AGENCY FOR INTERNATIONAL DEVELOPMENT
WASHINGTON, D. C. 20523

BIBLIOGRAPHIC INPUT SHEET

FOR AID USE ONLY

1. SUBJECT CLASSIFICATION

A. PRIMARY: Agriculture

B. SECONDARY: Cereal Crops

2. TITLE AND SUBTITLE

Photosynthesis and Translocation in Relation to Plant Development

3. AUTHOR(S)

Eastin, Jerry D.

4. DOCUMENT DATE	5. NUMBER OF PAGES	6. ARC NUMBER
1972	33p.	ARC 633.34-E13

7. REFERENCE ORGANIZATION NAME AND ADDRESS

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8. SUPPLEMENTARY NOTES *(Sponsoring Organization, Publishers, Availability)*

Published in Sorghum in the Seventies, New Delhi, 1972

9. ABSTRACT

The objective is to discuss physiologic activities in sorghum including photosynthesis and translocation. Meaningful discussion of such physiological activities as they bear on yield can be no better than the perspective within which they are viewed so far as plant developmental pattern limiations. Therefore, some time is devoted to discussing developmental characteristics in sorghum in general to be followed by a consideration of photosynthesis, translocation, etc. in the context of yield analyses when possible. Our understanding of the sorghum crop still remains quite limited. The store of information regarding the crop is steadily increasing. However, knowledge of physiologic responses is inadequate yet to state the order of yield limiting physiologic functions with the degree of certainty which seems desirable for cultural and genetic improvement purposes. Our perspective is improving regarding limitations in the various developmental stages. Rapid, simple developmental stage evaluations are permitting a more precise field evaluation of both the time production factors and metabolic efficiency production factors in sorghum. Hopefully this is true to the extent that it will be useful in plant breeder selection work. Progress in photosynthesis and assimilate transport work is continuing as it relates to intraplant competition. Much work needs to be done on respiration. A potentially productive procedure for evaluating photosynthesis in the canopy as a whole has been devised and likely will be a useful tool for plant-type-field stand geometry investigations in the near future. The need exists for developing additional field screening techniques. Also much work needs to be done at the molecular level to advance our understanding of control mechanisms regarding differentiation of floral parts and control of the major physiologic processes.

10. CONTROL NUMBER

PN-AAB-086

11. PRICE OF DOCUMENT

12. DESCRIPTORS

Physiologic Activities, Sorghum, Yield, Cultural and Genetic Improvement, Metabolic Efficiency Factors

13. PROJECT NUMBER

931-17-130-575

14. CONTRACT NUMBER

AID/CM-ta-c-1068

15. TYPE OF DOCUMENT

Research Bulletin

AID 590-1 (4-74)

Photosynthesis and Translocation in Relation to Plant Development

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Reprinted from
Sorghum in Seventies (Editors : N. G. P. Rao & L. R. House),
Oxford & IBH Publishing Co., New Delhi, 1972.

15. PHOTOSYNTHESIS AND TRANSLOCATION IN RELATION TO PLANT DEVELOPMENT

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I. Introduction

The realization that crop production was dependent on key physiological plant processes was clear well over a century ago (Liebig, 1840). However, as recently as some 40 years ago an eminent scientist, Professor F. G. Gregory, commented rather pointedly regarding the limitations of our knowledge in relating key physiologic activities to understanding yield limitations in the field. Permit me to share Professor Gregory's thoughts with you as related by Asana and Mani (1950).

> "During a discussion on the choice of developmental observations for forecasting yield, Gregory (1929) pointed out that plant physiologists were not in a position to state which physiological activities were in the direct line of yield, and therefore such observations as were arbitrarily undertaken, and without appreciation of their significance under a particular environment, for the purpose

Published as paper No. 3324, Journal Series, Nebraska Agricultural Experiment Station.

of interpreting differences in yield may not serve much useful purpose."

No doubt Professor Gregory's remarks provided a good assessment of production research when they were made some 40 years ago. While much progress has since been made in understanding plant function we generally remain unable to state the rate-limiting order of essential yield-related physiologic processes or activities with satisfactory certainty. This is true under either near optimal or stress conditions in the field and particularly so with the sorghum crop. Concentrated physiologic research effort on rice largely in Japan and at the International Rice Research Institute has proven very useful to rice breeders. Hopefully, such an approach will likewise be productive regarding the sorghum crop. Presumably our efforts at this symposium are directed toward assessing the limited knowledge we have regarding sorghum and pointing to where additional research effort is likely to be most productive.

My objective is to discuss physiologic activities in sorghum including photosynthesis and translocation. Meaningful discussion of such physiological activities as they bear on yield can be no better than the perspective within which they are viewed so far as plant developmental pattern limitations. Therefore, some time will be devoted to discussing developmental characteristics in sorghum in general to be followed by a consideration of photosynthesis, translocation, etc. in the context of yield analyses when possible.

I shall preface the discussion to follow with the generalization that sorghum yield improvement achieved in the past, at least in temperate climates, usually resulted more from an increase in seed number than in seed size. An attempt will be made to interpret physiologic activities in terms of how to exploit them for the purpose of increasing seed number and/or seed size when possible. Unfortunately our sketchy knowledge of sorghum will make this impossible more often than possible. Consequently, reference to some of the available data will at best recognize existing knowledge falling into Professor Gregory's categorization of "arbitrarily undertaken" research. Such research undertaken to elucidate basic mechanisms undergirding essential physiologic processes should not carry a bad connotation in applied research areas. While it may not be generally understood where some of the information fits for purposes of interpreting yield limitations, a portion of the data included will likely be of practical value as they become complemented by additional data. Within this general perspective, the first physiologic observations to be considered are developmental characteristics.

II. Developmental Characteristics

A. Growth Stages

Development of the sorghum crop could be categorized in a number of ways. A fairly simple and somewhat arbitrary categorization will be used based on three growth stages (GS_1, GS_2, GS_3) described as follows:

GS_1—Planting to panicle initiation (PI)
GS_2—Panicle initiation to bloom
GS_3—Bloom to physiological maturity

B. Vegetative Stage

Growth stage 1 is strictly a vegetative period. Relatively little information appears to be available concerning how this early vegetative period influences sorghum yield. Bunting (1971) expertly focused attention on this early vegetative phase in crops by posing questions concerning its necessity in cereal production. Discussion of GS_1 will be somewhat limited in view of the sparse literature on it. Its necessity is quickly recognized for generating sufficient leaf area and functional root system to support maximum grain development under whatever environmental limitations exist in any particular cropping situation. Events in GS_1 warrant a good deal of scrutiny regarding how they influence events in GS_2, particularly differentiation of floret number. Plant population influences on seed number differentiated appear to be exerted at least partially before and during PI (Goldsworthy, 1970a). Quinby and Shertz (1970) point to limitations on yield effected by unfavourable conditions limiting meristematic growth. Presumably influencing meristematic growth prior to PI might be a factor as well as after PI.

