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Three factors considered to be of importance in the control of yield, which are associated with the development of the inflorescence, are number of primary branch primordia, number of branches arising from each primary branch, and the timing of spikelet differentiation. Of these, the time sequence of acropetal differentiation of primary branch primordia followed by basipetal differentiation of spikelets may be the most important in controlling yield.

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ABSTRACT

A study of the morphology and development of the sorghum (*Sorghum bicolor* (L.) Moench) panicle was made from photographs of fresh apices and from stained sections of fixed material. From periodic collections, the transition from vegetative to reproductive stages indicated an acropetal initiation of primary branch primordia. Higher orders of branch primordia are commonly found on lower branch primordia. Differentiation of spikelets in the panicle is basipetal and is marked by the appearance of glume primordia. Both fertile and sterile spikelets of a pair are morphologically similar during their early development, but the floret parts of the latter degenerate as the inflorescence matures. A developmental stage system evaluating the degree of panicle development is proposed.

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Additional index words: Apex ontogeny, Spikelet differentiation, Phenology of the developing apex, Time of apex transition.

ALL parts of the sorghum (*Sorghum bicolor* (L.) Moench) shoot are developed from apical meristem, which at first initiates the leaf primordia and axillary buds at successive nodes. Buds may cease development early, whereas leaves may continue to develop until late in the growing season. While vegetative growth is still progressing at a rapid rate, the apical meristem shifts to the reproductive phase and initiates the inflorescence, which continues to develop until the end of the growing season. There are certain structural changes in the apical meristem at the beginning of the reproductive phase, and the resulting inflorescence differentiates as an integrated structure until it is a mature panicle.

Some developmental studies of the sorghum panicle have been published (Lane, 1963; Downes, 1972), but

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attention was largely confined to the initiation of the panicle and development of the caryopsis rather than to the complete differentiation of the panicle prior to anthesis. Winton (1903) gave an early description of the caryopsis of sorghum. Sanders (1955) studied the development of the endosperm, seed coat, and pericarp after pollination. Artschwager and McGuire (1949) also described the development of the caryopsis, but they were also concerned with macrosporogenesis, microsporogenesis, fertilization, and the development of the embryo. Chen (1938) recorded the time from germination to floral transition. Paulson (1962) described the first evidence of panicle initiation as the visual appearance of protuberances (primary panicle branch primordia) at the base of the apex. Goldsworthy (1970) apparently judged panicle initiation by growing-point elongation to 0.3 to 0.5 mm in length. Lane (1963) evaluated the influence of light quality on panicle initiation and maturity. Downes (1972) made some reference to stages of panicle development between initiation and bloom. Studies of inflorescence development in other cereals have been published by Bonnett (1966).

Higher seed number has generally been the component of yield associated with yield improvement (Stickler and Pauli, 1961; Quinby, 1963; Kambal and Webster, 1966; Beil and Atkins, 1967; Doggett, 1970; Blum, 1967, 1970). However, potential yield improvement through increasing the seed size component of yield must not be ignored (Voight, Gardner and Webster, 1966; Malm, 1968).

This investigation was undertaken to more carefully detail the course of events during early development of the panicle. Such ontogenetic evaluations appear basic to subsequent investigations on how to maximize the seed number component of yield under both optimal and stress environments.

MATERIALS AND METHODS

The panicle development of *Sorghum bicolor* (L.) Moench was studied in several strains (RS 608, 610, and 671). Grain was planted at the University Experimental Farms in Lincoln, Nebr. in 1969 and at Mead, Nebr. during the 1970 and 1971 growing seasons. Four weeks after planting seedlings having eight visible leaves were marked for further examination. At intervals of 2 or 3 days the visible leaf number of 10 plants from those marked earlier was recorded. Also several plants were removed and taken to the laboratory for study.

Shoot apices were dissected under a binocular stereomicroscope and photographed while fresh and alive, using the method described by Sharman (1947). The stereo dissecting microscope employed for photography used 12× oculars and 2× and 6× paired objective lenses. Fresh apices were also fixed in formal-acetic alcohol (FAA) and subsequently embedded in paraffin for later sectioning on a rotary microtome. Sections cut at 8 μ were stained with safranin, orange G, tannic acid, and iron alum according to Sharman (1943).

