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PHOTOSYNTHESIS AND SHADE TOLERANCE IN TROPICAL RANGE GRASSES AND LEGUMES

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SUMMARY

Seventeen tropical grasses (*Bothriochloa bladhii, Brachiaria mutica, Brachiaria decumbens, Brachiaria brizantha, Cenchrus ciliaris, Cenchrus setiger, Chloris gayana, Chrysopogon fulvus, Dichanthium annulatum, Heteropogon contortus, Panicum maximum* cv. IGFRI, *Panicum maximum* cv. PGG 289, *Paspalum notatum, Panicum antidotale, Pennisetum polystachyon, Setaria sphacelata,* Tri - specific Hybrid (TSH) [(*Pennisetum americanum* x *P. purpureeum*) x *P. squamulatum*] and two legumes [*Stylosanthes hamata* (Caribbean stylo), and *Macroptilium atropurpureum*] were studied for their physiological attributes under different light intensities in rain-fed semi-arid conditions. Rate of photosynthesis (P_N) and stomatal conductance (C_S) decreased with decreasing light intensity and reached the minimum level under high shading (25% light intensity). TSH, *P. antidotale*, *P. maximum* and *S. sphacelata* maintained the highest P_N and C_S under shade followed by *B. mutica, P. polystachyon* and *C. ciliaris* indicating their adaptation to shade. In legumes, *S. hamata* maintained higher P_N than *M. atropurpureum* under moderate shading (50%) and can be grown with trees having sparse canopies in tree-crop inter-cropping systems. Transpiration rate (T_R) at 25% light intensity was half that in full sunlight. TSH, *B. mutica, P. maximum, P. antidotale, S. sphacelata, P. polystachyon* and *S. hamata* relatively maintained higher carboxylation efficiency and water-use efficiency (WUE) under shade followed by *C. ciliaris, C. setiger, C. fulvus* and *B. bladhii.* Chlorophyll content (a + b) was maximum under 50-75% shading in most of the species.

Key words: **Chlorophyll, grasses, legumes, photosynthesis, shade tolerance, stomatal conductance, water use efficiency.**

INTRODUCTION

The grasslands in India are under excessive pressure from grazing, fire, shifting cultivation, soil erosion and invasion by weeds. As a result, grass and legume species are declining in productivity. The cover of the dominant grass species (*Panicum, Sehima, Cenchrus, Heteropogon, Dichanthium, Paspalum, Bothriochloa* and *Brachiaria*) and other range legumes in the tropics and subtropics of the Indian Sub-Continent is decreasing. Tree-grass and grass-legume combinations are being introduced in inter-cropping and silvo-pastoral systems to increase the productivity per unit area. Most of the grasses are perennials with a very broad ecological range. Photosynthesis is an important component of growth and productivity (Ledig and Botkin 1974, Dey *et al*. 1989), which depends on availability of both solar radiation and water. Relative increases in accessory pigments like chlorophyll b and carotenoids are an adaptive response of plants to variable photon flux density (Anderson *et al*. 1988, Bhatt and Sinha 1990, Misra 1995, Misra and Misra 1997). For recommending a pasture species for use in agroforestry/ silvi-pastoral systems, it is essential to understand the potential of the species to produce under low light intensities. Considering adaptive features and characters, 17 dominant grass species and

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2 legumes were selected and their physiological attributes like rate of photosynthesis, transpiration, stomatal conductance, chlorophyll content and adaptation to shaded environments were examined.

MATERIALS AND METHODS

Seedlings of 16 grass species (Table 1) were raised in the nursery at IGFRI, Jhansi (25^0 25'N, 78^0 35'E; 275 masl), in India. Tri–specific hybrid [(*Pennisetum americanum* x *P. purpureeum*) x *P. squamulatum*] was also included. Uniform seedlings of all grasses were transplanted in the field at a spacing of 50 x 50 cm in July. To ensure reasonable nutrient levels, fertilizer (60 kg N and 30 kg P_2O_5/ha) was applied at planting. The soil of the experimental field was neutral with medium texture and contained 0.06% N and 11.8 ppm available P (Olsen *et al*. 1954). The seeds of 2 species of range legumes (Table 1) were sown at the time of transplantation of grasses. After establishment of the grasses and germination of the range legumes, the plots were covered by shading net (Agro shade net) to allow 3 different light intensities (25, 50 and 75% of full sunlight) and one treatment was kept in the open as a control with 3 replications. The light intensity under the shading net was measured by using Quantum/ Radiometer/ Photometer (Model LI-188, LICOR, USA) and the required light intensities were obtained by adjusting the height of the shading net. Microenvironmental parameters such as air temperature (AT), relative humidity (RH), vapour pressure deficit (VPD) and photosynthetically active radiation (PAR) were recorded.

