Free Phenolic Compounds and Tannins in Sorghum Caryopsis and Glumes During Development[1]

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ABSTRACT

Caryopses and glumes of sorghum cultivars varying in type (I, II, or III), and pericarp and glume colors were analyzed for easily extractable (free) phenolic compounds (FPC) and tannins at 15 stages of maturity, from anthesis through maturity. Maximum levels of FPC were observed at immature stages of development (5–22 days after anthesis). Levels of FPC in mature caryopses were significantly less than in developing caryopses. Apparently, the phenolic compounds were increasingly bound to cellular components during maturation. Sorghums with a pigmented testa, dominant spreader gene, and darker pericarp and glume colors contained more FPC and tannins than other sorghums. Sorghums with higher levels of FPC generally had increased weathering and midge resistance.

Phenolic compounds in sorghum caryopsis improve resistance to birds, insects, and molds as well as preharvest germination (Bullard and Elias 1980, Dreyer et al 1981, Rooney and Miller 1982). However, these preharvest advantages are coupled with postharvest problems, i.e., binding and precipitation of proteins, decreased digestibility, off-color and off-flavors in feed and foods (Butler 1982a; Hahn et al 1984; Hahn and Rooney 1986). Sorghums need to be developed that exhibit improved preharvest characteristics and decreased postharvest problems. To accomplish this, the type of phenolic compounds, their concentration and location during caryopsis development, and their bioactivity need to be determined.

Phenolic compounds, i.e., phenolic acids, flavonoids, anthocyanidins, and tannins, are located primarily in the pericarp and testa layers of the sorghum caryopsis (Hahn et al 1984) and in the glumes and leaves of sorghum (Ring 1984). The genetics of caryopsis and glume color were reviewed in terms of polyphenols in sorghum (Rooney et al 1980, Hahn et al 1984). The appearance of the pericarp is affected by B_1-B_2-*S*-*R*-*Y*-*I*-*Z*- genes. Dominant B_1-B_2- yield a pigmented testa containing tannins (types II and III sorghums); dominant *S*- gene increases brown tannin pigments in the testa and pericarp; dominant *R*-*Y*- genes yield red anthocyanidins (luteolinidin) in the pericarp, while *rr Y*- genes yield a yellow chalcone (eriodictyol) in the pericarp, and *R*-*yy* or *rryy* genes yield a white pericarp with no visible pigments. Dominant *I*- gene affects the intensity of pericarp color, and a dominant *Z*- gene gives the caryopsis a thin, translucent pericarp with little or no mesocarp. Yellow endosperm sorghum (dominant *Ye*- genes) contain a high level of carotenoid pigments. The secondary plant and glume colors (*P*-*Q*- genes) affect pigmentation in leaves, stalks, glumes, and possibly even caryopses. Dominant *P*-*Q*- and *P*-*qq* combinations are associated with purple or red pigments, whereas *ppqq* genes are associated with sienna or brown pigments.

The concentration of phenolic compounds in caryopses has been determined at immature stages of development greater than 10 days after anthesis (Tipton et al 1970, Johari et al 1977, Price et al 1979, Davis and Hoseney 1979, Chavan et al 1979, Rooney et al 1980, Glennie 1981, Butler 1982b, Asquith et al 1983). Most researchers report higher levels of tannins and phenolic compounds before physiological maturity of the caryopsis. Little information is available, however, concerning phenolic compounds in caryopses during the first week after anthesis or concerning the effects of pericarp and glume colors. Other tissues in the developing spikelet probably contribute to disease and insect resistance of sorghums (Castor and Frederiksen 1980, Seitz et al 1983, Teetes 1985). Therefore, caryopses and glumes of diverse sorghum genotypes were analyzed for phenolic compounds from anthesis through maturity in this study. Changes in their microscopic structures and phenolic acids are reported separately (Earp 1984, Poe et al, *unpublished*).

MATERIALS AND METHODS

Sample Collection

Sorghum cultivars with different caryopsis and plant characteristics (Table I) were grown on the Texas A&M Plantation at College Station, TX, during 1983. Sorghum cultivars were planted in plots consisting of four rows, each 20-ft long. Panicles were tagged at anthesis, and samples were collected every day from anthesis through seven days after anthesis (DAA), and every fourth day from 10 to 34 DAA. Tissues from eight to 10 panicles were composited for each sample. Samples were immediately placed on ice, frozen within 2 hr after harvest, and stored in a freezer. Immature sorghum tissues were kept on ice during sample preparation. Fertile spikelets were separated from rachis branches and sterile florets for all samples. Caryopses were separated from other tissues in the fertile spikelet of samples 10 days or more after anthesis.