C. Panicle Initiation and Expansion

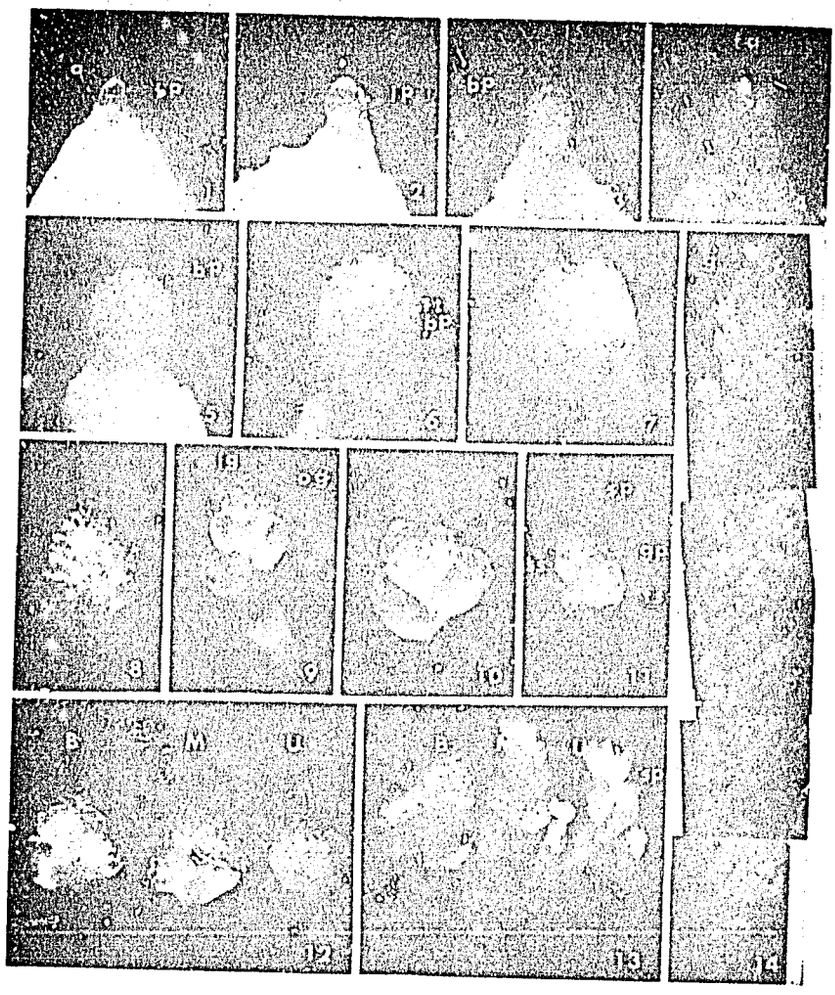
A major event in GS_2 is panicle initiation and subsequent expansion prior to bloom. This growth interval is critical since maximum potential seed number is set then and either expanded or partially aborted. Higher seed number has generally been the most important yield component associated with increasing yield in sorghum (Kamball and Webster, 1966; Stickler and Pauli, 1961; Blum, 1967 and 1970; Quinby, 1963;

Doggett; 1967, Beil and Atkins, 1967). Malm (1968) reported excellent yield improvement with R lines (in hybrid combination) developed from large-seeded exotic germ plasm. Seed size and yield of several hybrids from four steriles were high compared to hybrids of the 7078 check R line on the same respective male steriles. Malm's data (1968) were not reported in a manner that the influence of seed number could be analysed completely. However, large seed size appeared to be a substantial contributing factor in increasing yield. Voight *et al.* (1966) interpreted gene action for seed size to be mostly additive and concluded good progress should be possible in breeding for the seed size component of yield.

Since seed number has been an important factor in past yield improvement, it is well to consider available information on the panicle differentiation process. Chen (1938) reported work regarding time from germination to floral transition. Paulson (1962) described the first evidence of panicle initiation as the visual appearance of protruberances (primary panicle branch primordia) at the base of the apex. Steele's procedure for dating panicle initiation as used by Goldsworthy (1960a) was unavailable for reporting here. Apparently PI was judged as initiated when the growing point elongated to 0.3-0.5 mm. Paulson's (1962) studies were concerned more with caryopsis development than with panicle expansion prior to anthesis. In the absence of a good description of panicle expansion prior to bloom, pertinent investigations were initiated at Nebraska by Lee *et al.* (1970).

Figs. 15-1 through 15-14 illustrate the development of the panicle from inception through floret initiation for the variety Redlan. Fig. 15-1 shows the vegetative apex with a leaf primordium evident. The vegetative apex in Fig. 15-2 has begun expanding just prior to the appearance of primary panicle branch primordia illustrated in Fig. 15-3. Note that the acropetal development of primary branch primordia (Figs. 15-4 and 15-5) is followed by a similar acropetal development of secondary and higher order panicle branch primordia (Figs. 15-6 and 15-7). About 3 to 4 days were required to complete initiation of primary branch primordia under conditions of this experiment. A similar amount of time was required to initiate higher order branch primordia.

Lee *et al.* (1970) found that the acropetal development of panicle parts up to this point gives way to the basipetal development of florets which parallels the top to bottom of the head pollination process in sorghum (Ayyangar and Rao, 1931; Stephens and Quinby, 1934).



FIGS. 15-1 to 15-14. (See facing page).

FIG. 15-1. Leaf primordium (lp) and vegetative shoot apex (a) of sorghum.

FIG. 15-2. Beginning of the elongation of the apical meristem before floral development.

FIG. 15-3, 4. Differentiation of the primary branch primordia (bp_1) on the floral apex (fa).

FIG. 15-5. "Stage 3" of floral development showing primary branch primordia all over the apex.

FIG. 15-6. Initiation of secondary branch primordia (bp_2) from the primary branch primordia.

FIG. 15-7. Enlargement of floral apex due to the presence of more branch primordia of higher orders.

FIG. 15-8. Portion of a panicle branch, showing the division of the terminal portion of branch primorida (arrow) into two spikelet primordia.

FIG. 15-9, 10. Beginning of spikelet differentiation shown by the glume primordia initiation (og = outer glume ; ig = inner glume).

FIG. 15-11. Differentiation of sterile spikelet (ss) and fertile spikelet (fs), showing the appearance of stamen primordia (sp), and gynoecium primordia (GP).

FIG. 15-12. Young panicle branches from basal (B), middle (M) and upper (U) regions of the inflorescence showing their size differences. Spikelet differentiation has not proceeded at this stage yet.

FIG. 15-13. Panicle branches from the three regions with differrent degrees of floret differentiation. Stamen primordia (sp) appeared in the upper panicle branch (U), not in the middle panicle branch (M). The spikelet primordia at the basal branch (B) are at the stage in which glumes are being initiated.

FIG. 15-14. Low magnification of young inflorescence showing basipetal differentiation of spikelets. Note the glumes (g) have developed at the upper region of the inflorescence.

Spikelet primordia appear in pairs at points on the panicle branches illustrated in Fig. 15-8. Individual spikelets occur in pairs (Cowgill, 1926). One spikelet is sessile and fertile and one is pedicelled (Cowgill, 1926 and Doggett, 1970) and usually sterile. The fertile spikelet normally contains two florets, one fertile and one sterile.

Fig. 15-8 illustrates division of the ultimate branch primordia into two parts, the two paired spikelet primordia. Individual spikelet differentiation becomes obvious with the appearance of the two ridges giving rise to glumes (Fig. 15-9) encircling the floret primordium. Floret parts appear as in Figs. 15-10 and 15-11 with the stamen primordia arising around the pistil primordia which differentiates last.

Basipetal floret development is clearly illustrated in Figs. 15-12 and 15-13. Similar stages of development appear in Fig. 15-12. Stamen primordia are obvious in Fig. 15-13 in the upper panicle branch, elongation has occurred in the mid-inflorescence panicle branch and little change occurred in the basal branch. The period from setting spikelet primordia to floret development required about 10 days in this investigation. Peduncle elongation occurs at about the time floret differentiation is completed. Sorghum appears particularly susceptible to environmental stress damage at this stage (Hultquist, 1971). Panicle expansion and peduncle elongation proceed at a rapid pace up to bloom. Experiments will be discussed later to get an idea of the relative competition for assimilates between vegetative and floral parts between PI and bloom. A significant observation by Lee *et al.* (1970) was that floret abortion under favourable field conditions from the time of inception was less than 1% in Redlan and RS 671 except in panicle branches at the base of the rachis. Basal panicle branches frequently abort florets (Fig. 15-14). Also fertile floret abortion after bloom was insignificant except at the inflorescence base.

It is doubtful that the extremely low incidence of floret abortion before and after bloom observed under Nebraska conditions remains the case as the southern U. S. and the tropical areas are approached. The times of floret loss should be documented in areas of interest as a part of any attempt to analyse physiologic yield limitations. In other words both time and efficiency factors are involved.

D. Physiologic Maturity

Ultimate yield is obviously a function of both the length of the grain filling period and metabolic or synthetic efficiency during that period if

either seed number or potential size are not limiting. Precise, rapid determination of physiologic maturity is of interest since it permits accurate measurement of the grain filling period or time factor of yield. The determination of physiologic maturity in sorghum apparently has been done largely on the basis of measuring maximum dry weight date determined by repeated sampling and drying (Pauli *et al.*, 1964; Collier, 1963; Clegg *et al.*, 1958; Wikner and Atkins, 1960; Kersteng *et al.*, 1961). This approach is rather tedious and time consuming. Consequently the practice in the field has been to use bloom dates as an index to physiologic maturity as reported by Dalton (1967).