The experiments were conducted for 3 years. Observations on photosynthesis (P_N), transpiration (T_R), stomatal conductance (C_S), inter-cellular CO_2 concentration (Ci) and leaf temperature (LT) in 2^{nd} – 3^{rd} leaves were made with the help of the LI 6200 Portable Photosynthesis System (LI-COR, USA) during the mid-day hours at full vegetative growth (Sep-Oct) each year. Photosynthetic pigments (chlorophyll) in fresh leaves were estimated by the following method of Duxbury and Yentsch (1956) and fractions of chlorophyll were calculated according to AOAC (1970). The average values for 2 years are reported in this article.

RESULTS AND DISCUSSION

Air temperature (AT) and vapour pressure deficit (VPD) decreased with decreasing light intensities, whereas relative humidity increased. The difference in AT and VPD was 3.5 ^{0}C and 7.53, respectively, under 25% light intensity compared with the open, while relative humidity (RH) increased by 2.09%. The available photosynthetically active radiation (PARs) under the 4 light intensities (100, 75, 50 and 25%) were 1610, 1150, 760 and 360 μmol $m^{-2}s^{-1}$, respectively. As expected, leaf temperature (LT) decreased with decreasing light intensity and minimum LT was recorded under high shading in all plant species. On an average, LT decreased by 3.5 - 4.5^{0}C under low light intensity, which may be due to lower PAR and decrease in AT. The variation in LT might be due to lower availability of PAR, which influences transpiration rate (T_R) (Vandana and Bhatt 1999) and is species-dependent (Lange 1965, Bhatt *et al*. 1991).

Photosynthetic rate (P_N) decreased with decreasing light intensity in both grasses and legumes (Fig.1). Maximum P_N was recorded at 100 % light intensity in an open environment in all species except *S. hamata*.

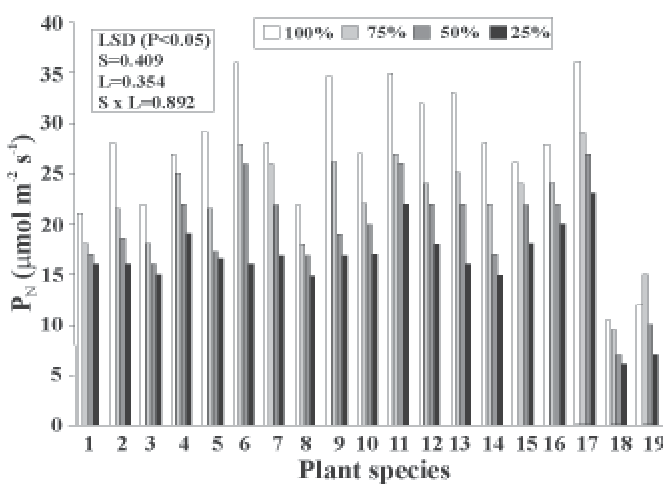

Fig. 1. Rate of photosynthesis (P_N) in some range grasses and legumes under different light intensities (25 - 100%). 100% represent full sunlight. (S – Species, L – Light intensity). (1. *Both. bladhii;* 2. *Br. brizantha;* 3. *Br. decumbens;* 4. *Br. mutica;* 5. *Ce. ciliaris;* 6. *Ce. setiger;* 7.*Ch. gayana;* 8. *Chry. fulvus; 9. Dich. annulatum;* 10. *H. contortus;* 11. *Pan. antidotale;* 12. *P. maximum cv.* IGFRI*;* 13. *Pas. notatum,* 14. *P. maximum (PGG 289);* 15. *Pen. polystachyon;* 16. *S. sphacelata*; 17. *Trispecific hybrid;* 18. *M. atropurpureum*; 19. *S. hamata*)

