Chlorophyll, Dry Matter, and Photosynthetic Conversion-Efficiency Relationships in Warm-season Grasses

U.G. BOKARI

Abstract

This study was conducted to determine the relationship between leaf chlorophyll content, dry matter production, and the photosynthetic conversion efficiency in several warm-season grasses. These included Old World bluestems (Bothriochloa spp.), eastern gamagrass [*Tripsacum dactyloides* (L)L.], and weeping lovegrass (Eragrostis curvula (Schradd) Nees.). Warm-season grasses usually operate on the C_4-photosynthetic pathway and are considered photosynthetically more efficient than the cool-season grasses under high temperature and high light intensity conditions. Samples for chlorophyll analysis and dry matter production were taken from 3 to 5, 0.5 M^2 quadrates per pasture at each phenological stage. Photosynthetically active irradiance (400-700 nm) was measured with a quantum sensor. Results indicated close correlation between chlorophyll and dry matter production. Increase in total chlorophyll was associated with increase in dry matter. Chlorophyll a/b ratio remained almost constant throughout the growing season. Solar energy conversion-efficiency ranged from 0.54% to 0.73% for various strains of Old World bluestems, 0.51% for eastern gamagrass and 0.44% for weeping lovegrass. It was demonstrated through this study that warm-season grasses, like many other plants, are not very efficient utilizers of the enormous amounts of incoming solar energy. These grasses maintained high productivity throughout the growing season by maintaining high levels of chlorophyll in the leaves.

Old World bluestems (Bothriochloa spp.), eastern gamagrass [*Tripsacum dactyloides* (L.) L.], and weeping lovegrass [*Eragrostis curvula* (Schrad.) Nees.] are warm-season grasses with C_4-photosynthetic pathway. These plants maintain higher rates of photosynthesis at higher temperature and light intensity than do the C_3-plants (Downton 1971, Bjorkman 1971, Slatyer 1970). Several workers have demonstrated a direct correlation between chlorophyll content and dry matter production in several plant species (Bray 1960, Brougham 1960, Bokhari 1976). This relationship varies considerably among plant species within and between different growing seasons. Bray (1960) found a significant positive correlation between chlorophyll and herbaceous stand height while negative correlations were reported for corn (*Zea mays* L.) and crested wheatgrass, [*Agropyron desertorum* (Fisch.)] (Schult.) (Oelke and Andrew 1966, Johnson and Miller 1940, Miller and Johnson 1938). Chlorophyll concentration usually decreases with age, but these trends in chlorophyll concentration have not been positively related to changes in photosynthetic rates (McGregor and Kramer 1963). However, Sestak and Catsky (1962) found that rates of photosynthesis and chlorophyll content increase to maximum values during the first phase of leaf development in tobacco (*Nicotiana tabacum,* L.) and then decrease. Rauzi and Dobrenz (1970) reported that both chlorophyll a and b total chlorophyll decreases in blue grama, [*Bouteloua gracilis* (H.B.K.) (ag. ex steud)] and western wheatgrass (*Agropyron smithii,* Rydb.) with age.

The objectives of this study were: to investigate (1) the relationship between chlorophyll content and dry matter accumulation and (2) solar-energy conversion efficiency of eastern gamagrass, weeping lovegrass, and several Old World bluestem grasses at different phenological stages.