Experimental Methods

Free phenolic compounds (FPC) were determined in triplicate by an automated Folin-Ciocalteu procedure (Kaluza et al 1980) using gallic acid as the standard. Two subsamples of 15 caryopses, 15–30 glumes or spikelets (0.1–0.3 g) were homogenized with a Polytron homogenizer (PT-10 probe, Brinkman Instruments, Westbury, NY) for 15 sec at maximum speed in 50-ml screw cap centrifuge tubes containing 20 ml of 1% HCl in methanol. Homogenized samples were shaken for 2 hr (20° C) and centrifuged (10 min, 2,500 × *g*).

Tannins were determined in triplicate by an automated, acidic-vanillin method (Maxson and Rooney 1972, McDonough et al 1983) using catechin as the standard. Two subsamples of caryopses, glumes, and spikelets (0.1–0.3 g) of cultivars containing a pigmented testa were homogenized (as described above) and incubated for 30 min at 27° C before analysis.

Moisture content was determined by drying samples (0.2–0.3 g) for 4 hr at 70° C then overnight at 135° C in a forced-air oven (AACC 1979).

RESULTS AND DISCUSSION

Spikelets, at all stages of development, had higher FPC and tannin levels than caryopses or glumes alone. Therefore, caryopses and glumes were separated and analyzed independently. Separation of immature caryopses (<10 DAA) from other tissues in the spikelet, i.e., glumes, lemma, palea, etc., was very tedious and time-consuming; hence, only one cultivar, Hegari, was

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separated and evaluated during its very early development. The remaining cultivars were analyzed as spikelets for 0–7 DAA and as caryopses and glumes (other tissues in the spikelet) from 10 to 34 DAA.

Dry weight and chemical analyses of Hegari revealed that glumes changed less than caryopses during early development (Table II). Glumes of Hegari weighed between 1.8 and 2.3 mg throughout development, while the caryopsis increased from 0.15 to 27.5 mg. Therefore, FPC values are reported on a per unit basis to normalize the rapidly changing weight of the caryopsis. Additional information is provided when FPC data are expressed on a per unit basis, i.e., compound biosynthesis, polymerization, and binding properties during caryopsis development. Caryopses of Hegari contained more FPC than were found in glumes (on a per unit basis). Phenolic compounds started increasing 3 DAA in caryopses, whereas FPC in glumes were stable through 7 DAA. Therefore, FPC in glumes were estimated from values of spikelets at anthesis and glumes at 10 DAA in other cultivars. Values of FPC in caryopses (0–7 DAA) were calculated by subtracting values for glumes from spikelets.

Average dry weights of sorghum caryopses and glumes are presented in Figure 1. Weights of glumes changed little after anthesis (1.5-fold increase from 1.8 to 2.8 mg/glume); however, caryopses increased in weight between 160- and 180-fold during development (0.15 mg at anthesis, 8.5 mg at milk stage [10 DAA], and 25.0 mg at combine harvest maturity [34 DAA]). Similar increases in caryopsis weights during development have been reported (Paulson 1969, Butler 1982b, Newton et al 1983).

Effect of Maturity

Sorghum caryopsis and glume tissues were analyzed for FPC and tannins during development. Sorghums with a pigmented testa layer had significantly higher levels of FPC in both tissues during most developmental stages when compared to other sorghums (Fig. 2). All sorghums had relatively low levels of FPC and tannins at 1 to 3 DAA. FPC continued to accumulate through 10–14 DAA (milk stage), whereas tannins continued to accumulate through 14–18 DAA (soft dough stage). Then, the concentration of FPC and tannins decreased continuously through physiological (22 DAA) and combine harvest maturities (34 DAA).

