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

Yield Considerations in Selected Cereals

3. AUTHOR(S)

Eastin, Jerry D. and Sullivan, Charles Y.

4. DOCUMENT DATE	5. NUMBER OF PAGES	6. ARC NUMBER
1974	7p.	ARC 633.174-E13a

7. REFERENCE ORGANIZATION NAME AND ADDRESS

University of Nebraska
Department of Agronomy
Lincoln, Nebraska 68503

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

Published in the Royal Society of New Zealand 1974

9. ABSTRACT

Seed number usually correlates positively with cereal grain yields. Environmental stresses at the time spikelet components are differentiated in sorghum seriously reduce grain number and yield. Competition for assimilates between simultaneously expanding floral and vegetative parts at this time may put a strain on development of spikelet differentiation and expansion, and suppressing vegetative expansion, appears to have merit. A second area meriting research relates to delaying senescence in grain in order to lengthen the grain filling period and increase total assimilate supply for grain production.

10. CONTROL NUMBER	11. PRICE OF DOCUMENT
PN-AAB-079	

12. DESCRIPTORS

Seed Number, Environment, Senescence, Spikelet Components, Growth Regulation, Vegetative Expansion

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)

MECHANISMS OF REGULATION OF PLANT GROWTH, R. L. Bieleski, A. R. Ferguson, M. M. Cresswell, eds. Bulletin 12, The Royal Society of New Zealand, Wellington 1974. Pages 871–877.

Yield Considerations in Selected Cereals[1,2]

JERRY D. EASTIN[3] and CHARLES Y. SULLIVAN[4]

ABSTRACT

Seed number usually correlates positively with cereal grain yields. Environmental stresses at the time spikelet components are differentiated in sorghum seriously reduce grain number and yield. Competition for assimilates between simultaneously expanding floral and vegetative parts at this time may put a strain on development of spikelet parts. Growth regulation research aimed at maximising spikelet differentiation and expansion, and suppressing vegetative expansion, appears to have merit. A second area meriting research relates to delaying senescence in grain in order to lengthen the grain filling period and increase total assimilate supply for grain production.

Limitations of space prohibit an extensive review of pertinent literature for this broad subject area. Comments will be restricted largely to grain sorghum, and documentation will not be exhaustive even there. In addition, modes of growth regulation or physiological control mechanisms *per se* will not be discussed. Rather we will consider how cereals develop and at what stages in their development, regulation of growth may enhance grain yield under particular environments. The "how" of growth regulation has been discussed during this symposium at some length by those with expertise in that area.

We first consider yield components. Plant breeders ordinarily analyse production in terms of the two yield components, seed size and seed number per unit land area. (Sometimes seed number per unit area may be expressed in terms of inflorescences per unit area and seeds per inflorescence.) Of these components seed number usually correlates far more positively with grain yield in sorghum (Arnon and Blum 1962; Quinby 1963; Kamball and Webster 1966; Beil and Atkins 1967; Doggett 1967; Kirby and Atkins 1968; Quinby and Liang 1969; Blum 1970; Quinby 1970). However, Voight *et al.* (1966) and Mahn (1968) consider that yield increases may also be obtained through seed size increases.

Eastin (1972) recently considered some of the developmental factors that relate to maximising seed number and size in order to enhance yield. The development of sorghum was divided into three growth stages defined as follows:

GS_1 — planting to panicle initiation (PI)
GS_2 — PI to bloom
GS_3 — bloom to physiological maturity

This division of developmental processes can be made quite precisely in terms of anatomical or morphological observations. However, in a discussion of developmental events limiting seed size and number, the division is rather arbitrary, since events occurring in GS_1 influence events in GS_2 which in turn influence ultimate grain production during GS_3. Nonetheless, we shall use this division to facilitate discussion.

[1]Contribution from the University of Nebraska, Departments of Agronomy and Horticulture and Forestry, with the approval of the Director, Nebraska Agric. Exp. Sta.
[2]Financial support for this work was by the Rockefeller Foundation, the DeKalb AgResearch Foundation, and the U.S. Department of Agriculture. Mention of trade names does not imply endorsement by these agencies or the University of Nebraska.
[3]Department of Agronomy, University of Nebraska, Lincoln, Nebraska, 68503; 1973 N.Z. Climate Laboratory Fellow.
[4]Department of Horticulture and Forestry, University of Nebraska.