Materials and Methods

Plant materials used in these studies were obtained from established, replicated pastures and field plot studies of each of the following grasses: 2 varieties of Old World bluestems, Plains (*B. ischaemum* L. Keng), caucasian (*B. caucasica* C.E. Hubb); 3 experimental blends of *B. intermedia* var. *indica,* (Harlan et al. 1969), designated "B", "L" and "T"; eastern gamagrass [*T. dactyloides* (L) L.], and 2 weeping lovegrass strains [*E. curvula* (Schrad.) Nees], Morpa and an experimental selection designated 813. Each Old World bluestem grass was established in pure stands in replicated 2-ha pastures in 1972. Eastern gamagrass was established in 4 replicated 12 × 6-m plots in 1975 and each of the 2 weeping lovegrass strains in 3 replicated 6 × 9 m plots in the spring of 1979. The soil type at each establishment site was classified as a Dale fine-silty, mixed, thermic, Pachic Haplustolls with a pH of approximately 6.8. Soil analysis of the test locations in 1979 showed that they contained 140 to 210 kg/ha of the available phosphorus, 760 to 1,086 kg/ha of available potassium, and about 5 kg/ha of nitrate nitrogen. During the 1979 and 1980 growing seasons, each pasture was fertilized in April at a rate of 40 kg N and 20 kg P/ha. During the growing season 3 to 5 quadrate samples for chlorophyll analysis and dry matter determination were taken at different phenological stages in each Old World bluestem pasture, eastern gamagrass, and the 2 weeping lovegrass plots. Phenological stages were defined as follows: vegetative stage—older plants leaves only, stem not elongated; boot stage—inflorescence enclosed in flag leaf sheath; late dough stage—endosperm doughy, well-developed seeds; ripe seed—seeds ripe, leaves green, heads intact. Dry matter was determined on a subsample from each quadrat dried at 70° C for 72 hr and weighed. One gram of an aliquot of the frozen or fresh material was taken for chlorophyll analysis. Chlorophyll was extracted with 80% acetone. Aliquots were drawn and diluted if necessary to measure absorbance of the solution at 663, and 645 nm using a Bausch & Lomb spectrometer 710[1]. Chlorophyll a,b (Chla, Chlb) and total chlorophyll (Chla + b) was determined according to the formula suggested by Arnon (1949). Solar energy conversion-efficiency (CE) was determined according to the following relationship. CE = [Chemical Energy Produced/Radiant Energy Received • 100.]

Author is research agronomist, USDA, ARS, Southwestern Livestock and Forage Research Station, El Reno, Okla. 73036.

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[1]Mention of a trade name or specific equipment does not imply its approval by the U.S. Department of Agriculture to the exclusion of other products that may also be suitable.

Table 1. Chlorophyll concentration (mg • g^{-1} • dry weight) in Old World bluestems at different phenological stages.

Developmental stage	Varieties/blends				
	Plains	Caucasian	"B"	"L"	"T"
Vegetative					
Chla	2.74	3.28	3.10	3.23	2.44
Chlb	1.00	0.98	0.90	1.01	0.78
Chl (a+b)	3.74	4.27	4.01	4.24	3.22
Chla/b	2.73	3.34	3.43	3.20	3.14
Boot					
Chla	2.17	3.55	3.57	4.05	4.10
Chlb	0.77	1.19	1.26	1.23	1.28
Chl (a+b)	2.95	4.74	4.82	5.29	5.38
Chla/b	2.81	2.99	2.84	3.29	3.19
Late dough					
Chla	6.02	7.59	7.55	6.63	6.37
Chlb	2.00	2.53	2.63	2.35	2.12
Chl (a+b)	8.02	10.12	10.18	8.98	8.49
Chla/b	3.01	3.00	2.87	2.82	3.00

Chemical energy produced represents the amount of photosynthetically active radiation converted into dry matter during a given time interval. This amount was determined by converting the dry matter produced into chemical energy on the basis of 4.7 KCal per gram dry weight.

Radiant energy received was determined by measuring the photosynthetically active radiation (400-700 nm) at ground level without vegetation cover by using a Lambda Corporation, quantum sensor LI 188[1]. Radiant energy was measured at 800 and 1200 hours at weekly intervals throughout the growing season.

Analysis of variance and a general linear model procedure were used to test differences among chlorophyll, dry matter, and photosynthetic conversion-efficiency. Significant differences among cultivars and treatments were determined at 5% and 1% level by using L.S.D.

Results and Discussion

Chlorophyll concentration (mg/g• dr • wt) in different strains of Old World bluestems at various phenological stages is shown in Table 1. Greater amounts of chlorophylls were recorded during anthesis than during vegetative or flowering stages in all the strains. Chl a/b ratio remained almost constant throughout the growing season. Concentration of Chl$_a$ was always greater than Chl$_b$. Total chlorophyll (Chl$_{a+b}$) peaked at anthesis (Table 1), which coincided with peak dry matter production in all the strains (Table 2). The percent of the total increase in chlorophylls between the vegetative and late dough stage for Plains, Caucasian, "B", "L" and "T" was 114%, 139%, 154%, 111%, and 164% respectively. During this growth period, from vegetative to late dough stage, the percent of the total increase in dry matter production of Plains, Caucasian, "B", "L" and "T" was 163%, 266%, 245%, 103% and 413%, respectively.

Table 2. Relationship between chlorophyll and dry matter production in Old World bluestems.