OBSERVATIONS

By dissecting away the maturing leaves of a sorghum plant to obtain the vegetative apex, 1 to 3 leaf primordia were found on the apices. The apex of sorghum, therefore, belongs to the short type (Sharman, 1942). Figure 1 shows the dome-shaped vegetative apex of a 3-week-old seedling enclosed by a leaf primordium. The size of the apex increases both in width and height as the seedling develops. Figure 2 shows a 5-week-old shoot apex. The changes in size of the apices of three hybrids are shown in Table 1. During transition from vegetative to early reproductive stages, the size of the apices increases about three to four times in both width and height.

After functioning for about 40 days as a vegetative meristem, the apex is transformed into a floral meristem. The first indication of the initiation of the inflorescence from the vegetative apex is the elongation of the shoot apex above the last formed leaf (Fig. 3). At about this time the volume of the shoot apex increases to almost 50 times that of the vegetative apex. The next and positive indication of the shift is the appearance of protuberances which are the primary branch primordia (Fig. 4). They are initiated both spirally and acropetally on the apex (Fig. 5 and 6).

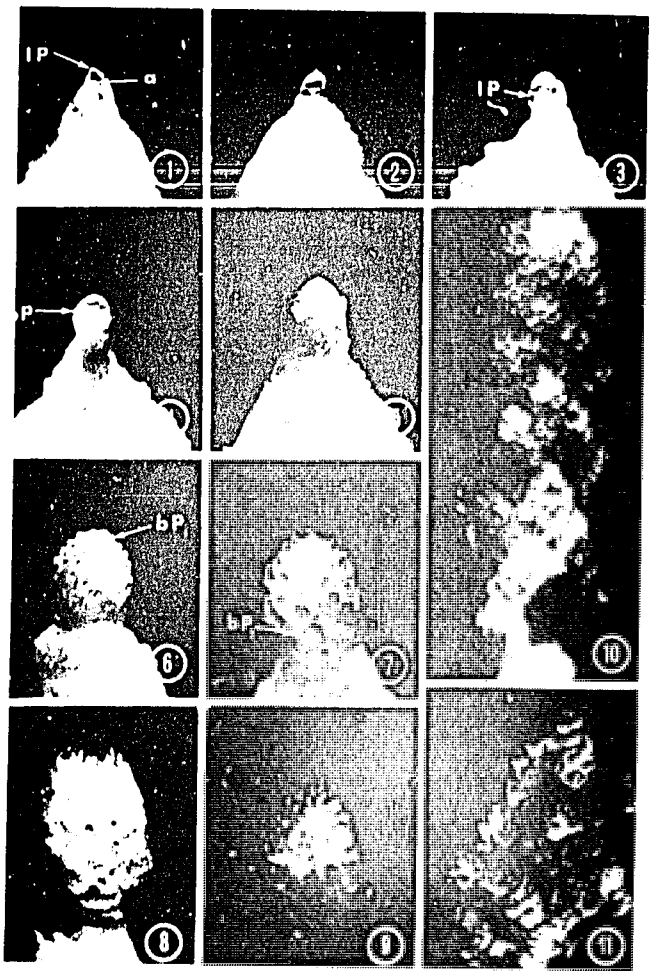

Fig. 1-11. (1) Leaf primordia (lp) and shoot apex (a) of a 3-week-old seedling. 24×; (2) Leaf primordia and shoot apex of a 5-week-old plant. 24×; (3) Beginning of elongation of the apical meristem before floral development, lp = leaf primordia. 24×; (4) Initiation of primary branch primordia (bp) at the lower portion of the apex. 24×; (5) Floral apex with many primary branch primordia. 24×; (6) Floral apex completely covered with primary branch primordia. 12×; (7) Initiation of secondary branch primordia (bp) from the primary branch primordia. 12×; (8) Enlargement of floral apex due to the presence of more branch primordia of higher orders. 8.4×; (9) A close view of a side branch. 12×; (10) A young inflorescence at the beginning of spikelet differentiation. 5.4×; (11) A close view of a side branch taken from the inflorescence shown in Fig. 10. 15.6×.

Table 1. Change in size of apical meristems of sorghum hybrids during transition from vegetative to reproductive activity; 1969.

Date of collection	Days after planting	Hybrid number	Size, μ Range of width	Range of height
June 24	15	671	48 to 61	43 to 61
		610	51 to 64	48 to 70
		608	54 to 64	45 to 48
July 2	23	671	67 to 83	61 to 80
		610	70 to 74	67 to 86
		608	64 to 83	48 to 77
July 6	27	671	81 to 96	51 to 93
		610	70 to 80	64 to 77
		608	83 to 93	70 to 90
July 10*	31	671	134 to 252	138 to 279
		610	96 to 233	112 to 186
		608	74 to 211	77 to 224

* Some of the apical meristems were floral apices with primary branch primordia.