Daynard and Duncan (1969), reflecting on earlier work by Johann (1935) and Kiesselbach and Walker (1952), proposed using the formation of a black closing layer in the placental region of corn kernels as an indicator of assimilate translocation cutoff and hence physiologic maturity. Daynard *et al.* (1971) further speculated that this may be a feasible approach to judging length of grain filling period and hoped it would correlate well with yield. Rench and Shaw (1971) have shown that initial dark closing layer formation correlates well with maximum grain dry weight. However, moisture varied considerably among genotypes at the time of black layer formation.

Maunder (1970) and Quinby (1971) considered use of the black layer formation in sorghum as an indication of physiologic maturity. Eastin *et al.* (1971) have also collected data bearing on this point. Sorghum pollinates from the tip to the base of the head and consequently matures in the same directional fashion. RS 626 test plants were chosen where external evidence of the dark closing layer was obvious in kernels from the head tip., Ten plants were fed $^{14}CO_2$ in the flag leaves and left 24 hours before harvest. Panicle branches from the middle of the head were analyzed for ^{14}C content. Four kernels chosen from the tip toward the middle of the panicle branch had external visible evidence of the dark layer. Very slight darkening at the fifth kernel tip was evident. The six through eighth kernels (progressing from the middle to basal portions of the panicle branch) had no apparent black layer on the basis of external visual judgment.

The quantity of ^{14}C translocated into each kernel selected appears in Fig. 15-15. Note that the four tip kernels (visual black layer) took up essentially no radioactivity while ^{14}C content of the lower four kernels (no readily visible black layer) increased progressively toward the base of the panicle branch. There appears to be an excellent correlation between an external judgment on black layer appearance and the time

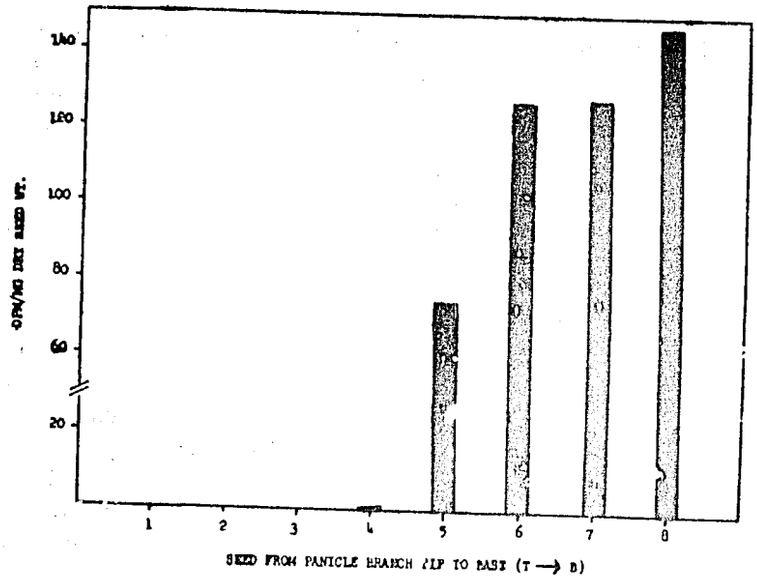


FIG. 15-15. ^{14}C labelled leaf assimilates transported to seeds located between the tip (1) and base (8) of a maturing panicle branch.

translocates are cut off to the kernel. This marks the time of maximum kernel dry weight and can be designated physiological maturity for most, if not all, purposes.

Additional data were obtained on the same heads by choosing kernels from tip (black layer obvious), middle (no black layer) and basal portions of the same RS 626 heads. Essentially no activity was noted in the tip kernels. Sizable activity in the mid-head kernels was only one-third the activity in kernels at the base. Similar results were obtained using Dekalb's E57 hybrid.

Data available to date are not complete in description of events associated with black layer formation but do suggest it will likely be a rapid and useful indicator of physiologic maturity and hence grain filling period for breeding purposes. Yield, along with determination of physiologic maturity, provides an accurate means of determining the efficiency of grain dry matter accumulation on a field basis. Efficient plants can be selected for breeding work and contrasting types (efficient and inefficient) can be field selected for detailed physiologic analyses concerning reasons for their metabolic differences.

E. Comparative Development Among Genotypes

Sorghum literature does contain information regarding the three developmental stages which we have designated as GS_1, GS_2 and GS_3. However, often the information given is not particularly useful in explaining yield differences noted among genotypes, particularly between hybrids and pure lines. Factors controlling panicle initiation and subsequently flowering will be alluded to first and then differences among genotypes for GS_1, GS_2 and GS_3 considered as to their potential association with field yields.

Doggett (1970) reviewed much of the literature regarding factors influencing panicle initiation and flowering. Miller *et al.* (1968a) conducted experiments on tropical photoperiod influence on sorghum growth by planting every month of the year. Miller *et al.* (1968b) tested the influence of known maturity genes on flowering under short days in Puerto Rico. Comparisons on daylength effects on maturity between the tropics and temperate areas probably are confounded by temperature effects. Maturity differences amongst sorghum varieties are thought to be due to differences in photoperiod and temperature responses (Quinby, 1967). However, Doggett (1970) points out that neither classic photoperiodic responses plus temperature responses or interactions between the two satisfactorily explain time of flowering reactions (and hence related PI time) of some Nigerian sorghum varieties.

These references point up the general state of our knowledge regarding control of panicle initiation and flowering and suggest the need for added research in this complex area. The desire to know more about control of PI stems from the knowledge that altering planting date can alter PI date and supposedly factors influencing maximum potential floret differentiation. The seed number component of yield no doubt relates closely to these differentiation factors in some environments.

The date of sowing spring cereals (wheat and barley) has been shown to influence seed number and hence yield (Jessop and Ivins, 1970). Temperature and daylength effects are known to influence seed number in wheat during both before panicle initiation and before bloom once the panicle is initiated (Thorne *et al.*, 1968). Much work is in order on grain sorghum regarding how pre-panicle initiation events influence seed number. With these background remarks some variations in the time spent in various developmental stages will be considered.

Paulson (1962) found days to floral transition varied from 32 to 44

days from a May 31 Iowa planting of 12 genotypes. He also checked the influence of planting date on panicle initiation as illustrated in Table 15-1. The genotypes used are quite photo-insensitive. Later planting reduced days to PI over 40 per cent. June 12 is a relatively late planting date. However, a spread of about 10 days to PI exists simply by adjusting the planting date between mid-May and early June, the normal planting period for Iowa conditions.

TABLE 15-1. *Date of Floral Transition and Anthesis in relation to Date of Planting*

Planting Date	Genotype	Days to Floral Transition	Days to 50% Full Bloom	Days from Transition To 50% Bloom
May 1	RS 610	52	90	38
	Kafir 60	52	92	40
May 15	RS 610	36	71	35
	Kafir 60	38	73	35
May 28	RS 610	27	65	38
	Kafir 60	29	67	38
June 12	RS 610	28	59	31
	Kafir 60	30	61	31

(Taken from I. W. Paulson, 1962, Embryogeny and Seedling Development to Floral Transition of Sorghum vulgare Pers., Ph. D. Thesis, Iowa State University).

Quinby and Liang (1969) determined that panicle initiation occurred an average 2.6 days earlier in CK 60A × Tx 7078 and Redlan A × 7078 hybrids than in their parents. Flowering also averaged 3.8 days earlier in the hybrids. The hybrids were judged earlier than their parents on these bases. Paulson's (1962) data in Table 15-1 show RS 610 (CK 60A × 7078) to be about 2 days earlier than CK 60 (Kafir 60) on the basis of both PI and bloom dates.

Pauli *et al.* (1964) checked the influence of planting date (temperature plus daylength effects) on bloom and length of grain filling period for a number of lines and two hybrids. Maturity judgments were based

on date of maximum dry weight. We studied a series of 5 hybrids and their parents for PI, bloom and physiologic maturity in addition as judged by the apparent coloring of the placental area (Kisselbach, 1939; and Rost and Lersten, 1970) to give the so-called black layer. In the 1970 data which follow (Tables 15-2 and 15-3) a maturity judgement was made on the basis of black layer formation in the tip kernels rather than base of the head as in 1971. These comparative judgements between years are obviously in error since pollination may proceed down the heads at a different rate than the maturation process proceeds. However, data between genotypes for each year are comparative.