Tannin levels in immature caryopses have been reported (Price

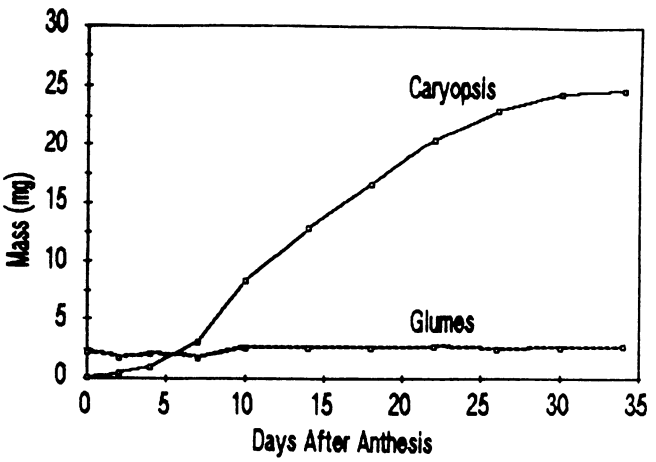

Fig. 1. Average dry weight of caryopsis and glume tissues of sorghums from anthesis to combine harvest maturity (mg/unit).

TABLE I
Descriptive Characteristics and Genetics of Sorghum Cultivars

Cultivar	Glume Color	Pericarp	Pigmented Testa	Appearance of Kernel	Weathering Rating[a]	Genetics[b]
SC103-12	purple	red, thick	yes	dark brownish-red	1.5	*B1B1B2B2SSRRYYIIzzyeyePPQQ*
Dobbs	purple	white, thick	yes	brown	1.8	*B1B1B2B2SSRRYYiizzyeyePPQQ*
RTx2566	purple	red, thin	yes	brownish-red	1.8	*B1B1B2B2ssRRYYIIZZyeyePPQQ*
Hegari (PI34911)	purple	white, thick	yes	chalky white	2.2	*B1B1B2B2ssRRyyiizzyeyePPQQ*
BTx378	purple	red, thick	no	red	2.3	*b1b1B2B2SSRRYYIIZZeyePPQQ*
SC630-11E(II)	purple	red, thin	no	dark red, pearly	1.2	*b1b1B2B2SSRRYYIIZZyeyePPQQ*
RTx7000	purple	red, thick	no	red	3.2	*b1b1B2B2SSRRYYiizzyeyePPQQ*
RTx2767	purple	red, thin	no	yellow	2.5	*b1b1b2b2SSRRYYiiZZYeYePPQQ*
SC748-5	purple	yellow, thin	no	brownish-yellow	2.5	*b1b1B2B2ssrrYYIIZZyeyePPQQ*
BTx3197	purple	white, thick	no	chalky white	3.2	*b1b1B2B2SSRRyyiizzyeyePPQQ*
CS3541	tan	white, thin	no	white, pearly	2.5	*B1B1b1b2SSRRyyIIZZyeyeppqq*

[a] Ratings of weathering conducted by R. Monk, two weeks after harvest maturity: 1 = clean, normal appearance (no weathering) to 5 = moldy, discolored kernels (weathered).
[b] Details of sorghum genetics are discussed in the text.

TABLE II
Free Phenolic Compounds and Tannins in Caryopsis and Glume Tissues of the Sorghum Cultivar, Hegari (PI34911), from Anthesis Through Combine Harvest Maturity

Days After Anthesis	Dry Weight		Free Phenolic Compounds[a]		Tannins[a]	
	(mg/caryopsis)	(mg/glume)	(mg/caryopsis)	(mg/glume)	(mg/caryopsis)	(mg/glume)
0	0.15	2.0	0.010	0.014	0.024	0.004
1	0.39	1.8	0.007	0.015	0.011	0.004
2	0.45	1.8	0.018	0.022	0.016	0.005
3	0.80	1.8	0.024	0.021	0.184	0.006
4	1.0	2.1	0.147	0.027	0.348	0.010
5	1.7	1.9	0.160	0.021	0.898	0.006
6	2.0	1.8	0.235	0.025	0.927	0.009
7	3.2	1.8	0.278	0.033	0.628	0.018
10	8.4	2.2	0.281	0.070	0.473	0.020
14	14.4	2.1	0.236	0.059	0.497	0.015
18	20.6	2.2	0.218	0.083	0.426	0.011
22	25.0	2.1	0.165	0.119	0.268	0.006
26	27.5	2.0	1.141	0.076	0.170	0.004
30	26.6	2.2	0.162	0.065	0.187	0.005
34	26.7	2.2	0.139	0.056	0.160	0.005