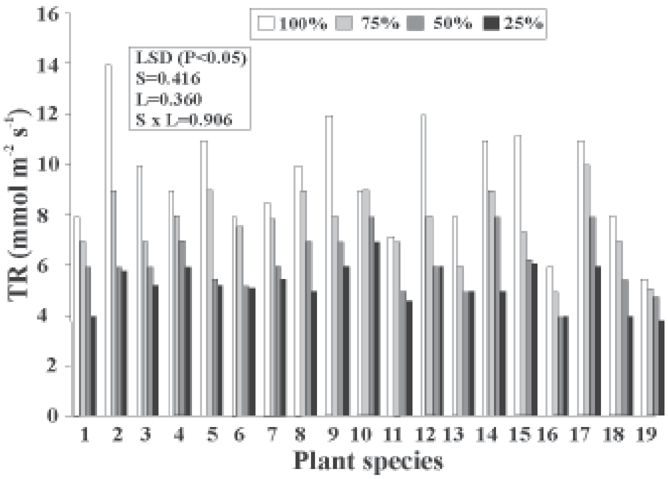

Fig. 2. Rate of transpiration (T_R) in some range grasses and legumes under different light intensities (25 - 100%). 100% represent full sunlight. (S – Species, L – Light intensity). (1. *Both. bladhii;* 2. *Br. brizantha;* 3. *Br. decumbens;* 4. *Br. mutica;* 5. *Ce. ciliaris;* 6. *Ce. setiger;* 7.*Ch. gayana;* 8. *Chry. fulvus; 9. Dich. annulatum;* 10. *H. contortus;* 11. *Pan. antidotale;* 12. *P. maximum cv.* IGFRI*;* 13. *Pas. notatum,* 14. *P. maximum (PGG 289);* 15. *Pen. polystachyon;* 16. *S. sphacelata*; 17. *Trispecific hybrid;* 18. *M. atropurpureum*; 19. *S. hamata*)

Overall the reduction in PN with a reduction in light intensity from 75% to 50%, was less than the reduction from 100% to 75%. TSH, *P. antidotale, S. sphacelata* and *P. maximum* maintained good PN followed by *B. mutica*, *P. polystachyon* and *C. ciliaris*, *S. hamata* showed their potentiality towards shade adaptation and may be suitable under shading environment in tree-crop, silvi-pastoral system. The lower P_N in shade - grown plants may be attributed to the lower activity of the photosynthetic enzyme, RUBP carboxylase (Ushuda *et al*. 1985). Reduction in PN under shade occurred due to lower stomatal conductance (C_S). PN is strongly dependent on available PAR (r = 0.6068), and C_S (r = 0.5925). On the basis of plant density, ground cover (%), herbage mass and sward canopy height, Firth *et al*. (2002) recommended potential legumes and grass species as ground cover for macadamia orchards in subtropical Australia.

Stomatal conductance of all grasses and legumes also reduced under high shading due to lower availability of PAR, which causes partial closure of stomata (Table 1). The stomatal functioning depends on the availability of PAR as evidenced by the significant positive correlation between C_S and PAR (r = 0.5366). As compared with P_N, the intercellular CO_2 concentration (Ci) increased as the degree of shading increased in all species, indicating lower fixation of CO_2 (Table 1). The lower values for Ci were recorded in those species exhibiting a higher rate of CO_2 assimilation. Maximum Ci was recorded in *C. fulvus* and *S. hamata* under high shading indicating their lower PN. TR decreased as shading increased (Fig. 2). The reduction in T_R at low light intensity is a result of low PAR and lower C_S. T_R is mainly dependent on changes in micro-environmental parameters, particularly PAR, as evidenced by strong correlation with these parameters (r = 0.6123).

The P_N/Ci ratio, which indicates the carboxylation efficiency (Farquhar and Sharkey 1982), decreased gradually with decreasing light intensities in all grasses and legumes.TSH, *B. mutica, P. antidotale, S. sphacelata, P. polystachyon* and *P. maximum* maintained higher carboxylation efficiency under reduced light intensity indicating their potential to produce under shade. However, *S. hamata* showed higher carboxylation efficiency under a moderate shading environment and hence is also suitable for a tree-crop intercropping system. The P_N: T_R ratio (the moles of CO_2 fixed per mole of water transpired) is termed as water use efficiency (WUE) and increased under a shading environment in most of the plant species. S. *sphacelata, P. antidotale* and *B. bladhii* showed the highest WUE followed by TSH, *C. ciliaris, B. mutica, C. setiger, P. maximum, P. polystachyon* and *C. fulvus* under shade. In range legumes, WUE was higher in *S. hamata* than in *M. atropurpureum* under shade, further confirming its potential adaptation to shady situations (Table 1). These above mentioned grass and legume species maintained high levels of WUE even under heavy shade, suggesting that these can be grown in heavy shade environment under trees provided other resource factors are at optimum levels.

Accumulation of Chl a and Chl b increased with decreasing light intensities in all grasses and legumes. Total chlorophyll content was higher in plants grown under shade than in those in full sun and maximum values were observed at 50 % shading in some grasses and 75 % in other grass species (Table 2). The increased Chl a and Chl b in shaded leaves has been attributed to the increase in number and size of chloroplasts and better

Table 1. Stomatal conductance (C_S), intercellular CO_2 concentration (Ci), water- use efficiency (P_N/T_R) and economy coefficient (P_N/Ci) in range grasses and legumes under various shading treatments.