After the primary branch primordia have attained a certain size, secondary branch primordia arise distichously from them (Fig. 7 and 8), giving each primary branch a flattened laminar appearance. However, the secondary branch primordia are usually initiated before the distal portion of the apex has been completely covered up by the primary branch primordia. Tertiary- and quarternary-branch primordia are commonly formed on the lower branches, but they seldom occur on the uppermost branches. Thus, further branching decreases acropetally. For convenience, the primary branch is designated here as a side branch, the secondary and higher order branches as branchlets. As the higher orders of branch primordia develop, the laminar shape of side branches is no longer maintained, but is transformed to a voluminous, fleshy structure with many irregularly oriented primordia (Fig. 9). Also, the young inflorescence begins a very rapid increase in dimensions (Fig. 10). This increase in size is due partly to the elongation of the rachis and partly to the elongation of the upper side branches and their branchlets. Figure 11 shows an upper side branch with well-defined branchlets. The openness or compactness of the panicle is dependent mostly on the elongation of the primary branches and their branchlets.

The ultimate units of the branchlets are the spikelets. In sorghum and other Andropogoneae, the spikelets are in pairs. One is sessile and perfect, the other is pedicellate and sterile. The first and second glumes of each spikelet enclose two potential florets, one of which is sterile and represented only by a lemma (third glume). The fertile floret has a lemma and a palea. Usually opposite the palea are two lodicules. The androecium consists of one whorl of three stamens. The gynoecium is central and consists of one pistil with a branched style bearing two feathery stigmas. The mature stalked spikelet consists of outer and inner glumes and usually a sterile lemma. At the tip of a primary branch sometimes three spikelets occur, two of which are pedicellate and sterile and one sessile and fertile. Occasionally, there are a few vestigial spikelets at the base of side branches, especially in the lower part of the rachis. They are designated here as aborted spikelets (Fig. 12). However, they are only a small fraction of the total number of spikelets.

In the early stages of development, as far as external appearance is concerned, there is no difference between those primordia that become the lateral

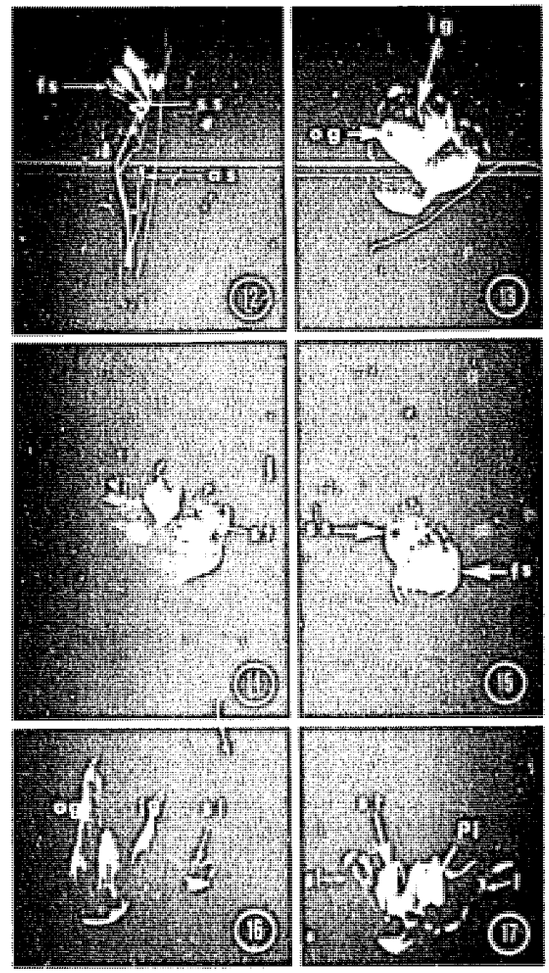

Fig. 12-17. (12) Portion of a side branch of a mature inflorescence, showing the fertile spikelet (fs), sterile spikelet (ss) and aborted spikelet (as). .9×; (13) Initiation of glumes from the spikelet primordia, og = outer glume; ig = inner glume. 27.6×; (14) Differentiation of floret parts in the spikelets, st = stamen primordia. 27.6×; (15) The paired spikelets at the same developmental stage, ss = sterile spikelet, fs = fertile spikelet. 24×; (16) Components of a well-developed sterile spikelet, og = outer glume, ig = inner glume, sl = sterile lemma. 3.6×; (17) Floret parts from the sessile spikelet, sl = sterile lemma, l = lemma, st = stamen, pi = pistil. 33×.