Developmental stage	Species/blends				
	Plains	Caucasian	"B"	"L"	"T"
Vegetative					
DM (kg/ha)	5117	3911	3077	6181	2265
CHL (kg/ha)	19.13	16.69	12.30	26.20	7.28
DM/Chl	267	234	250	236	311
Late dough					
DM (kg/ha)	13462	14324	10626	12553	11629
Chl (kg/ha)	108	145	108	113	98
DM/Chl	124	98	98	111	118

Table 3. Chlorophyll concentration (mg • g^{-1} • dry wt.) in eastern gamagrass and weeping lovegrass at different phenological stages.

Developmental stage	Species		
	Eastern gama grass	Weeping lovegrass "813"	Weeping lovegrass "Morpa"
Vegetative	9.17	12.10	15.50
Chlb	2.86	3.21	4.00
Chl (a+b)	12.03	15.30	14.50
Chla/b	3.20	3.76	3.87
Boot			
Chla	7.75	10.05	10.84
Chlb	2.58	4.38	3.37
Chl (a+b)	10.33	19.43	14.21
Chla/b	3.00	3.44	3.22
Late dough			
Chla	7.32	7.93	7.55
Chlb	2.15	1.95	1.72
Chl (a+b)	9.47	9.88	9.26
Chla/b	3.41	4.06	4.40
Ripe seed			
Chla	7.38	4.74	3.65
Chlb	2.00	1.24	1.01
Chl (a+b)	9.30	6.00	4.65
Chla/b	3.68	3.81	3.63

The dry matter/chlorophyll ratio in Old World bluestems was higher at the vegetative stage than at the late dough stage, indicating faster rate of increase in chlorophyll than dry matter at the late dough stage. Other growth factors being adequate, the production of dry matter in pasture crops depends upon the total leaf area that is active in light interception and the amount of chlorophyll in the exposed leaves. Brougham (1960) developed a simple index of growth rate/total chlorophyll to determine the relationship between chlorophyll and dry matter production in a number of dicotyledons and cereal plants. Bray (1960) found significant differences in chlorophyll content of diverse plant communities and a positive linear relationship between chlorophyll and dry weight of various stands of different plant communities.

Usually chlorophyll a,b and Chl a/b ratio decrease faster in plants with maturity (Sanger 1971) due to the addition of more fibrous materials and the breakdown of chlorophylls. This does not seem to be the case with Old World bluestem plants at least up to the time of peak dry matter production. However, both Chla and Chlb in weeping lovegrass (Table 3) declined significantly (P=0.01) towards maturity. The ratio of Chl a/b did not change significantly except for a slight decline in the case of weeping lovegrass during late dough and ripe seed stage. Maximum amounts of chlorophylls in eastern gamagrass and weeping lovegrass were recorded during vegetative and boot stages, which did not coincide with maximum amount of dry matter production in these species (Table 4).

Table 4. Relationship between chlorophyll and dry matter production in eastern gama and two strains of weeping lovegrass.

Developmental stage	Eastern gama grass	Lovegrass 813	Lovegrass morpa
Vegetative			
DM (kg/ha)	3850	3262	3380
CHL (kg/ha)	46.31	50.00	49.00
DM/Chl	83	65	69
Late dough			
DM (kg/ha)	9860	8575	8680
CHL (kg/ha)	93.38	84.72	80.40
DM/Chl	105	101	108

There was no significant increase (P=0.05) in chlorophyll concentration of eastern gamagrass from vegetative to boot stage (Table 3); however there was significant (P=0.01) increase (156%) in dry matter production during the vegetative and late dough stage (Table 4). DM/Chl ratio also increased from 83 to 105. During the vegetative and boot stage, the increase in chlorophyll concentration in lovegrass-813 was about 27%; and in lovegrass-Morpa, there was no change (Table 3). Dry matter of accession-813 and of Morpa lovegrass increased about 162% from vegetative to the late dough stage. During the same period the DM/Chl ratio for 813 increased from 65 to 101 and for Morpa from 69 to 108.

The DM/Chl ratio in eastern gamagrass and lovegrasses increased from vegetative to late dough stage, indicating slower rate of chlorophyll synthesis, but more dry matter per kg chlorophyll.

All the species studied in this experiment are warm-season grasses and operate on the C_4-photosynthetic pathway. These plants maintain higher rates of photosynthesis at high light intensity and at high temperature. However, there are differences in the chlorophyll contents among these species and varieties that contribute to differences in dry matter production. Such differences have been reported among both C_4- and C_3-plants (Bokhari 1976, Rauzi and Dobrenz 1970, Black and Mayne 1970, Holden 1973, Chang and Traughton 1972).