[a] Phenolic compounds and tannins were quantitated by the Folin-Ciocalteu and acidic-vanillin methods, respectively.

et al 1979, Chavan et al 1979, Bullard et al 1981, Glennie 1981, Butler 1982b, Asquith et al 1983). Chavan et al (1979) and Butler (1982b) reported maximum FPC and tannin levels in caryopses on a dry weight basis, at 7 and 16 DAA, respectively. Others reported maximum levels between hard dough stage and physiological maturity. Maximum levels of FPC and tannins in this study were observed between 5 and 15 DAA (milk stage) when expressed on a dry weight basis.

Glumes contained lower levels of FPC and tannins than caryopses at most stages of development (Fig. 2) except the early developmental stage. Tannins and FPC accumulated in glumes until physiological maturity, then declined through combine harvest maturity, similar to caryopses. Glumes contained relatively high amounts of FPC (average 2.0–3.9%) and tannins (average 0.5 to 8.9%) on a dry weight basis. Even though FPC levels in glumes changed little during development, glumes at all developmental stages contained significant levels of easily extractable, potentially bioactive phenolic compounds.

Effect of Pericarp and Glume Color

Sorghums without a pigmented testa (type I sorghums) were compared to determine the effect of pericarp and glume colors. The level of FPC in caryopses during development was associated with pericarp color (Fig. 3). Caryopses with a darker pericarp color (red or yellow) contained more FPC than caryopses with a white pericarp. Glume color, however, was not associated with different levels of FPC in caryopses with a white pericarp.

The level of FPC in glumes during development was associated with glume color (Fig. 3). Purple glumes contained more FPC than tan glumes. Levels of FPC in glumes was not associated with pericarp color of sorghums with purple glume color. Rooney and Miller (1982) observed that pigments leach from the glumes of sorghum at different rates. Apparently, the glumes of the yellow pericarp cultivar (SC748-5) leached FPC more rapidly than the other cultivars.

Two separate biochemical mechanisms for phenolic compound synthesis appear to function in developing sorghum spikelets, one located in caryopses and another in glumes. Apparently, the *R* and *Y* genes, which determine pericarp color, dominate the production of phenolic compounds in developing sorghum caryopses. The *P* and *Q* genes, which determine glume color, apparently regulate phenolic compounds in glumes.

Effect of Pericarp Color and the Spreader Gene

Sorghums with a pigmented testa layer (types II and III) were compared to determine their relationships with pericarp color and the spreader (*S*) gene. Presence of a dominant *S* gene (type III sorghum) corresponded to increased levels of FPC and a longer period of deposition of FPC in the caryopsis (Fig. 4). Darker pericarp color of type II sorghums (recessive *ss* gene) corresponded to increased FPC levels from 10 to 26 DAA. However, pericarp color of type III sorghums was not associated with changes in FPC levels.

Free phenolic compounds in glumes of sorghum with a pigmented testa were not significantly different at any stage of