The time required to reach PI (Table 15-2) or complete GS_1 was less for hybrids than their respective parents and required from 26 to 36%

TABLE 15-2. *Days in Each Growth Stage for Hybrids and Parents in 1970*

Genotype	Planting to Maturity	Days to Bloom	Growth Stage in Days With % of Total in Parenthesis		
			GS_1	GS_2	GS_3
RS 671*	110	70.7	34 (31)	36.7 (33)	39.3 (36)
Redlan	114	75.2	41 (36)	34.2 (30)	38.8 (34)
Tx 415	110	71.0	37 (34)	34.0 (31)	38.8 (35)
RS 626	107	64.0	28 (26)	36.0 (34)	42.6 (40)
CK 60	108	68.2	33 (31)	35.2 (33)	39.8 (37)
Tx 414	105	67.2	34 (32)	33.2 (32)	37.8 (36)
RS 625	107	64.3	29 (27)	35.3 (33)	42.7 (40)
Martin	105	66.8	32 (30)	34.8 (33)	38.2 (36)
Tx 414	105	67.2	34 (32)	33.2 (32)	37.8 (36)
RS 610	108	64.0	29 (27)	35.0 (32)	44.0 (41)
CK 60	108	68.2	33 (31)	35.2 (33)	39.8 (37)
7078	106	66.2	30 (28)	36.2 (34)	39.8 (37)
TR	110	69.1	33 (30)	36.1 (33)	40.9 (37)
Redlan	114	75.2	41 (36)	34.2 (30)	38.8 (34)
Tx 414	105	67.2	34 (32)	33.2 (32)	37.8 (36)

*Genotypes in each subset are hybrid, female, and male, respectively.

of the life cycle. About one-third of the life cycle was required to complete panicle expansion (GS_2). There was a slight tendency for hybrids to use more days in expanding the panicle than the parents which is opposite to the results of Quinby and Liang (1969). Considerable variation is noted in GS_3. Hybrids RS 626, RS 625 and RS 610 had appreciably longer grain filling periods than did their parents. Smaller differences were noted between RS 671 and TR and their parents. Redlan is a parent common to both hybrids. Maturities based on the black layer

TABLE 15-3. *Grain and Stover Data for Hybrids and Respective Parents 1970*

Genotype	Germination to Maturity	Yield kg/ha	Seasonal Production Rate			Grain Filling Period Production Rate		
			kg/ha/day	% of Hybrid Over Parent	Days	% of Hybrid Over Parent	kg/ha/day	% of Hybrid Over Parent
RS 671[1]	108	7461[2]	69.1		39.8		187.5	
Redlan	112	6747[4]	60.2	14.7	38.8	2.5	173.9	7.8
Tx 415	108	5817	53.9	28.2	38.8	2.5	149.9	25.0
RS 626	105	7816[2]	74.4		42.6		183.5	
CK 60	106	6277	59.2	25.6	39.8	7.0	157.7	16.3
Tx 414	103	6184	60.0	24.0	37.8	12.6	163.6	12.3
RS 625	105	8053[2]	76.7		42.7		188.6	
Martin	103	7288[3]	70.8	8.3	38.2	11.7	190.8	−1.6
Tx 414	103	5925	57.5	33.3	37.8	12.9	156.7	20.3
RS 610	106	8250[2]	77.8		44.0		187.5	
CK 60	106	6464	61.0	27.5	39.8	11.0	162.4	15.4
7078	104	6521	62.7	24.0	39.8	11.0	163.8	14.4
TR	108	6982	64.6		40.9		170.7	
Redlan	112	6891	61.5	5.0	38.8	5.4	177.6	−4.0
Tx 414	103	6280	61.0	5.9	37.8	8.2	166.1	2.8

[1]The first genotype of a set is the hybrid followed by the female and then pollinator parent.
[2]Significant difference between hybrid and parent mean (P. 01).
[3]Significant difference between parents (P. 01).
[4]Significant difference between parents (P. 05).

judgment place hybrids at least as late as the earliest parent, sometimes in between the parents and in one case later than the parents. More traditional judgement based on bloom date has been that parents are earlier since they normally bloom earlier.

Table 15-3 contains 1970 yield data which permit grain production efficiency estimates. Seasonal grain production rates for all the hybrids except TR average on the order of 20% higher than the parent average. The TR hybrid did not yield significantly more than its parent mean and had a seasonal production rate of only 5.5% over the parent average. A similar pattern occurs for production efficiency during grain filing. Hybrid production rates exceed the parent average by about 9 to 16% during grain filling except in the case of TR. Interestingly, the Martin variety was as efficient as any hybrid during grain filling.

The same hybrid-line comparison experiment was run in 1971. Hybrid maturities generally were a little earlier or fell intermediate between the parents. Grain filling periods for hybrids either exceeded those of the parent with the longest grain filling period or fell in between the parents. Hybrids tended to accumulate grain more efficiently than the parents except for the efficient variety Martin.

Dalton (1967) capably demonstrated the positive regression of yield on maturity in sorghum hybrids where growing conditions were favourable in the Texas panhandle. He used days to half bloom as a maturity index. The regression of yield on days to half bloom was negative both years in our hybrid-parent line experiments (also non-significant r values). However, the regressions of yield on days in GS_3 (Figs. 15-16 and 15-17) were positive both years. The significant r values regarding the association between yield and days in GS_3 were 0.80 and 0.62 for 1970 and 1971, respectively. From about one-third to two-thirds of the variability in yield related to variability in the grain filling period under favourable conditions. Significant correlation between days in GS_3 and yield does not hold under stress conditions. The b values given in kg/ha/day (Figs. 15-16 and 15-17) indicate the importance of a few extra grain filling days.

A number of years will be required yet to properly evaluate the utility of GS_3 characterization. However, it appears black layer formation determination will provide a fairly rapid, routine plant breeding method for evaluating and classifying genotypes regarding time production factors and efficiency production factors. If so, this approach might be useful in making both crossing block selections and genotype selections for detailed metabolic efficiency studies as they relate to yield.

If days in GS_3 is to be a useful screening criterion for plant improvement the question arises immediately as to how much variability exists amongst available genotypes. A random mating population of 30 R lines synthesised by P. T. Nordquist and C. O. Gardner was chosen as a

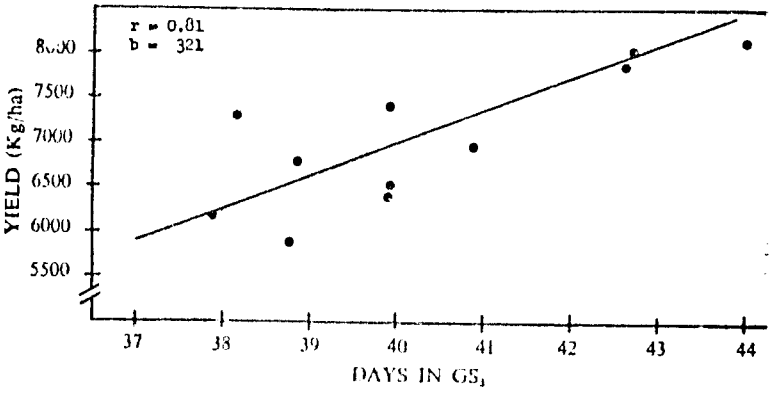


FIG. 15-16. Regression of yield on grain filling period in a 1970 hybrid-parent test with the b value in kg/ha/day.

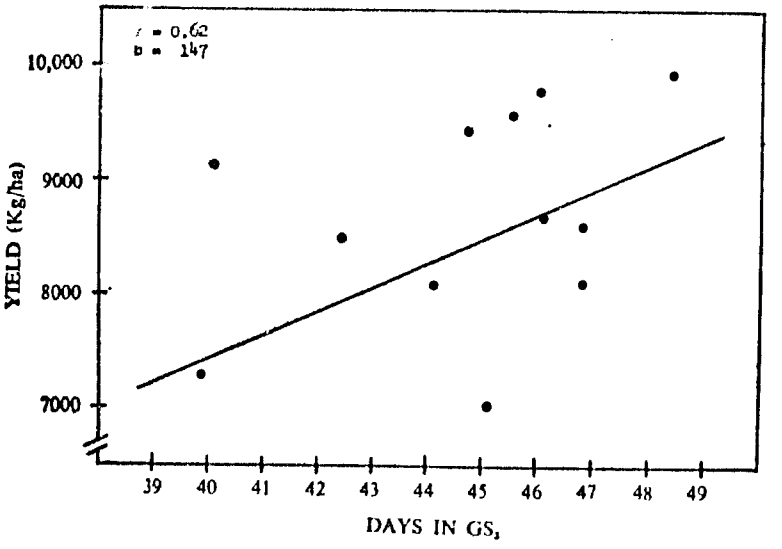


FIG. 15-17. Regression of yield on grain filling period in a 1971 hybrid-parent test with the b value in kg/ha/day.

test group for this character. An excess of 700 single plants checked for grain filling period produced a normal curve-type distribution (Fig. 15-18). The possibility of selection for GS_3 days appears good.