Plant species	C_S (cm s^{-1})				Ci (ppm)				P_N/T_R [μmolCO_2 (mmol $H_2O)^{-1}$]				Pn/Ci			
	Light intensities (%)															
	100	75	50	25	100	75	50	25	100	75	50	25	100	75	50	25
Range grasses																
Bothrichloa bladhii	0.59	0.48	0.46	0.39	199	210	222	230	2.62	2.57	2.83	4.00	0.105	0.086	0.076	0.073
Brachiaria brizantha	0.98	0.77	0.66	0.52	180	192	198	216	2.00	2.39	3.08	2.75	0.155	0.112	0.093	0.074
Brachiaria decumbens	0.72	0.71	0.64	0.56	229	232	241	250	2.20	2.57	2.67	2.88	0.096	0.077	0.066	0.060
Brachiaria mutica	0.58	0.49	0.44	0.41	126	132	142	166	3.00	3.12	3.14	3.16	0.214	0.189	0.155	0.114
Cenchrus ciliaris	0.95	0.76	0.52	0.51	204	205	230	235	2.65	2.38	3.14	3.17	0.143	0.104	0.075	0.070
Cenchrus setiger	0.64	0.62	0.52	0.41	166	178	188	205	4.50	3.68	5.00	3.13	0.217	0.157	0.138	0.078
Chloris gayana	0.68	0.61	0.52	0.44	180	188	186	192	3.29	3.29	3.67	3.09	0.155	0.138	0.118	0.088
Chrysopogon fulvus	0.75	0.71	0.50	0.41	241	244	252	266	2.20	2.00	2.43	3.00	0.091	0.074	0.067	0.056
Dichanthium annulatum	1.10	0.91	0.70	0.70	201	218	232	242	2.89	3.27	2.71	2.83	0.173	0.120	0.082	0.070
Hetropogon contortus	0.92	0.72	0.71	0.61	199	205	216	222	3.00	2.44	2.50	2.42	0.136	0.107	0.092	0.076
Panicum antidotale	0.52	0.48	0.46	0.44	159	166	177	199	4.86	3.86	5.20	4.78	0.220	0.163	0.147	0.110
Panicum maximum (IGFRI)	0.61	0.59	0.41	0.39	210	215	217	220	2.66	3.00	3.66	3.00	0.152	0.112	0.101	0.089
Panicum maximum (PGG)	0.78	0.72	0.56	0.52	127	138	156	170	2.54	2.44	2.12	3.00	0.220	0.159	0.109	0.088
Paspalum notatum	0.64	0.61	0.56	0.52	160	170	165	188	4.12	4.16	4.40	3.20	0.206	0.147	0.133	0.085
Pennisetum polystachyon	1.00	0.82	0.71	0.58	124	180	180	190	2.32	3.24	3.55	3.00	0.149	0.133	0.122	0.094
Setaria sphacelata	0.52	0.48	0.42	0.41	204	215	215	220	4.67	4.60	5.50	5.00	0.137	0.112	0.102	0.090
Tri-specific hybrid (TSH)	0.81	0.77	0.56	0.41	122	130	135	155	3.27	2.90	3.37	3.83	0.295	0.223	0.200	0.148
(*Pennisetum americanum* X *P. purpureum*) X *P. squamulatum*]																
Range legumes																
Macroptilium atropur-pureum	0.48	0.41	0.38	0.29	213	222	226	232	1.31	1.36	1.27	1.50	0.049	0.043	0.030	0.026
Stylosanthes hamata	0.36	0.34	0.32	0.28	236	242	248	266	2.18	2.94	2.08	1.84	0.051	0.062	0.040	0.026
LSD (P< 0.05)																
Species		0.034				9.5				0.0023				0.0101		
Light intensity		0.074				20.6				0.0041				0.0220		
Species X Light intensity		NS				NS				NS				0.0088		

Table 2. Photosynthetic pigments in range grasses and legumes under various shading treatments.