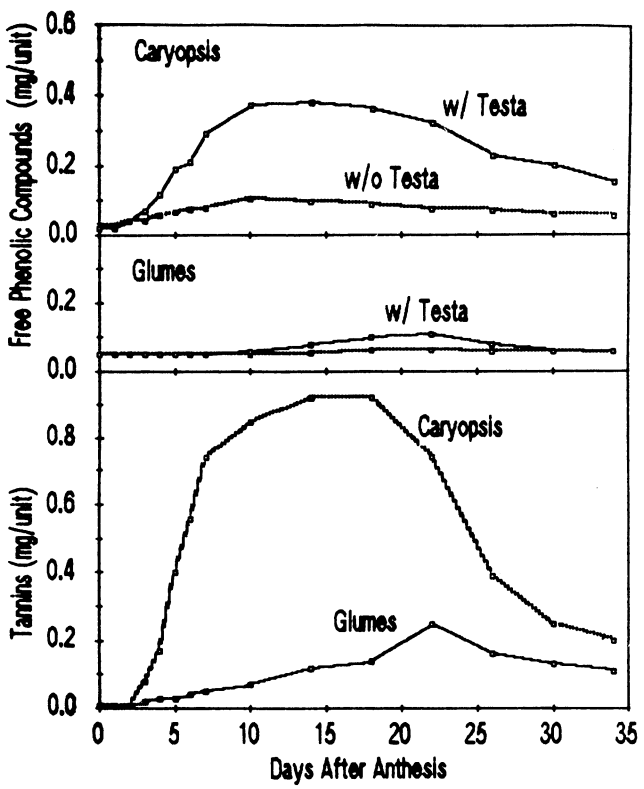

Fig. 2. Effect of sorghums with a pigmented testa on average levels of free phenolic compounds (FPC) and tannins in caryopsis and glume tissues from anthesis to combine harvest maturity: **top,** FPC in caryopses; **middle,** FPC in glumes (unlabeled curve = w/o testa); and, **bottom,** tannins in caryopses and glumes (of type II and III sorghums, only).

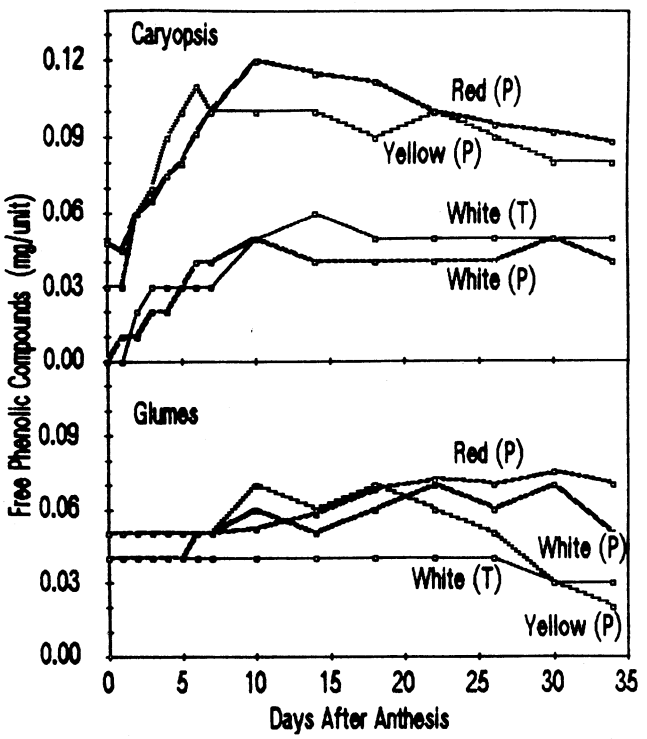

Fig. 3. Effect of pericarp and glume colors on FPC in caryopses (**top**) and glume tissues (**bottom**) of type I sorghums during development. Pericarp colors were red, yellow, and white, and glume colors were purple (**P**) or tan (**T**).

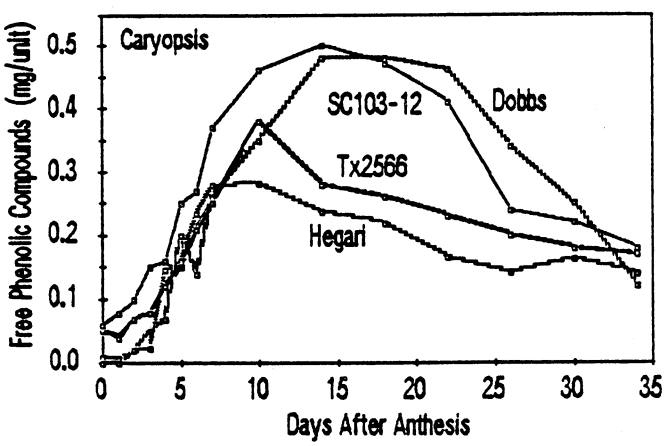

Fig. 4. Effect of pericarp color and spreader gene on FPC in caryopses of type II and III sorghums. (Kernel characteristics and genetics are presented in Table I.)

development. Maximum levels of FPC were observed between 18 and 26 DAA (Fig. 1). However, FPC levels in glumes were higher in cultivars with a pigmented testa than in other sorghums (Figs. 2–4), i.e., dominant B_1 and B_2 genes were associated with increased FPC in glumes of sorghum. The relationship of glume color with FPC was not evaluated because all type II and III cultivars had the same plant color (purple).