The relationship between chlorophyll and dry matter production is meaningful only when the leaf area that is active in interception of light is known. The shape, height, and orientation of leaves along the vertical profile of the plant community are important factors which contribute to the total dry matter production (Whittaker and Garfine 1962, Jahnke and Lawrence 1965).

Old World bluestem plants exhibited greater efficiency in conversion of solar energy into dry matter (Table 5) during July and August at the time of peak standing biomass. During May and June, the average efficiency of conversion was 0.42%, which increased to 1.3% during July and August followed by a decline to 0.18% during September and October. There were varietal differences among different strains of Old World bluestems throughout the growing season from May to August; however, these differences were not significant (P=0.05) near the end of the growing season. Average conversion efficiency for the growing season varied from a minimum of 0.54% for "B" blend to a maximum of 0.73% for caucasian. Average conversion efficiency for all the Old World bluestem strains was .64%. These values appear to be very low compared to the total amount of energy received during a given period of time; however, most ecosystems whether natural or managed are inherently very inefficient in utilization of incident solar irradiance. Ovington and Lawrence (1967) reported conversion efficiency of 0.32% and 0.35% for maize (*Zea mays* L.) and maize plus weed communities. Noble (1972) reported conversion efficiencies for irrigated and nonirrigated pastures consisting of perennial ryegrass (*Lolium perenne* L.) and white clover (*Trifolium repens* L.) for the period 1948-66. Maximum conversion efficiency for irrigated pastures was 0.63% during 1960-61 and for nonirrigated pastures it was 0.54% during 1959-60 growing season. The values found for Old World bluestem plants in this study are, therefore, in general agreement with those from other studies.

Maximum conversion efficiencies of 1.12% in eastern gamagrass, 0.98% in 813 and 0.95% in Morpa lovegrasses (Table 6) were recorded during July-August, and May-June respectively.

Table 5. Solar energy conversion-efficiency (%) of Old World bluestems.

Time	Species/blends					
	Plains	Caucasian	"B"	"L"	"T"	Ave.
May-June	0.48	0.48	0.34	0.53	0.28	0.42
July-Aug.	1.52	1.50	1.12	1.33	1.22	1.33
Sept.-Oct.	0.13	0.23	0.16	0.16	0.25	0.18
Average	0.71	0.73	0.54	0.67	0.58	0.64

Table 6. Solar energy conversion-efficiency (%) of eastern gamagrass and weeping lovegrass.

Time	Eastern gamagrass	Weeping lovegrass	
		813	Morpa
May-June	0.32	0.98	0.95
July-Aug.	1.12	0.25	0.26
Sept.-Oct.	0.11	0.12	0.13
Average	0.51	0.45	0.44

Seasonal average efficiency was 0.51% for eastern gamagrass and about .44% for the two lovegrass strains. These values are slightly lower than that for the Old World bluestems, but are supported by the differences in dry matter production between Old World Bluestem and lovegrass and between Old World bluestems and eastern gamagrass.

The values presented here, do not include below ground production or consumption of dry matter by primary or secondary consumers, nor do they represent losses due to respiration. Here, the conversion efficiency represents only the aboveground-harvestable biomass which is potentially available for primary consumers during a given time interval including cattle and insects that feed on aboveground biomass. The potential conversion efficiency would be slightly higher if roots were included and losses were excluded.

The growth habit and morphological characteristics of Old World bluestems are quite different from eastern gamagrass and weeping lovegrass. Old World bluestems have erect growth habit with the majority of the leaves in an upright position while leaves of weeping lovegrass and eastern gamagrass are usually prostrate. Plants with prostrate leaves have a greater opportunity to intercept the incoming irradiance than plants with erect leaves. However, a majority of the leaves in plants with prostrate leaves are shaded and their efficiency is drastically reduced while in the case of erect leaves that are not placed closely to each other, as is the case in Old World bluestem plants, the efficiency of conversion is relatively higher. For example, more than 60% of the incoming solar irradiance was intercepted by the upper foliage of lovegrass during May-June, 50% by eastern gamagrass, and 35% by Old World bluestems during July-August in the 1980 growing season. In this study, chlorophyll analyses were performed on a representative aliquot from a composite sample which included both the upper and lower foliage. In future studies it will be interesting and useful to divide the foliage into upper and lower compartments along the vertical height of the plant and so do separate chlorophyll and light interception studies to investigate the efficiency of conversion of separate compartments. Warm-season grasses are generally believed to be more efficient utilizers of available resources than cool-season grasses. However, the results of the study indicate that even in the presence of adequately available resources, the solar energy harvesting and assimilating capacity of these grasses may actually be the limiting factor for increasing productivity. Chlorophyll, the solar energy harvesting apparatus in the leaves of these grasses, does not appear to be limiting at any stage during plant growth and neither is solar energy. In order to be able to incorporate the abundance of available solar energy into useful plant products, genetic manipulation of these grasses along with improved management practices to maintain a desired level of plant population is needed.

