fig. 2; Appendix II).

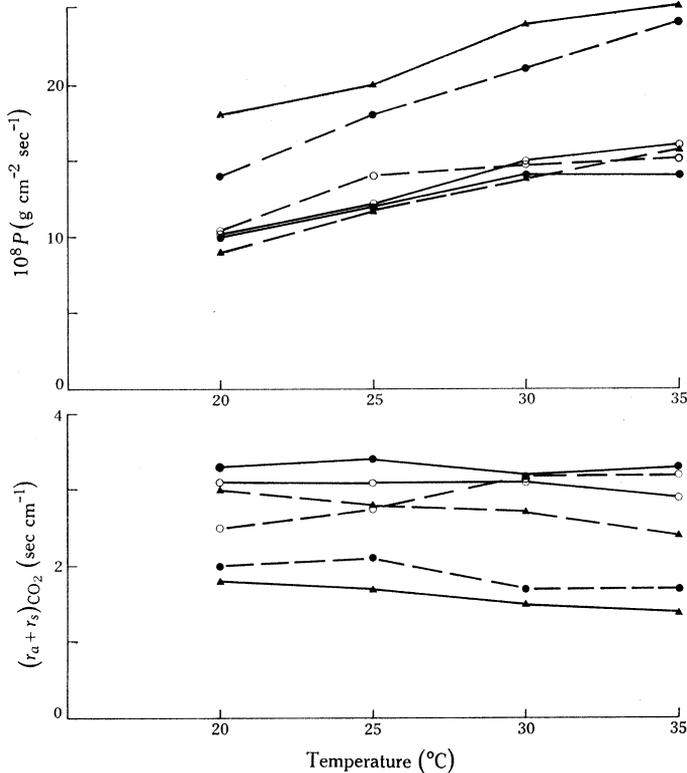


Fig. 2.—Photosynthetic rate and resistance of three sorghum species which respond differently to leaf temperature, under high radiation conditions, depending on their light intensity adaptation. (Data for all 10 species are included in Appendix II.) ● *S. arundinaceum*. ○ *S. stipoides*. ▲ *S. bicolor*. — Adapted to full sunlight. --- Adapted to half sunlight.

(c) Anatomical Observations

Leaf thickness varied from 70 to 140 μm , with *S. intrans* having the thickest leaf (Table 1). The average diameter of parenchyma bundle sheath cells in transverse section 6 μm thick varied between 16 and 26 μm with *S. arundinaceum* having the largest cells. Although in most cases plastids almost filled the parenchyma bundle sheath cells, *S. arundinaceum* had fewer plastids in these cells, in a thin centrifugally arranged layer. Centrifugally disposed plastids were observed in all species.

IV. DISCUSSION

In many cases the light intensity conditions to which plants were conditioned modified the relationship between P and light intensity detected in test conditions, as reported previously in *S. sudanense* (Downes 1971). *S. arundinaceum* was a notable exception in that plants were capable of higher P values if pretreated in half

sunlight. This species occurs in the relatively low radiation conditions of equatorial forests in West Africa and it appears likely that its response has been determined by natural selection in its habitat. The effect appears to have been mediated through stomatal response to environmental conditions. Whereas stomata of other *Sorghum* species tend to remain closed in low light, *S. arundinaceum* stomatal resistance is low if plants have been conditioned to a low light regime. Such a change is necessary in a species with the C₄ pathway of photosynthesis (Hatch, Slack, and Johnson 1967) and associated syndrome (Downes 1970b) in a shaded habitat since species with the C₃ (Calvin) pathway of photosynthesis would otherwise have competitive advantage. Their stomatal resistance to gas exchange is low under these conditions (Downes 1969).

Other species which occur in high radiation environments, e.g. *S. virgatum* (Egypt) and *S. sudanense* and *S. bicolor* (both south-west United States of America), appear to be genetically adapted to these conditions since they respond to high light intensity. Although its origin is unknown, the Mediterranean form of *S. halepense* tested may have been exposed to high radiation conditions in summer in its original habitat. An exception was provided by the *S. aethiopicum* accession which was less responsive to high light conditions though it is apparently a desert-adapted species (De Wet, Harlan, and Price 1970). The accession was termed *S. aethiopicum*-like by Harlan (personal communication) so it may not be representative of the species.

The Australian species *S. intrans* and *S. stipoides* occur in savannah woodland and tall grass communities of low latitudes which experience varying radiation conditions in the rainy season. This appears to be reflected in their relative insensitivity to light-intensity conditioning. Unfortunately, the accession of *S. verticilliflorum* studied was characterized by a longitudinal leaf striping. The effect of this possible mutation in the material may have masked species characteristics.

From the limited sample of species and accessions tested, it appears that ploidy has little bearing on gas exchange responses. Wild species varied considerably in their responses and the *P* values of cultivated species were comparable with the highest of the wild ones. In this respect *Sorghum* appears to differ from *Triticum* (Evans and Dunstone 1970; Khan and Tsunoda 1970). Rather, it appears that generally it is the light regime to which a genotype is adapted that determined the responses detected here. All of the species exhibited higher *P* values at 30 or 35°C than at 25°C which is nearer the temperature at which they were grown (27°C during the day), suggesting that temperature adaptation is less significant than adaptation to light intensity.