branches and those from which the spikelets will be differentiated. At the beginning of spikelet development, the ultimate branch primordium divides into two parts, forming the two paired spikelet primordia. The appearance of two ridges across the spikelet primordia indicates the differentiation of the spikelet (Fig. 13). These ridges are the glume primordia, one slightly above the other and each semicircling the meristematic tissue of the spikelet primordium. The floret parts are differentiated acropetally as is common in many flowers (Fig. 14). The lemma is the first to differentiate, followed by the palea and the lodicules. Later the stamens appear as circular papillae, and finally the pistil differentiates from the remaining region of the floret primordium. If one compares the early stages of the paired spikelet development, there is no difference between them. The floret parts are initiated in both fertile and sterile spikelets

at almost the same time. The only external difference between them is that the sterile spikelet is slightly stalked above the fertile spikelet (Fig. 15). Thus, the degeneration of the floret parts in the sterile spikelet occurs after their original initiation. Figure 16 shows a mature sterile spikelet in which the outer glume, inner glume, and sterile lemma are well defined, but the floret is vestigial. To the contrary, the floret parts in the fertile spikelet are well developed (Fig. 17). The composition of the fertile spikelet is shown in Fig. 18.

As noted above, the origin of primary branch primordia is acropetal. Grasses differ considerably, however, in the order of development of the spikelets. Evans and Grover (1940) have reviewed this situation for a number of grasses. The bristlegrasses (*Setaria* sp.) and maize (*Zea mays* L.) exhibit acropetal development of the spikelets. Bluegrass (*Poa* sp.) has basipetal spikelet development, and rye (*Secale cereale*) has a mixed type in which the spikelet development begins about the center of the spike and develops both upward and downward. From our observations we would conclude that in sorghum spikelet development is basipetal; that is, the spikelets in the upper branches develop before those of lower branches. The spikelets at the upper end of a branch develop slightly earlier than the lower ones on the same branch. It is shown in Fig. 19 that the side branches from different regions of the inflorescence (base, middle and upper) are more or less at the same developmental stage prior to spikelet differentiation. In Fig. 20, the florets from the upper portion of the inflorescence are more advanced in development than those of the other regions. The stamen primordia are clearly seen, whereas in the basal portion of the inflorescence the glumes are just being initiated from the spikelet primordia. After the floret parts have been initiated, the side branches, branchlets and the rachis all elongate very rapidly (Fig. 21). Later, anthesis is seen to progress from the top of the inflorescence to the base, as does seed maturation, following the order of spikelet development.

Based on the external morphology of the apical meristem, a sequence of developmental stages may be given in general terms to agree with our observations on various strains of our cultivated grain sorghums (Table 2). It should be noted that some of the eight stages are not completely separate from each other, and there is possible overlapping between successive stages. For example, there is considerable overlapping in time between stage 5 and stage 6. Since the differentiation of spikelets is basipetal, the basal region of the inflorescence may be at stage 5 while stage 6 has been attained in the upper region. These stages may be expressed also in terms of the number of expanded leaves for RS 671 during the 1971 growing season. Stage 2 occurs with the presence of 15 or 16 expanded leaves; stage 5 occurs with 18 to 19 leaves, and stage 7 occurs with 21 expanded leaves.

DISCUSSION

Growth and development of the sorghum plant have been generally categorized in two phases: vegetative and reproductive. Knowledge concerning the vegetative phase is obtained mainly from anatomical and