Literature Cited

Arnon, D.I. 1949. Copper enzymes in isolated chloroplasts. Plant Physiol. 24:1-15.

Bjorkman, O. 1971. Comparative photosynthetic CO^2 exchange in higher plants. In Photosynthesis and Photorespiration, ed. M.D. Hatch, C.B. Osmond and R.O. Slatyer, Wiley-interscience, New York. 18-32.

Black, C.C., Jr., and B.C. Mayne. 1970. P_{700} activity and chlorophyll content of plants with different photosynthetic carbon dioxide fixation cycles. Plant Physiol. 45:738-741.

Bokhari, U.G. 1976. Influence of various temperatures, water stress and nitrogen treatments on chlorophyll and dry matter of western wheatgrass. J. Range Manage. 29:127-131.

Bray, J.R. 1960. The chlorophyll content of some mature and managed plant communities in central Minnesota. Can. J. Bot. 38:313-333.

Brougham, R.W. 1960. The relationship between the critical leaf area, total chlorophyll content and maximum growth rate of some pasture and crop plants. Ann. Bot. 24:463-474.

Chang, F.H., and J.H. Traughton. 1972. Chlorophyll a:b ratio in C_3- and C_4-plants. Photosynthetica 6:57-65.

Downton, W.J. 1971. Adaptive and evolutionary aspects of C^4 photosynthesis. *In:* Photosynthesis and Photorespiration, ed. M.D. Hatch, C.B. Osmond, and R.O. Slatyer. Wiley-interscience, New York, p 3-17.

Harlan, L.R., W.L. Richardson, and J.M.J. deWet. 1969. Improving Old World bluestems for the South. Prog. Rep. 1963. Oklahoma Agr. Exp. Sta. processed series p. 480, p. 14-27.

Holden, Margaret. 1973. Chloroplast pigments in plants with the C_4 dicarboxylic acid pathway of photosynthesis. Photosynthetica 7:41-49.

Jahnke, L.S., and D.B. Lawrence. 1965. Influence of photosynthetic crown structure on potential productivity of vegetation, based primarily on mathematical models. Ecology 46:319-326.

Johnson, I.J., and E.S. Miller. 1940. Leaf pigment concentration and its relation to yield in Fairway Crested Wheatgrass and Parkland brown grass. J. Amer. Soc. Agron. 32:302-307.

McGregor, W.H.D., and P.J. Kramer. 1963. Seasonal trends in rates of photosynthesis and respiration of loblolly pine and white pine seedlings. Amer. J. Bot. 50:760-765.

Miller, E.S., and I.J. Johnson. 1938. The relation between leaf tissue pigment concentration and yield in corn. J. Amer. Soc. Agron. 30:941-946.

Noble, P.F. 1972. The efficiency of pastures and forage crops in photosynthetic conversion of solar radiation in the Waikato district, New Zealand. N.Z.J. Agr. Rex. 15:676-686.

Oelke, E.A., and R.H. Andrew. 1966. Chlorophyll relationships for certain sweet corn genotypes in different environments. Crop Sci. 6:113-116.

Ovington, J.D., and D.B. Lawrence. 1967. Comparative chlorophyll and energy studies of prairie, savana, oakwood and maize field ecosystems. Ecology 48:515-524.

Rauzi, F., and A.K. Dobrenz. 1970. Seasonal variation of chlorophyll in Western Wheatgrass and blue grama. J. Range Manage. 23:372-373.

Sanger, J.E. 1971. Quantitative investigation of leaf pigments from their inception in buds through autumn coloration to decomposition in falling leaves. Ecology 52:1075-89.

Sestak, Z. and J. Catsky. 1962. Intensity of photosynthesis and chlorophyll content as related to leaf age in Nicotiana sanderae hort. Biol. Plantarum 4:131-140.

Slatyer, R.O. 1970. Comparative photosynthesis, growth and transpiration of two species of atriplex plants. Planta 93:175-189.

Whittaker, R.H., and V. Garfine. 1962. Leaf characteristics and chlorophyll in relation to exposure and production in Rhododendron maximum Ecology 43:120-125.