GS_1 involves vegetative development only. GS_2 involves the differentiation of the inflorescence and its expansion along with expansion of the last six to eight leaves in "combine height" (usually less than 1.5 m tall) sorghums. During this stage the maximum seed number potential is determined. The final stage, GS_3, begins with pollination and ends at physiological maturity, when maximum dry weight is achieved. Post-maturity dry-down will not be considered.

GROWTH STAGE 1

The influences of GS_1 events on maximising the seed number potential that is achieved during GS_2 are not well defined. Quinby and Schertz (1970) pointed out that there would probably be limitations in yield when meristematic growth was limited. Presumably this would apply both before and after PI in sorghum. Goldsworthy and Tayler (1970) felt that population influences on seed number differentiated appear to be exerted before as well as during PI. More recently Downes (1972) reported a definite pre-PI GS_1 temperature influence on seed number, but the mechanism of action is unknown. Sinnott (1921) stated that the size of a plant organ depends on the size of the growing point from which it develops; and Quinby (1970) suggested that larger leaves amongst sorghum plants measured (up to about leaf 12) may have reflected correspondingly larger growing points. With this in mind, Castleberry (1973) reasoned that potential leaf area may be determined during GS_1 since all leaves are initiated prior to PI. Further there is limited evidence (to be discussed in the next section) that simultaneously expanding floral and vegetative structures may compete, under certain conditions, for available assimilates during GS_2, and that seed number can be influenced as a result. Therefore, if leaf size potential and stalk size potential are determined during GS_1 then the potential competition between simultaneously expanding vegetative and floral parts during GS_2 is determined during GS_1. The significance of any such competition on seed number potential generated during GS_2 remains to be evaluated.

GROWTH STAGE 2

The critical GS_2 event is the setting of the maximum seed number potential since seed number usually has a high positive correlation with yield. Perhaps the first indication that seed number can suffer due to competition for assimilates between simultaneously expanding floral and vegetative parts came from a height line experiment we did. Discussion of that experiment should be prefaced by a generalised review of how combine height sorghums develop (Lee *et al.* 1974).

1. 16 to 20 leaves develop, with the 10th to 12th leaf just appearing in the whorl at PI, leaving 6 to 8 leaves to be expanded while the panicle is developing. A new leaf appears about every 3 days.
2. Panicle branch differentiation proceeds acropetally, and is completed in 7 to 10 days.
3. Spikelet primordia are initiated within 2 weeks after PI.
4. Differentiation of spikelet components proceeds basipetally from about 14 to 21 days after PI, during which time peduncle elongation commences.
5. Panicles emerge from the flag leaf sheath (boot) about 1 week before bloom, which proceeds from the tip to base.
6. Total time from PI to beginning of bloom will be of the order of 35 days in Nebraska. Times required to encompass the above events can easily vary by ± 20% depending on year and genotype.

Our experiment was conducted in 1970 (Eastin 1972) on dry matter production in isogenic height lines of the sorghum hybrid RS 626. Sorghum has four dwarfing genes, with presence of all four genes giving the shortest

plants (Quinby 1967). In this hybrid series the females were 2-, 3- and 4-dwarfs crossed to a 3-dwarf pollinator. Grain yields of the 2 × 3-, 3 × 3- and 4 × 3-dwarf hybrids were 7528, 7988, and 7741 kg/ha, respectively, and were not significantly different. However, seed size of the tall (2 × 3) hybrid was 30% larger than in the two shorter (3 × 3 and 4 × 3) hybrids. Consequently, seed number must have been 30% lower in the tall hybrids since yields were not different. Note in passing that the 30% larger seed size in the tall isogene suggests that a good deal of unused sink capacity exists in sorghum; this point will be considered later.

Either the tall hybrid did not differentiate as many florets during GS_2 as its shorter counterparts, or else it aborted 30% more florets. The latter seems unlikely under conditions of this experiment. Therefore we sought for reasons for the differentiation of fewer florets. Vegetative dry matter production in the tall hybrid exceeded the average of the shorter hybrids by 17.5%. Since the three hybrids cannot be distinguished from each other in the field until after PI, this difference in vegetative dry matter production must have occurred in the period between PI and bloom, when panicle parts were being differentiated and the maximum seed number potential was being set. Lower seed number in the tall isogene apparently resulted from assimilate competition between simultaneously expanding vegetative and floral parts. The phrase "assimilate competition" is probably insufficiently descriptive to characterise events leading to differential seed numbers. However, it appears that in the tall hybrid some combination of regulatory factors limited the polarisation of assimilate translocation that would favour differentiation or expansion of floret numbers.