Plant species	Chl a				Chl b				Chl a+ Chl b				Chl a: Chl b			
	Light intensities (%)															
	100	75	50	25	100	75	50	25	100	75	50	25	100	75	50	25
Range grasses	(mg chl/g fresh wt)															
Bothriochloa bladhii	1.15	1.83	2.12	1.85	0.42	0.59	0.67	0.58	1.57	2.42	2.79	2.43	2.73	3.10	3.16	3.19
Brachiaria brizantha	0.84	0.51	0.37	0.49	0.29	0.27	0.24	0.28	1.13	0.78	0.61	0.77	2.89	1.88	1.54	1.75
Brachiaria decumbens	0.59	1.13	1.19	0.93	0.13	0.32	0.29	0.27	0.72	1.45	1.48	1.20	4.53	3.53	4.10	3.44
Brachiaria mutica	0.79	0.87	0.91	0.94	0.27	0.31	0.29	0.30	1.06	1.18	1.20	1.24	2.92	2.80	3.13	3.13
Cenchrus ciliaris	0.76	0.79	1.13	1.10	0.13	0.14	0.23	0.20	0.89	0.93	1.36	1.30	5.84	5.64	4.91	5.50
Cenchrus setiger	0.95	1.20	1.32	1.65	0.16	0.17	0.24	0.32	1.11	1.37	1.56	1.97	5.93	7.50	5.50	5.15
Chloris gayana	0.87	1.13	1.11	1.50	0.23	0.34	0.32	0.33	1.10	1.47	1.43	1.33	3.78	3.32	3.46	3.03
Chrysopogon fulvus	0.86	1.42	1.50	1.49	0.29	0.52	0.54	0.51	1.15	1.94	2.04	2.00	2.96	2.73	2.77	2.92
Dichanthium annulatum	1.37	1.43	2.03	2.16	0.19	0.36	0.41	0.44	1.56	1.79	2.44	2.60	7.20	3.97	4.95	4.90
Hetropogon contortus	1.31	1.72	2.90	1.95	0.31	0.43	0.57	0.50	1.62	2.15	3.47	2.45	4.22	4.00	5.08	3.90
Panicum antidotale	1.15	1.23	1.17	1.73	0.19	0.21	0.20	0.32	1.34	1.44	1.37	2.05	6.05	5.85	5.85	5.40
Panicum maximum (IGFRI)	0.83	0.99	1.07	1.14	0.32	0.43	0.46	0.48	1.15	1.42	1.53	1.62	2.59	2.30	2.32	2.37
Panicum maximum (PGG)	0.93	1.32	1.75	1.49	0.29	0.50	0.59	0.42	1.22	1.82	2.34	1.91	3.20	2.64	2.96	3.54
Paspalum notatum	0.29	0.33	0.37	0.42	0.13	0.18	0.22	0.19	0.42	0.51	0.59	0.61	2.32	1.83	1.68	2.21
Pennisetum polystachyon	0.71	0.92	0.89	0.73	0.19	0.28	0.31	0.36	0.90	1.70	1.20	1.09	3.73	3.28	2.87	2.02
Setaria sphacelata	0.49	0.57	0.63	0.65	0.39	0.50	0.54	0.63	0.88	1.07	1.17	1.28	1.25	1.14	1.16	1.03
Trispecific hybrid (TSH)	0.63	0.73	0.89	0.90	0.31	0.31	0.34	0.32	0.94	1.04	1.23	1.22	2.03	2.35	2.61	2.80
[(*Pennisetum americanum* X *P. purpureeum*) X *P. squamulatum*]																
Range legumes																
Macroptilium atropurpureum	1.20	1.13	1.51	1.43	0.49	0.51	0.54	0.50	1.69	1.64	2.05	1.93	2.44	2.21	2.79	2.86
Stylosanthes hamata	1.32	1.63	1.80	1.63	0.33	0.40	0.46	0.53	1.65	2.03	2.26	2.22	4.00	4.07	3.91	3.18
LSD (P< 0.05)																
Species	0.036				0.017				0.058				0.228			
Light intensity	0.077				0.036				0.127				0.497			
Species X Light intensity	0.033				0.014				0.050				2.828			

grana development (Boardmann *et al.* 1977). Under shade the accumulation of Chl a and Chl b increased predicting the shade adaptation in these plant species. Shaded plants have a higher concentration of Chl b than the plants grown in full sunlight (Eagle 1960, Bhatt and Sinha 1990 and Singh 1994). Chl a / b ratio reduced under low light intensities in most plant species, but increased in other plant species which may be due to an increase in Chl a accumulation under high shading conditions.

On the basis of physiological attributes, the grass species *viz.*, *P. maximum, P. polystachyon, S. sphacelata*, TSH and *B. mutica* are suitable species for high shading environment and *B. decumbens, C. setiger, C. ciliaris, C. fulvus, D. annulatum, P. notatum S. hamata* and *M. atropurpureum* for moderate shading and therefore, these grass and legume species are recommended for shading environment under silvo-pastoral system in semiarid tropical region.

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