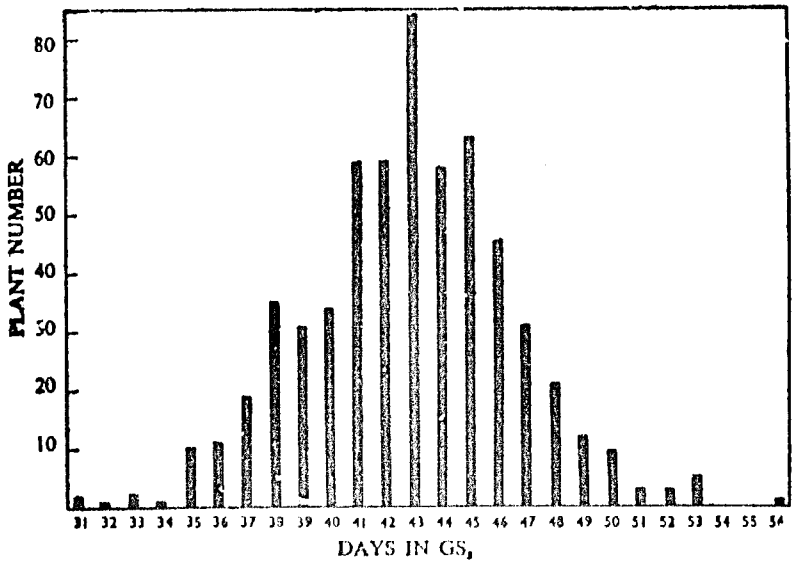


FIG. 15-18. Grain filling period variability in a random mating population of 30 sorghum R lines. The population was in its third random mating.

The association between yield and events in GS_3 appears not too close in U.S. hybrids at this point. However, some data on yields of isogenic height line hybrids are of interest in this respect. Eastin *et al.* (1970) tested the influence of height genes in hybrid combination (RS 626 in 2 × 3-, 3 × 3- and 4 × 3-dwarf versions) on yield. The question of interest was how does reducing internode length and consequently reducing the space between leaves affect performance. Data are given in Table 15-4. Grain-stover ratio of the 2 × 4-dwarf was lower due to its higher stover production. Grain production rates in kg/ha/day did not vary amongst the 3 heights. Total dry matter production in kg/ha/day did differ with the 2 × 3-dwarf exceeding the others by about 16 to 19%.

Seed weight differences are most interesting. Note that the 2 × 3-dwarf has about 29 or 30% larger seed (Table 15-4) than the others. Since yields of all genotypes were the same the 2 × 3-dwarf has to have about a 25 to 30% lower seed number. Obviously, the 2 × 3-dwarf was

able to compensate for the lower seed number by increasing seed size some 25 to 30%. Seed size potential is not being utilized.

TABLE 15-4. *Comparative Production Data for Tall (2-dwarf), Normal (3-dwarf) and Short (4-dwarf) RS 626**

	Grain Height Stover Ratio**	Dry Weight in kg/ha			Kg Dry Matter/Day				% of 2 dw over Others
		Grain	Total	% of 2 dw	Grain	Total	% of 2 dw	g/1000 Seeds	
2 dw	0.76	7741	17,940	100	73.3	169	100	29.3	
3 dw	1.14	7988	15,080	84	75.4	142	84	22.7	29
4 dw	1.08	7528	14,501	81	71.0	137	81	22.5	30

*Germination to maturity was 106 days. Dry matter is adjusted to 14% moisture.
**Ratio is higher than normal due to leaf loss in a heavy unseasonal snow before final harvest.

The cause of the reduced seed number can probably be deduced from dry matter accumulation curves. Plant weights were not taken at PI on June 24 but no height differences could be detected then. Vegetative expansion ceases before bloom except for possibly a little peduncle elongation. Therefore, the extra 16 to 19% vegetative dry matter accumulation by the 2×3-dwarf occurred after PI and prior to bloom. Note the b values in Table 15-5 indicating a more rapid dry matter accumulation for the 2 × 3-dwarf genotype. Lower seed number apparently resulted due to competition for assimilates between vegetative and floral parts during this period.

Panicle initiation occurred on June 24. Since the genotypes are isogenic height hybrids and since no height differences were apparent at PI, it is reasonable to assume the potentials for seed number among genotypes were the same at PI. Panicle branch primordia developed by about July 1. Judging from the time sequence development of the inflorescence described earlier by Lee *et al.* (1970), appearance of floral parts primordia would have been completed by or before July 17. Expansion

TABLE 15-5. *Correlation Coefficients and Regression of Dry Matter Accumulation on Days from Planting (1970) for RS 626*

Hybrid	Samples*	r	b ± $CL_{.05}$ in g/plant/day
2×3 dwarf	18	0.980	1.523 ± 0.0124
3×3 dwarf	18	0.945	1.267 ± 0.0123

*Plots were sampled every 4 days beginning 36 days after planting.

of floral parts continued until about July 30. It appears that the competition between vegetative and floral parts between July 5 and July 30 resulted in either the formation of fewer florets or else floret abortion occurred during expansion of the panicle before bloom. This apparently places the 2 × 3-dwarf at a disadvantage when yield levels appreciably exceed the 8,000 kg/ha level under our conditions.

The tall late Nigerian sorghum (*Farafara*) which Goldsworthy (1970) used produced about three times as much total dry matter per unit area as did the American NK 300 short, early sorghum. However, grain yield in *Farafara* was about half the yield of NK 300. *Farafara* consistently produced a lower seed number at several populations than did NK 300. The lower seed number of *Farafara* may be related to large vegetative growth compared to NK 300. However, a vegetative production comparison with NK 300 is difficult since *Farafara* grew over a much longer time period.

Obviously seed number and seed size components remain essential factors in sorghum yield analyses. Several authors were cited earlier regarding the fact that increases in seed number have been paramount in increasing yields by improving genotypes. Environmental influences within genotypes are also interesting as they relate to seed number. Clegg (1970) collected data over three somewhat diverse years on three genotypes concerning yield and yield components (Table 15-6).

Seed number and seed size data were taken in 1969 and 1970. The yield differences were closely paralleled by changes in seed number within the same genotypes both years. By way of contrast only small changes in seed weight occurred despite the great variation in yield. These kinds of data on genotype and environment yield effects make it

TABLE 15-6. *1968, 1969 and 1970 Averages of Yield and Yield Related Components for Four Sorghum Genotypes*

Year	Yield (kg/ha)	Grain/Head (g)	1000 Seed Wt. (g)	No. of Seeds per Head	Plant Height (cm)	Days to 50% Flowering
1968	5766	21.6	—	—	110	—
1969	9221	31.7	20.6	1532	130	71.5
1970	7038	23.1	21.4	1070	119	68.5

clear that seed number considerations must be given careful thought in both genetic and cultural approaches to sorghum improvement in the future. However, seed size probably should receive more consideration than seems apparent currently. The isogenic height line data discussed earlier (Eastin *et al.*, 1970) suggest that 20 to 30% yield increases due to increased seed size are easily possible. Experiments on manipulating head size (Muhammad Tufail, 1971; Fischer and Wilson, 1971d) suggest the same thing. Therefore, considerable effort seems in order regarding the mechanisms which cause sorghum to senesce and limit seed size by terminating the grain filling period. Malm's (1968) success using large seeded exotics is encouraging. The relative importances of seed number and seed size in further advancing yield are difficult to quantitate. However, it appears obvious that both merit a great deal of consideration and essential physiologic process variation should be considered in terms of how it influences seed number and size.