The precise time at which the lower seed number limitation occurred was not clear from this experiment. A second experiment therefore explored assimilate distribution in sorghum during panicle development. Beginning at PI, $^{14}CO_2$ was fed to the last fully expanded leaf of irrigated RS 626 plants approximately every four days for seven periods. Specific activity (S.A.) of the expanding panicle was measured and compared with that of the most rapidly expanding vegetative tissue. This was the untelescoped internodes to which the panicle was attached and was called the juvenile stem complex 1 (JS1). Labelled assimilates had to pass through this stem section en route to the panicle. The ratio (panicle S.A.)/(JS1 S.A.) was considered an index of competitiveness between the two tissues for assimilates. The ratio declined from 1.8 at PI to 0.9 at the beginning of floret differentiation, then further declined to about 0.5, where it remained through the late boot stage. This suggested that the panicle decreased in competitive ability as its development proceeded. S.A. comparisons between tissues as an index of competition leave something to be desired when relative growth rates of the tissues vary and these data must be viewed somewhat cautiously.

We are indebted to Dr R. M. Castleberry and Dr Joe H. Hultquist whose subsequent research has further clarified the sequence of critical events during GS_2.

Castleberry (1974) conducted a series of thinning treatments beginning two weeks after emergence in irrigated sorghum. Approximately at weekly intervals sample areas of a 300 000 plants/ha population (three genotypes) were thinned to 180 000 plants/ha. The effects on seed number per plant, seed size per plant and grain/ha were noted. Thinning treatments 1, 2, and 3 were carried out during GS_1, and treatments 4, 5, 6, and 7 during GS_2. Panicle initiation occurred between treatments 4 and 5. Observations will

be limited to two only of the three genotypes tested since the third genotype fell in a different maturity class.

First, the rate of dry matter accumulation per plant generally increased quickly after thinning, suggesting that the increase in light energy available to each plant had resulted in an increase in photosynthetic supply per plant. Second, seeds per panicle increased significantly in thinning treatments made before mid-GS_2. Third, yields/ha did not decline as a result of thinning treatments made before mid-GS_2 because seed number per plant increased. After mid-GS_2 the genotypes lost their ability to compensate yields by adjusting seed number upward, and increases in seed size were not sufficient to maintain yield per unit area. Fourth, the data suggested there is little direct relationship between growing point size at PI and panicle yield.

Castleberry's (1973) results strongly suggest that the time of differentiation of spikelet components ordinarily occurring between two and three weeks after PI (mid-GS_2) is a critical period relating to seed number potential. These thinning treatment results (enhancing photosynthate supply) agree well with the shading treatment results (decreasing assimilate supply) of Pepper and Prine (1972) which show that lowering light levels reduce seed numbers.

Hultquist (1973) investigated the panicle development process from a different angle. Whiteman and Wilson (1965) had shown that in general, stress prior to PI merely delayed PI without greatly influencing yield per plant. Hultquist (1973) tested the influence of water stress on yield components at PI, at floret differentiation, and at early grain fill. Two hybrid genotypes, C-42Y and RS 626, were used. A severe reduction, about 60%, in seed number per head resulted from stress imposed during PI. No primary panicle branch loss was expected or noted when the stress came during early grain fill, but there was a 25% loss in seed number through floret abortion.

Seed size compensation following the 60% seed number loss from the PI stress was about 30%. There was no seed size compensation following the early seed fill stress. This may possibly have resulted from rigidity induced in endosperm cell walls as a result of the stress.

Hultquist (1973) found sensitivity to panicle damage much more pronounced at floret differentiation. The RS 626 hybrid appeared to react somewhat differently than did C-42Y at this stage. Up to about half a panicle could be killed by the stress effect and the remaining half panicle would still exert (develop) in RS 626. Upon rewatering, nodal tillering accompanied panicle extension. When the primary panicle was damaged more severely it would not emerge from the flag leaf sheath, but the plant survived and developed nodal tillers. In C-42Y the reactions were more extreme. Either panicles emerged and appeared relatively undamaged, or—if the panicle was damaged—it did not emerge and the plant appeared dead within a few days. No nodal tillering occurred.