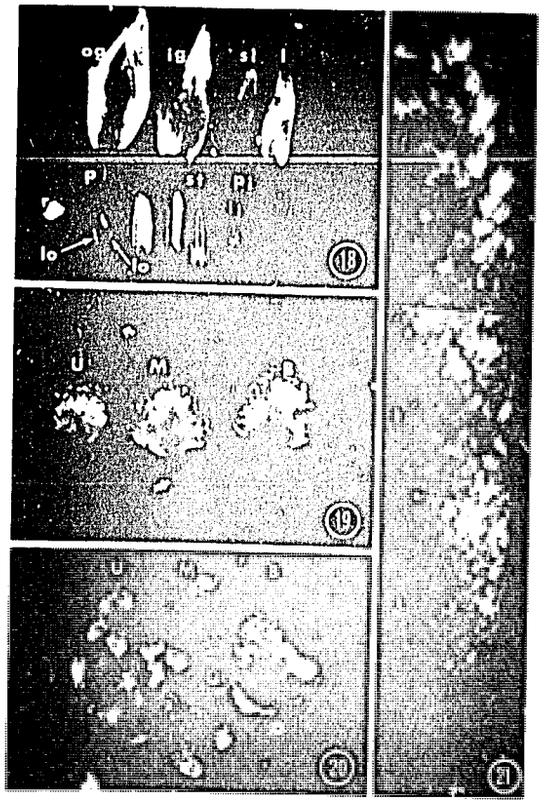

Fig. 18-21. (18) Components of fertile spikelets, og = outer glume, ig = inner glume, sl = sterile lemma, l = lemma, r = receptacle, p = palea, lo = lodicule, st = stamen, pi = pistil. 3.6×; (19) Young panicle branches from basal (B), middle (M) and upper (U) regions of the inflorescence showing their size differences. Spikelet differentiation has not begun at this stage. 10.2×; (20) Panicle branches from the three regions with different degrees of floret differentiation. Stamen primordia are shown in the upper panicle branch (U), not in the middle panicle branch (M). The spikelet primordia on the basal branch (B) are at the stage in which glumes are being initiated. 10.2×; (21) A young panicle showing the basipetal differentiation of spikelets. 4.2×.

Table 2. Developmental stages of panicle initiation based on 1970 study.

Developmental stage	Morphology of the apex	Time interval
1	Vegetative phase of apex producing leaves and shoot tissue	From embryo development through 18 days of growth following germination
2	Beginning of transition to the reproductive phase with the enlargement of the apex	About 18 days after germination
3	Initiation of primary branch primordia acropetally from the base of the shoot apex	About 5 days after the beginning of Stage 2.
4	Secondary and higher order branch primordia arise laterally at the base of branch primordia	
5	Initiation of spikelet primordia	About 5 days after the start of Stage 3.
6	Appearance of glumes on the upper spikelet primordia	
7	Spikelet development present along the whole inflorescence (it has progressed to the basal portion of the inflorescence.)	About 11 days from Stage 5
8	Elongation and emergence of the inflorescence	

developmental studies of organs and tissues (Artschwager, 1948; Lee and Lommasson, 1968). Information on how this period influences the later development of the panicle and yield is scarce. In general, it is recognized that sufficient leaf area and functional root systems are necessary to support maximum grain production. Nevertheless, termination of this phase by the apical meristem not only affects leaf number and plant size, but also marks the start of the reproductive phase. Quinby (1963) reported that four genes controlled the duration of the vegetative phase and subsequently the time of floral initiation. However, the expression of these genes is influenced by other environmental factors, such as temperature and photoperiod (Stickler, Pauli, and Casady, 1962; Coleman and Belcher, 1952).

From our observations there seem to be three important developmental factors in panicle initiation which contribute directly or indirectly to the yield of sorghum. The first factor is the number of primary branch primordia initiated. Since these primordia are acropetally initiated, their total number depends on the available space on the apical dome. Our study indicates that the size of the apex increases as the duration of the vegetative phase is prolonged. Thus, there is a significant influence of the vegetative period upon floral development. The second factor is the number of secondary, tertiary, and higher order branches initiated from each primary branch promordium. The external morphology of the mature panicle indicates that there is an obvious decrease in number of branches and branchlets from the base to the upper parts of the inflorescence. Accordingly, the number of grains per branch also decreases (Blum, 1967). The reduction in number of branchlets in the upper branches is clearly related to the third factor, that is, the timing of spikelet differentiation. It is indicated from the present study that the differentiation of the spikelets is basipetal, whereas the initiation of branch and branchlet primordia is acropetal. Therefore, the remarkable reduction in grain carrying capacity by the upper branches is understandable if spikelet differentiation starts too soon after the intiation of primary branch primordia. On the other hand, its delay will enhance the branchlet developmental potential of both the upper branches and the lower branches. Since the average number of grains per upper branch varies among different strains, it is suggested that this timing also may be under genetic control comparable to the maturity genes of the vegetative phase.

Spikelet abortion under favorable field conditions was insignificant and usually found on the lowest branches. It is interesting, however, that the early differentiation of both fertile and sterile spikelets is similar, yet the stalked spikelet is invariably sterile and the sessile spikelet fertile. Nutritional competition between these two kinds of spikelets may not be the only explanation. Research on the control of spikelet development and its sterilization should be a profitable and significant approach in relation to increase in yield.

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