The major point in the entire discussion thus far is that sorghums are typically complex economic plants and can be expected to react variably to differing environmental conditions. Physiologic studies regarding yield limitations in any particular environment are likely to be most productive if attempts are made to initially define yield component limitations in terms of limiting developmental characteristics. In other words, defining the time periods when seed number and seed size limitations occur, under the environment of interest, necessarily precedes any efficient effort directed toward associating specific physiologic process limitations (photosynthesis, translocation, etc.) with seed size and number limitations. Keeping this generalization in mind we will consider some limited aspects of translocation and photosynthesis in sorghum.

III. Translocation

A. Vascular System

The general morphology and anatomy of sorghum have been described by Cowgill (1926) and Artschwager (1948). Unpublished data (Hultquist, 1971; Lommasson and Lee, 1970) suggest that sorghum translocation pathways are similar to the dual system of corn as described by Kumazawa (1961). Both peripheral and central systems appear to exist in sorghum as judged by ^{14}C movement. Translocates from minor parallel leaf veins appear to move into the peripheral system and travel upward or downward rather quickly. Most assimilates labelled with ^{14}C entering the stalk move primarily to the central portion of the entry node. Assimilate travel (after bloom) then moves down generally for 1 to 4 internodes before entering upward moving central system streams. Peripheral upward travel normally precedes central system upward travel. Assimilate movement appears quite similar to both the flag leaf and leaf 3 from the top. Discussion of morphological and anatomical peculiarities of the translocation system will not be pursued since as yet we have no evidence regarding assimilate transport capacity being a yield-limiting physiologic function in sorghum.

B. Carbon Assimilate Distribution Patterns

Assimilate distribution will be considered both before and after bloom. Before bloom considerations are of interest because they are associated with panicle expansion and seed number. We have fed $^{14}CO_2$ about every four days to leaves from PI up to bloom in order to partially evaluate potential intraplant competition between simultaneously expanding vegetative and floral parts.

Plants were harvested 5 hours after feeding radioactive CO_2 to the last fully expanded leaf. Plant parts were sectioned and lumped together on the basis of expanding floral parts, expanding vegetative parts and fully expanded vegetative parts. Average panicle weights over five progressive sampling periods were 3.4, 18, 66, 154, and 637 mg. Specific activity in the panicle decreased rapidly at the 154 mg stage compared to the expanding vegetative parts reflecting a more favourable flow of assimilates to the expanding vegetative parts. The panicle was expanding rapidly at that point when comparative assimilate absorption to it was diminished at the same time possibly setting up a fairly delicate

balance between assimilate supply and panicle expansion potential. Some limited information suggests the panicle is particularly susceptible to stress damage in terms of floret loss about this time.

We have also conducted assimilate distribution studies on plants having all leaves fully expanded. A few of the distribution patterns in terms of mean percent of translocated disintegrations per minute (dpm) in aerial parts are illustrated in Figs. 15-19, 15-20 and 15-21. Plants were fed in leaves 1 (flag), 3 and 5, respectively. Note first that about the same percentage of translocatable assimilates ended up in the panicle from all the leaves fed. It appears that for a period prior to bloom

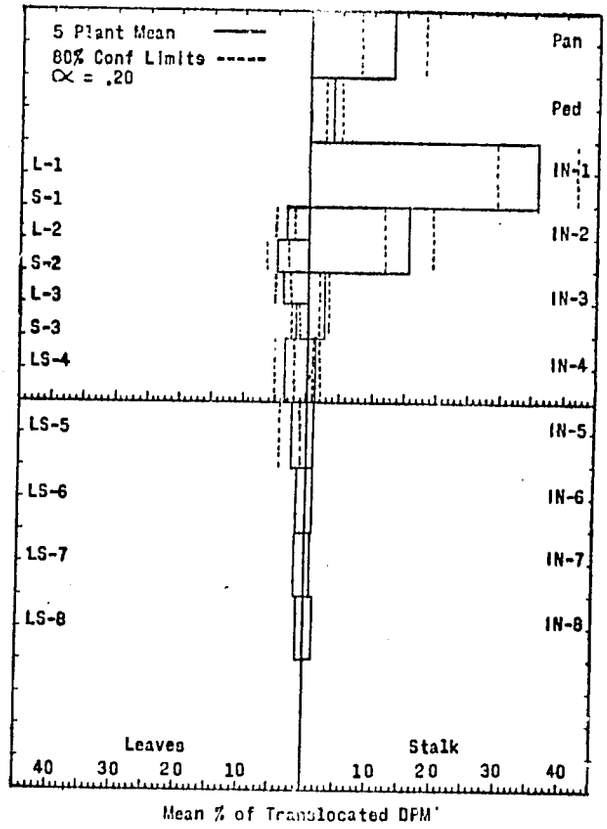


FIG. 15-19. Mean percent of labelled translocated assimilates in indicated plant parts four hours after feeding $^{14}CO_2$ to leaf 1 (variety Redlan).
L=leaf blade ; S=leaf sheath ; LS=blade+sheath ;
Pan=panicle ; Ped=peduncle ; and In=internode.

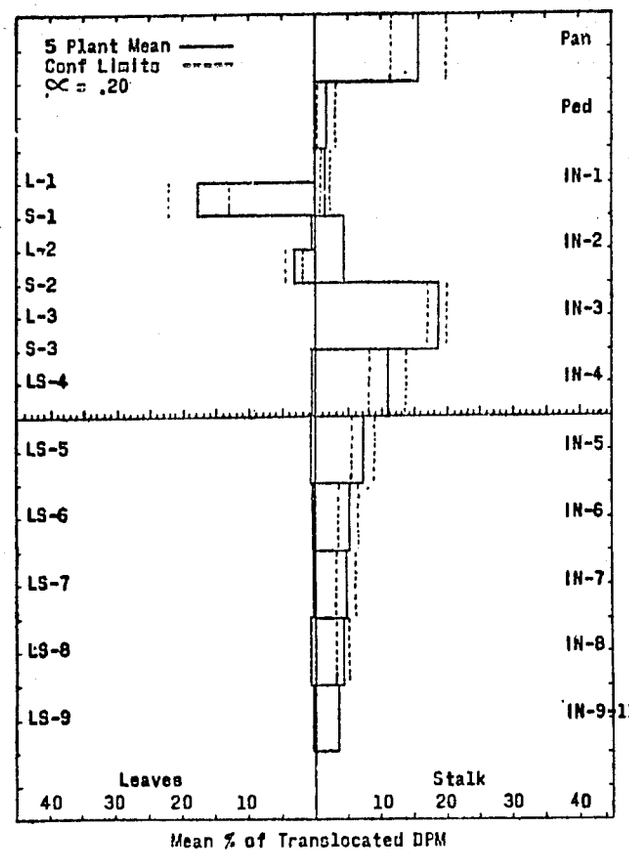


FIG. 15-20. Mean percent of labelled translocated assimilates in indicated plant parts four hours after feeding $^{14}CO_2$ to leaf 3 (variety Redlan).
L=leaf blade ; S=leaf sheath ; LS=blade+sheath;
Pan=panicle ; Ped=peduncle ; and In=internode.

several leaves feed the head about equally well and, therefore, the nature of light distribution within the canopy is not particularly critical relating to head development at this stage under good environmental conditions. This supposition assumes that assimilate movement to the root is not a first order limiting factor. A great deal more work is in order regarding translocation and root requirements particularly under stress.