Hultquist (1973) also measured photosynthesis in turgid controls, moderately stressed plants and plants stressed to zero net CO_2 exchange. The translocation of assimilates formed from photosynthesis of $^{14}CO_2$ was also followed immediately after each treatment and after 17 and 27 day recovery periods. As stress decreased photosynthesis it caused similar reductions in export of ^{14}C from labelled leaves. The patterns of export differed in the two varieties. The RS 626 hybrid exported more assimilate to lower nodes and roots and less to panicles than did C-42Y both during stress and

recovery. Polarisation of assimilate transport in C-42Y was geared more to panicle production while RS 626 transport was associated more with survival at the expense of panicle and seed production. An understanding of the mechanisms responsible for these different assimilate polarisation tendencies might aid development of sound management and plant improvement programmes for areas chronically subject to stress.

Speculatory summary thoughts follow:

1. Differentiation of spikelet components is a critical period, and seed number can be reduced drastically by unfavourable environmental factors at that time. Time of meiosis must likewise be a sensitive period.
2. Photosynthesis may be limiting during seed number differentiation and during subsequent development.
3. If photosynthesis is not limiting, an inability to polarise assimilate translocation and control development in favour of spikelet differentiation and expansion may frequently be limiting.

Regarding the last item, influence of temperature on differentiation of high seed numbers in several cereals and other grasses bears comment. Relatively low temperatures during spikelet formation generally enhance both high spikelet and floret numbers in barley (Tingle *et al.* 1970), wheat (Thorne *et al.* 1968; Cackett and Wall 1971; Owen 1971a, b), and perennial ryegrass (Ryle 1965). Cackett and Wall (1971) analysed selected wheat literature, including Rawson's (1970) work, and noted that in general low temperatures retarded ear development and lengthened the spikelet formation period giving an increase in spikelet number per ear. The influence of temperature on hormonal balance or other control mechanisms favouring formation of high seed numbers merits thorough consideration. Apparently slowing growth during GS_2 favours development of high seed numbers in many cereals. Whether or not this is accomplished at the expense of vegetative expansion, or whether it is in addition to normal vegetative growth, is uncertain.

GROWTH STAGE 3

Ultimate grain yield depends on the rate of dry matter accumulation and the length of the grain filling period. In other words, grain yield is a function of an efficiency component and a time component. The efficiency component is complex, being influenced by sink adequacy and a host of physiological processes. Further, some factors influencing the efficiency component may also influence the time component.

Since many of the processes influencing production efficiency or dry matter accumulation rate have already been discussed here at some length for other cereals, a discussion of these in sorghum will be omitted. The time component or length of grain filling period will be considered briefly.

The time of pollination or the initiation of grain filling is easy to determine. A quick and accurate determination of the time of physiological maturity has been impossible until recently. Sorghum apparently forms a dark closing layer in the placental area of kernel attachment similar to that in corn (Kiesselbach and Walker 1952), when physiological maturity has been reached. Daynard and Duncan (1969), Daynard *et al.* (1971), and Rench and Shaw (1971) have used appearance of this dark layer in corn to evaluate the length of the grain filling period in corn and the relation of this to yield. Eastin *et al.* (1973) checked the functional status of the apparent dark layer in sorghum by feeding $^{14}CO_2$ to the leaves and checking transport to the kernels. An abrupt cutoff occurs when the apparent dark layer development reaches a certain stage. Using this to determine

physiological maturity, and thus the length of the grain filling period, we have noted (from three years' unpublished data) that about one-third to two-thirds of the variability in yield correlates with variability in GS_3 length. This appears true only in the absence of rather severe or prolonged environmental stresses. Under severe stress conditions there is no correlation between yield and GS_3 length.

We found (Eastin 1972) appreciable variability in GS_3 length amongst heads selected at random in a random mating sorghum population. Presumably genetic control of GS_3 length is functionally effected through some kind of chemical control. Understanding the nature of this control might permit easier manipulation of GS_3, either genetically or culturally. The grain filling curve in hybrid sorghums is more or less linear (Collier 1963; Kersting *et al.* 1961; Eastin 1973). Delaying senescence by a few days could be quite productive since maximum seed size potential in sorghum is frequently not attained in the field.

ACKNOWLEDGMENT

Appreciation is extended to Drs R. M. Castleberry and Joe H. Hultquist for constructive reviews of this manuscript.

REFERENCES

ARNON, L.; A. BLUM. 1962. Israel J. Agr. Res. 12: 95-105.

BEIL, G. M.; R. E. ATKINS. 1967. Crop Sci. 7: 225-228.