The species varied considerably in leaf morphology and anatomy. Narrow-leaved *S. virgatum* and *S. sudanense* exhibited high *P* values yet so did the broad-leaved *S. bicolor*. In contrast to the finding of Wilson and Cooper (1967) in *Lolium*, there was no clear relationship between *P* and leaf thickness (Table I and Appendix I).

All of the species had gas exchange characteristics (Downes 1970a) of species having the C₄ pathway of photosynthesis (Hatch, Slack, and Johnson 1967). A subgenus of *Panicum* differs from the rest of the genus in having features associated with the C₃ (Calvin) pathway (Downton, Berry, and Tregunna 1969; Moss, Krenzer, and Brun 1969). In the subgenus, many species are forest grasses (Hitchcock 1950) and specialized plastids are absent from parenchyma bundle sheath cells (Brown

1958). The reduction in the plastid content of these cells in the forest *Sorghum* (*S. arundinaceum*) may indicate a tendency in this direction. However, the centrifugal arrangement of plastids in bundle sheath cells in all species in this study suggests a dependence on mesophyll plastids. In grasses with the C_4 pathway of photosynthesis, the C_3 pathway operates in the bundle sheath cells (Slack, Hatch, and Goodchild 1969) and if these lack photosystem II activity (Anderson, Woo, and Boardman 1971) they may depend on the mesophyll for reducing power (Downton, Berry, and Tregunna 1970).

Apparently the presence or absence of the C_4 pathway is not directly associated with evolutionary adaptation to shade (forest) conditions since different pathways are apparently used in forest *Panicum* and *Sorghum* species. However, it appears that the typical C_4 light-mediated stomatal response has been modified in *S. arundinaceum* to increase its fitness in this environment.

Since shade conditions operate in the crop canopy, the stomatal behaviour of *S. arundinaceum* might be valuable in crop sorghums but it is doubtful that this species has contributed to crop gene pools (De Wet, Harlan, and Price 1970) yet hybridization is possible among the Eu-sorghums (Celarier 1958). Another wild species of potential importance in plant breeding is *S. virgatum* which, because of its desert adaptation, may contribute to drought resistance. Though it is capable of high values of P , it too may have contributed little to cultivated sorghums to date (De Wet, Harlan, and Price 1970) though it has been noted as a source of resistance to attack by aphid [*Schizaphis graminum* (Rondani)] (Hackerott, Harvey, and Ross 1969). These observations suggest that it would be desirable to increase the representation of wild sorghums in sorghum gene pools (e.g. Murty, Arunachalam, and Saxena 1967).

V. ACKNOWLEDGMENTS

The able technical assistance of Mr. R. Davis in conducting the gas analysis studies is gratefully acknowledged. Dr. J. Harlan, University of Illinois, and Mr. R. Perry, Division of Land Research, CSIRO, kindly provided seed. Mr. R. Dunstone contributed advice and assistance in cutting and staining leaf sections.

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APPENDIX I

PHOTOSYNTHETIC RATE (P) AND RESISTANCE (R) IN 10 *SORGHUM* SPECIES, ADAPTED TO TWO LIGHT INTENSITY CONDITIONS, AND TESTED AT THREE LEVELS OF RADIATION AT 30°C

Units for P are $\text{g cm}^{-2} \text{sec}^{-1}$ and for R [$= (r_a + r_s)\text{CO}_2$] sec cm^{-1}