The approach described in the two experiments just mentioned illustrates how a knowledge of assimilate distribution can be useful in asses-

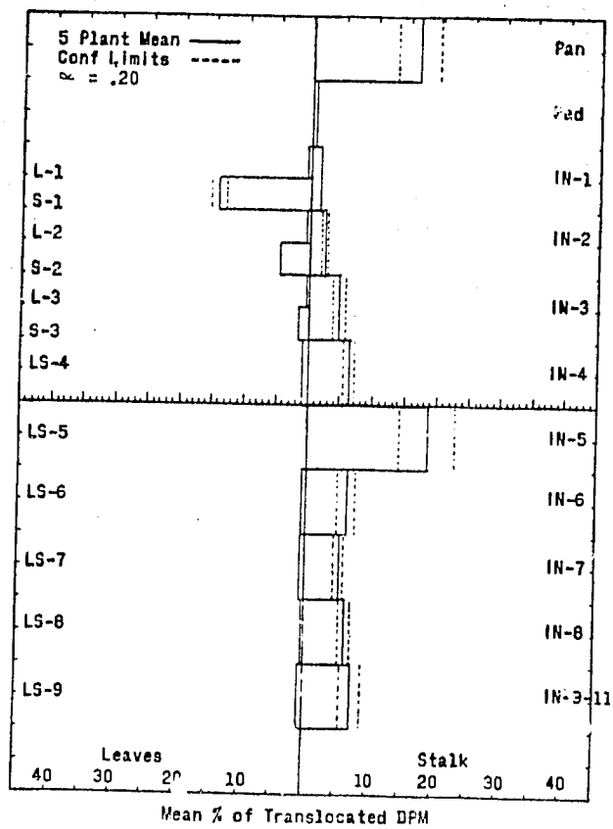


FIG. 15-21. Mean percent of labelled translocated assimilates in indicated plant parts four hours after feeding $^{14}CO_2$ to leaf 5 (variety Redlan).
L=leaf blade ; S = leaf sheath ; LS = blade + sheath ;
Pan=panicle ; Ped = peduncle ; and In = internode.

sing shifts concerning intraplant competition for assimilates. Intraplant competition can arise due to a variety of stresses including environmental stresses, disease stresses and insect stresses. We have barely begun to study the effects of these kinds of stresses on intra-plant competition and how deleterious effects can be minimized by alte ing plant type or stand geometry.

Consideration will now be shifted from the GS_2 to GS_3 stage. Goldsworthy (1970c) concluded that most of the dry matter entering the grain was produced after anthesis. Fischer and Wilson (1971a) deduced

from radiotracer experiments that assimilates produced prior to anthesis constitute about 12% of the grain dry matter.

Fischer and Wilson (1971b) carried out more extensive work on assimilate fate during grain filling. They estimated contribution to grain of the head and top 4 leaves to be about 18 to 20% each. Data are given in Table 15-7 along with leaf efficiencies per unit leaf area. This experiment was conducted in a glass house where conditions no doubt diverge considerably from the field particularly with respect to light

TABLE 15-7. *Contribution to Sorghum Grain Yield of the Head and Four Leaves and the Efficiency per Unit Leaf Area (From Fischer and Wilson, 1971b)*

Source	Contribution To Grain Yield	Efficiency per Unit Area (cpm cm^{-2})
Flag Leaf	18.0	118
Leaf 2	17.4	70
Leaf 3	18.6	57
Leaf 4	20.8	68
Head	17.9	

environment. However, Duthie *et al.* (1971) at the same location reported similar results from field experiments with populations of 50,000 and 250,000 plants/acre. They explained their results on the premise that incident radiation was not much different amongst the top four leaves except for the flag leaf which received more radiation.

Eastin (1968) presented data showing differing contributions to the head from the flag leaf and leaf three (Table 15-8) in field stands. The data are not directly comparable since the total panicles were analyzed as opposed to grain only. Also the latter experiments are short term experiments. Points of note in Table 15-8 are that the percent of total activity in the heads from flag leaf fed plants is 2 to 3 times as high as for leaf 3 fed plants during the pollination period. Little difference exists during the dough stages. Leaf efficiency expressed as percentage

contribution/cm^{-2} is quite variable. The flag leaf was from 3 to 10 times more efficient than leaf 3 as a contributor to the panicle. Leaf 3 was about 3 times the size of the flag leaf. By virtue of leaf 3 size and

TABLE 15-8. *Specific Activity (SA in dpm/mg), Percent of the Total Plant Activity in Heads and Percentage Contribution to the Head/cm^{-2} of Leaf Area Four Hours after Feeding $C^{14}O_2$ in Leaf 3 (from Top) and the Flag Leaf*

Flag Leaf			Growth Stage	Leaf 3		
SA	% total	% cont. /cm^{-2}		SA	% total	% cont. /cm^{-2}
			1965			
			Heads emerging from boot	4,446	29.3	
4,446	25.8		Pollination at tip	2,202	18.1	
1,719	37.4		Pollination at base	710	12.0	
1,433	76.8		Late soft dough	1,316	66.6	
			1966			
			Flag leaf emerging	1,796	1.9	
			Heads at boot tip	3,997	40.9	
1,047	19.9	.41	Pollination at tip	552	5.7	.04
515	17.3	.35	Pollination at base	103	6.7	.05
1,251	36.9	.75	Milk stage	517	22.7	.16
814	46.8	.95	Hard dough	896	45.5	.31

location, it is reasonable to suspect that differences in photosynthetically active radiation received by the two respective leaves explains a good portion of the efficiency differences. Also the closer proximity of leaf 3 compared to leaf 1 to the root may be a factor.

IV. Photosynthesis

A. LEAVES

Sorghum falls in the group of tropical grasses which have an efficient

photosynthetic apparatus (El-Sharkaway and Hesketh, 1965) due in part to little or no photorespiration. Low photorespiration is associated with the C-4 dicarboxylic acid pathway of CO_2 fixation (Hatch and Slack, 1966). This pathway is known to exist in sorghum (Slack and Hatch, 1967; Hatch *et al.*, 1967). Some work has been reported concerning dark pathway intermediates in sorghum (Johnson and Hatch, 1969). Additional references could be cited regarding molecular and anatomical aspects relating to the photosynthetic apparatus of sorghum. Information in this area lending itself to field application is still somewhat limited as will be our discussion of the topic. However, important work is in progress on molecular aspects of photosynthesis in sorghum and should be expanded. The better the system is understood the better will be our chances of manipulating it in terms of increasing yield under both optimal and marginal conditions.

Sorghum, though apparently similar photosynthetically to corn (El-Sharkaway and Hesketh, 1965), has not been characterized in terms of a good light-CO_2 uptake curve. The corn curve is convex shaped (Hesketh, 1963). A similar curve would be expected in sorghum. Mr. R. M. Castleberry, in our group, is currently developing data on this point which are inconclusive so far. However, the plot of CO_2 uptake *vs.* light intensity appears to be a little more linear than expected. Determining the shape of this curve is an important factor. If the shape is convex then light is presumably used more efficiently per unit leaf area at moderate to lower light levels. The canopy then should be structured to distribute the available photosynthetically active radiation (PAR) over a larger portion of the total leaf area in deference to illuminating fewer leaves at higher PAR levels. Some field grain yield evidence does exist (Fischer and Wilson, 1971c; Goldsworthy, 1970a; M. D. Clegg, unpublished data) to support the suspicion that the tendencies toward larger sorghum leaf areas illuminated at lower intensities is more efficient. These field experiments are, however, sometimes difficult to interpret in terms of efficiency of photosynthesis when grain production is the performance criterion. This is so because sink capacity (seeds/unit ground area) is influenced as population is increased to increase the leaf area. Population extremes, both low and high, can result in differentiation of an inadequate grain number to utilize the photosynthetic capacity of the leaf area generated within the canopy in question. The matter of measuring photosynthetic efficiency by grain yield then becomes confounded with floret differentiation limitations which are probably not adequately understood. Consequently, additional data are

needed on CO_2 uptake as influenced by PAR intensity. Given this information a better evaluation of the potential of different leaf angles and various stand geometries will be possible.

Some might consider that sink size is not a limitation in sorghum production based on seed size observations. Eastin's data (1970) presented earlier on isogenic height lines suggested that seed size potential is not being fully utilized in existing field genotypes. Data of Fischer and Wilson (1971d) coming from floret removal suggests the same thing as does Tufail's (1971) partial head removal data. The supply of assimilates to the head appears limiting. This may well be due to a limitation in photosynthesis but the possibility of inadequate polarization of assimilate travel to the head cannot be ruled out under certain conditions. Indeed the polarization of assimilates from leaves to the head is quite variable at different stages of development (Table 15-8) ranging from about 6% of the total at pollination to 75% of the total at the dough stage. A good deal of attention is in order regarding factors that polarize assimilates transport to the head when the crop is grown under both productive and marginal environments.