BLUM, A. 1970. Crop Sci. 10: 28-31.

CACKETT, K. E.; P. C. WALL. 1971. Rhodesian J. Agr. Res. 9: 107-120.

CASTLEBERRY, R. M. 1973. Effects of thinning at different growth stages on morphology and and yield of grain sorghum (S. bicolor L. Moench). Ph.D. Dissertation, University of Nebraska, Lincoln.

COLLIER, J. W. 1963. Crop Sci. 3: 419-422.

DAYNARD, T. B.; W. G. DUNCAN. 1969. Crop Sci. 9: 473-476.

DAYNARD, T. B.; J. W. TANNER; W. G. DUNCAN. 1971. Crop Sci. 11: 45-48.

DOGGETT, H. 1970. Sorghum. Longmans, Green & Co., Ltd. London.

DOWNES, R. W. 1972. Austral. J. Agr. Res. 23: 585-594

EASTIN, JERRY D. 1972. Photosynthesis and Translocation in Relation to Plant Development. In N.G.P. Rao, L. R. House, eds., Proc. Sorghum in the 70s Symp., Hyderabad, October 1971. Oxford - India, New Delhi.

EASTIN, JERRY D. 1973. Efficiency of grain dry matter accumulation in grain sorghum. In J. I. Sutherland, R. J. Falasca, eds., Proc. Amer. Corn & Sorghum Res. Conf., December 1973. Amer. Seed Trade Assoc., Washington, D.C. In press.

EASTIN, JERRY D.; JOE H. HULTQUIST; C. Y. SULLIVAN. 1973. Crop Sci. 13: 175-178.

GOLDSWORTHY, P. R., R. S. TAYLER. 1970. J. Agr. Sci. Cambridge 74: 1-10.

HULTQUIST, JOE H. 1971. Physiologic and morphologic investigations of grain sorghum (S. bicolor L. Moench). Ph.D. Dissertation, University of Nebraska, Lincoln.

KANDALL, A. F.; O. J. WEBSTER. 1966. Crop Sci. 6: 513-515.

KERSTING, J. F.; F. C. STICKLER; A. W. PAULI. 1961. Agron. J. 53: 36-38.

KIESSELBACH, T. A.; E. R. WALKER. 1952. Amer. J. Bot. 39: 561-569.

KIRBY, J. S.; R. E. ATKINS. 1968. Crop Sci. 8: 335-339.

LEE, K. W.; R. C. LOMMASSON; JERRY D. EASTIN. 1974. Developmental studies on the panicle initiation in sorghum. Crop Sci. In press.

MALM, N. R. 1968. Crop Sci. 8: 295-298.

OWEN, P. C. 1971a. Exp. Agr. 7: 33-41.

OWEN, P. C. 1971b. Exp. Agr. 7: 43-47.

PEPPER, G. E.; G. M. PRINE. 1972. Crop Sci. 11: 782-786.

QUINBY, J. R. 1963. Crop Sci. 3: 288-291.

QUINBY, J. R. 1967. Adv. in Agron. 19: 267-305.

QUINBY, J. R. 1970. Crop Sci. 10: 251-254.

QUINBY, J. R.; G. W. LIANG. 1969. Canad. J. Gen. Cytol. 11: 275-280.

QUINBY, J. R.; KEITH F. SCHERTZ. 1970. Sorghum Genetics, Breeding, and Hybrid Seed Production. In J. S. Wall, W. M. Ross, eds., Sorghum Production and Utilization. Avi, Westport, Conn.

RAWSON, H. M. 1970. Austral. J. Biol. Sci. 23: 1-15.

RENCH, EUGENE; ROBERT H. SHAW. 1971. Agron. J. 63: 303-305.

RYLE, G.J.A. 1965. Ann. App. Bio. 55: 107-114.

SINNOTT, E. W. 1921. Amer. Naturalist 55: 385-403.

THORNE, G. N.; M. A. NORD; D. J. WATSON. 1968. Ann. Bot., NS 32: 425-446.

TINGLE, J. N.; D. G. FARIS; D. P. ORMROD. 1970. Crop Sci. 10: 26-28.

VOIGHT, R. L.; C. O. GARDNER; O. J. WEBSTER. 1966. Crop Sci. 6: 582-586.

WHITEMAN, P. C.; G. L. WILSON. 1965. Univ. Queensland Papers, Dept. Bot. 14(13): 233-239.