Species	Light Intensity 0.08 cal $\text{cm}^{-2} \text{sec}^{-1}$		Light Intensity 0.24 cal $\text{cm}^{-2} \text{sec}^{-1}$		Light Intensity 0.40 cal $\text{cm}^{-2} \text{sec}^{-1}$	
	10^3P	R	10^3P	R	10^3P	R
	Species adapted to full sunlight					
<i>S. arundinaceum</i>	8±0.8	6.6±0.6	14±1.0	3.3±0.5	16±1.0	2.5±0.3
<i>S. verticilliflorum</i>	7±0.9	7.3±0.7	15±1.2	3.2±0.6	17±1.3	2.5±0.3
<i>S. aethiopicum</i>	7±0.9	9.1±0.8	16±0.9	3.4±0.6	19±1.1	2.7±0.3
<i>S. virgatum</i>	8±0.7	5.1±0.5	23±0.8	2.1±0.4	29±1.2	1.7±0.2
<i>S. halepense</i>	8±0.7	6.2±0.6	20±1.0	2.6±0.5	26±1.2	1.8±0.3
<i>S. propinquum</i>	5±0.7	7.6±0.7	14±1.1	3.6±0.6	16±1.0	3.1±0.4
<i>S. intrans</i>	7±0.7	6.1±0.6	18±1.0	2.7±0.5	20±1.0	2.3±0.3
<i>S. stipoides</i>	6±0.7	8.2±0.8	13±1.0	3.7±0.6	15±1.0	2.9±0.3
<i>S. sudanense</i>	8±0.8	7.2±0.6	14±0.9	3.5±0.5	24±1.1	1.6±0.2
<i>S. bicolor</i>	8±0.8	7.2±0.7	16±0.9	2.5±0.4	23±1.0	1.7±0.3
Species adapted to half sunlight						
<i>S. arundinaceum</i>	10±0.9	5.2±0.6	20±1.1	2.5±0.7	23±1.0	1.9±0.2
<i>S. verticilliflorum</i>	6±0.9	7.7±0.7	10±0.9	4.4±0.6	11±1.2	3.7±0.5
<i>S. aethiopicum</i>	7±0.8	6.4±0.7	13±0.7	3.4±0.5	13±0.9	3.2±0.4
<i>S. virgatum</i>	8±0.7	5.7±0.7	18±0.8	2.8±0.5	22±1.0	2.1±0.2
<i>S. halepense</i>	8±0.7	5.4±0.6	13±0.9	2.5±0.5	19±0.9	2.1±0.3
<i>S. propinquum</i>	6±0.7	7.1±0.7	13±0.8	3.5±0.6	15±0.8	2.9±0.3
<i>S. intrans</i>	9±0.8	5.0±0.6	14±0.9	3.1±0.6	16±0.9	2.6±0.3
<i>S. stipoides</i>	7±0.7	6.5±0.7	12±0.9	3.5±0.6	16±0.9	2.9±0.4
<i>S. sudanense</i>	9±0.8	5.7±0.6	17±0.7	2.8±0.5	19±0.8	2.4±0.3
<i>S. bicolor</i>	7±0.8	6.1±0.7	13±0.8	2.9±0.5	15±0.9	2.4±0.3

APPENDIX II

PHOTOSYNTHETIC RATE (P), RESISTANCE (R), AND CO_2 CONCENTRATION DIFFERENCE (C) IN 10 *SORGHUM* SPECIES, ADAPTED TO TWO LIGHT INTENSITY CONDITIONS AND TESTED AT FOUR LEAF TEMPERATURES WITH PHOTOSYNTHETICALLY ACTIVE RADIATION CONSTANT AT $0.4 \text{ CAL CM}^{-2}\text{MIN}^{-1}$. Units for P are $\text{g cm}^{-2} \text{ sec}^{-1}$, for $R [= (r_a + r_s)\text{CO}_2]$ sec cm^{-1} , and for $C [= (C_a - C_i)]$ g cm^{-3} .

Standard deviations for P , R , and C are 1×10^{-8} , 0.5 , and 4.0×10^{-8} respectively

Species	Leaf Temperature 20°C			Leaf Temperature 25°C			Leaf Temperature 30°C			Leaf Temperature 35°C		
	10^8P	R	10^8C	10^8P	R	10^8C	10^8P	R	10^8C	10^8P	R	10^8C
	Species adapted to full sunlight											
<i>S. arundinaceum</i>	10	3.3	32	12	3.4	42	14	3.2	45	14	3.3	47
<i>S. verticilliflorum</i>	12	2.8	33	15	2.8	42	18	2.4	44	19	2.4	46
<i>S. aethiopicum</i>	14	3.0	41	16	2.5	42	20	2.2	44	18	2.2	40
<i>S. virgatum</i>	16	2.0	32	20	2.2	44	22	2.4	53	22	2.4	54
<i>S. halepense</i>	18	2.2	40	21	1.9	42	25	1.9	46	25	2.0	50
<i>S. propinquum</i>	8	6.3	49	10	4.8	50	12	4.1	51	13	4.0	53
<i>S. intrans</i>	12	2.2	27	16	2.6	42	18	2.7	49	20	2.5	51
<i>S. stipoideum</i>	10	3.1	32	12	3.1	37	15	3.1	45	16	2.9	47
<i>S. sudanense</i>	15	2.0	30	20	1.8	36	24	1.5	36	25	1.6	46
<i>S. bicolor</i>	18	1.8	32	20	1.7	35	24	1.5	37	25	1.4	37
Species adapted to half sunlight												
<i>S. arundinaceum</i>	14	2.0	29	18	2.1	38	21	1.7	37	24	1.7	40
<i>S. verticilliflorum</i>	6	5.6	36	7	5.6	42	9	4.8	45	10	4.6	48
<i>S. aethiopicum</i>	10	3.0	30	13	3.3	43	15	3.2	46	16	3.0	48
<i>S. virgatum</i>	15	2.5	37	19	2.2	42	21	2.2	48	23	2.1	49
<i>S. halepense</i>	11	2.9	33	15	2.6	40	18	2.2	41	20	2.1	43
<i>S. propinquum</i>	10	3.7	37	12	3.2	39	16	2.9	46	16	2.9	48
<i>S. intrans</i>	10	2.9	29	13	3.0	40	16	2.7	45	17	2.5	44
<i>S. stipoideum</i>	10	2.5	25	14	2.8	39	15	3.2	46	15	3.2	47
<i>S. sudanense</i>	9	3.0	27	12	3.0	36	15	3.0	45	16	2.6	42
<i>S. bicolor</i>	9	3.0	28	12	2.8	34	14	2.7	39	16	2.4	38