The photosynthetic capacity of sorghum leaves is of the order of 60 mg CO_2 $dm^{-2}hr^{-1}$ (El-Sharkaway and Hesketh, 1965). Environmental influences on CO_2 uptake were partially investigated by El-Sharkaway and Hesketh (1964). Carbon dioxide uptake increased from about 53 to 68 mg CO_2 $dm^{-2}hr^{-1}$ as leaf temperature was increased from 30°C to about 44°C at a light intensity of 1.3 ly min^{-1}. At 50°C, carbon dioxide uptake dropped to 40 mg CO_2 uptake $cm^{-2}hr^{-1}$ and reached zero at 55°C. From a comparison of cotton and sorghum they concluded that temperature optima are higher for plants having a high net photosynthesis compared to low photosynthesis plants. Also, they showed that CO_2 uptake dropped off sharply at about 10% water deficit at which time leaves were visibly curled. Stomatal width had a definite influence on CO_2 uptake.

Carlson (1969) checked CO_2 exchange in growth chamber plants in both light (about 1/5 full sun intensity) and dark as water potential decreased. The entire aerial portion of plants were monitored. Table 15-9 gives CO_2 exchange in the light. Uptake was cut by up to about 50% in plants stressed to about 20 atmospheres. Leaf diffusive resistance increased some at this point. Stress beyond 20 atmospheres essentially reduced CO_2 exchange to compensation levels which coincided with a large increase in leaf diffusive resistance.

Dark CO_2 evolution (Table 15-10) averaged a little less than 1 mg

TABLE 15-9. *CO_2 Exchange at Low Light Level as Affected by Water Stress*[1]

Water Potential Nonstressed		Water Potential Moderate Stress		Water Potential Severe Stress	
Uptake mg/dm²/hr ± st.dev.	ψ ± ave. dev.	Uptake mg/dm²/hr ± st.dev.	ψ ± ave. dev.	Uptake mg/dm²/hr ± st.dev.	ψ ± ave. dev.
8.90*	12.8 ± 2.2	9.34 ± 1.87***	18.6 ± 0.8	0.33 ± .08	20.3 ± 5.1
6.20 ± 0.15	13.0 ± 2.2	4.20 ± 0.72***	20.3 ± 1.5	0.45 ± .06	26.3 ± 1.5
9.62 ± 1.44	≤ 13.5**			0.20 ± .03	28.3 ± .25
9.20 ± 0.63	≤ 13.5**			0.69 ± .15	34.2 ± 1.9
9.80 ± 0.27	13.5 ± 0.4			0.27 ± .09	55.7 ± 0.0
9.87 ± 0.28	12.2 ± 0.1				

[1] The figures for mg CO_2 dm^{-2} hr^{-1} of uptake were averaged from readings taken every 1/2 hour during the first 8 hours of a regular 12 hour dark-12 hour light cycle.

* Single reading.

** Due to equipment failure, these water potential values were estimated from measurements on similar plants.

*** These figures were obtained by averaging 1/2 hour reading over the first 4 hours following darkness or light initiation.

CO_2 $dm^{-2}hr^{-1}$ in turgid plants. This was increased to about 1.3 mg CO_2 $dm^{-2}hr^{-1}$ at about 20 atmospheres. Carbon dioxide evolution in more severely stressed plants (> 20 atmospheres) was reduced less than 0.5 mg $dm^{-2}hr^{-1}$. This may be due to respiratory substrate limitations arising as stress is prolonged.

Carlson (1969) also assayed the activity of phosphoenolpyruvate carboxylase extracted from the same plant sets. Activity of the enzyme remained quite high even under severe stress. Apparently the enzyme is relatively stable. Treharne and Cooper (1968) demonstrated phosphoenolpyruvate carboxylase to generally have a high temperature maximum. Information regarding carboxylation activity is being

TABLE 15-10. *CO_2 Exchange in Darkness at Increasingly Severe Stages of Water Stress*[1]

Water Potential Nonstressed		Water Potential Moderate Stress		Water Potential Severe Stress	
Evolved mg/dm²hr st. dev.	ψ ave dev.	Evolved mg/dm²/hr st. dev.	ψ ave. dev.	Evolved mg/dm²/hr st. dev	ψ ave. dev.
0.92 ± .02	10.4 ± 0.4			0.35 ± .05	20.3 ± 1.5
1.08 ± .24	12.8 ± 2.2	1.30 ± .07	18.6 ± 0.8	0.42 ± .11**	26.3 ± 1.5
1.04 ± .06	13.0 ± 2.2	1.41 ± .09	19.6 ± 4.1	0.42 ± .06**	28.4 ± 2.5
0.47 ± .05	± 13.5*	1.21 ± .20	20.3 ± 5.1	0.28 ± .02	34.2 ± 1.9
0.63 ± .08	± 13.5*			0.13 ± .03	47.9 ± 5.0
0.81 ± .09	13.5 ± 0.4			0.14 ± .04	55.7 ± 0.0
0.79 ± .11	12.2 ± 0.1				

[1] The figures for mg CO_2 dm^{-2} hr^{-1} evolved were averaged from readings taken every 1/2 hour during the first 8 hours of darkness of a regular 12 hour dark-12 hour light cycle.

* Due to equipment failure, these water potential values were estimated from measurements on similar plants.

** These figures were obtained by averaging 1/2 hour readings over the first 4 hours following darkness or light initiation.

gathered gradually in sorghum. A great deal of research is needed regarding the characteristics of sorghum's carbon economy system as it relates to the plant's ability to go "dormant" under stress and resume activity when stress is alleviated.

One of the most novel and potentially productive approaches to date used in characterizing CO_2 uptake in sorghum canopies was devised by Fischer and Wilson. They enclosed a portion of a canopy and recirculated $^{14}CO_2$ labelled air throughout the canopy. Canopy parts were then dissected (Table 15-11) to get a CO_2 fixation profile in an undisturbed canopy. The amount of photosynthesis at the 80-100 cm level is higher than might have been expected. However, it is difficult to evaluate the results completely without knowing which leaves were in

the different strata and what the light levels were there. Note that some activity was picked up in the head.

TABLE 15-11. ^{14}C *Activity, Photosynthesis per Unit Land Surface and Leaf Area Index of Canopy Layers*

Height in Canopy (cm)	^{14}C Activity in Layer		Photosynthesis (mg CO_2 $dm^{-2}hr^{-1}$)		Leaf Area Index
	c. p. m.	Total %	Measured by CO_2 Uptake	Estimated from ^{14}C Activity	
140–160	476	1.8		0.06	(Inflorescence)
120–140	2,647	10.0	—	3.44	0.2
100–120	8,734	33.0	—	11.35	0.6
80–100	11,117	42.0		14.45	2.0
60–80	3,494	13.2	—	4.54	1.4
0–60	0	0	—	0	0
0–160	26,469	100.0	34.0		4.2

B. INFLORESCENCE

We have conducted some research on CO_2 uptake in inflorescence. A comparison was made between open and simulated semi-compact inflorescences. Further an attempt was made to compare leaves with inflorescences by measuring the area shaded by the head in a horizontal plane at the flag leaf collar level. Data indicate that when the sun is at a low angle the flag leaf is more efficient than either head type. At solar noon the simulated compact head is more efficient than either the open head or the flag leaf.

These data were taken at a time when head photosynthesis compared favourably with leaves. However, the head is this active for only perhaps half the bloom to maturity period (Eastin and Sullivan, 1969). Since the heads can intercept from 25 to 40% (Eastin, 1968) of the incoming PAR, more information regarding their CO_2 uptake and retention is needed. Perhaps heads should, in view of their short active photosynthetic period, be slightly recessed within the canopy to permit the most efficient utilization of available solar energy.

V. Outlook

Our understanding of the sorghum crop still remains quite limited. The store of information regarding the crop is steadily increasing. However, knowledge of physiologic responses is inadequate yet to state the order of yield limiting physiologic functions with the degree of certainty which seems desirable for cultural and genetic improvement purposes. Our perspective is improving regarding limitations in the various developmental stages. Rapid, simple developmental stage evaluations are permitting a more precise field evaluation of both the time production factors and metabolic efficiency production factors in sorghum. Hopefully this is true to the extent that it will be useful in plant breeder selection work. Progress in photosynthesis and assimilate transport work is continuing as it relates to intraplant competition. Much work needs to be done on respiration. A potentially productive procedure for evaluating photosynthesis in the canopy as a whole has been devised and likely will be a useful tool for plant-type-field stand geometry investigations in the near future. The need exists for developing additional field screening techniques. Also much work needs to be done at the molecular level to advance our understanding of control mechanisms regarding differentiation of floral parts and control of the major physiologic processes.

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