Tannin levels in caryopses and glumes of sorghum during development were associated with darker pericarp color and dominant *S* gene (Fig. 5). Caryopses with a dark pericarp color (red) generally contained more tannins than white caryopses. Presence of a dominant *S* gene increased tannin levels and lengthened the period of deposition of tannins in caryopses. However, at maturity, caryopses of all sorghums with a pigmented testa contained one-eighth to one-fourth of their maximum tannin levels. The solubility and chemical reactivity of tannins during development depend upon their rate of synthesis and their binding properties to cellular components. The marked decline of tannin levels is probably not due to degradation, but to their deposition into vacuoles (Price et al 1979, Earp 1984, Hahn et al 1984).

Tannins in glumes were observed in significant concentrations only for Tx2566 (red pericarp, type II) and Dobbs (white pericarp, type III). Hence, there is not sufficient data to compare the effects of pericarp and glume colors and *S* gene on tannins in glumes of sorghum. However, maximum levels of tannins (and FPC) in glumes were observed at physiological maturity. Thus, tannins were present in caryopses and glumes of sorghums with a pigmented testa and they varied markedly during maturation.

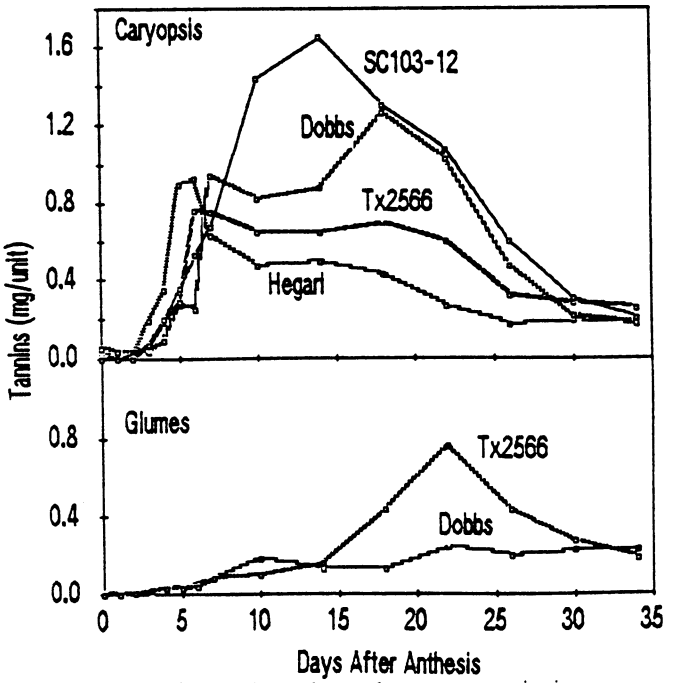

Fig. 5. Effect of pericarp color and spreader gene on tannins in caryopses (**top**) and glume tissues (**bottom**) of type II and III sorghums. (Kernel characteristics and genetics are presented in Table I.)

Biological Activity of Phenolic Compounds

Sorghums in this study varied in weathering and midge resistance. Caryopsis deterioration (weathering) during development can be caused by fungal invasion of immature caryopses (Castor and Frederiksen 1980). Less weathering (less mold, discoloration, or deterioration) was observed in caryopses that had an early increase in FPC levels compared to other sorghums. Further characterization of these phenolic compounds by high-performance liquid chromatography will provide correlations of weathering resistance with individual phenolic acids (Poe et al, unpublished). Corneous endosperm texture and more epicuticular wax also contribute to increased weathering resistance (Glueck and Rooney 1980).

Sorghums resistant and susceptible to midges (an insect) were grown in a separate field. Midges oviposit in sorghum spikelets at anthesis, and the larvae consume plant tissues and nutrients during maturation. The midge-resistant cultivar (RTx2767) contained more FPC, and FPC increased more rapidly in the immature caryopsis than in the susceptible cultivar (RTx7000) (Teetes 1985). Cultivar Tx2566, also midge resistant, has a pigmented testa and more phenolic compounds; however, FPC did not correlate with midge resistance in other type II and III cultivars. Correlations of midge resistance with phenolic acids in caryopsis during development is under investigation.

CONCLUSIONS

The Folin-Ciocalteu and acidic-vanillin methods effectively quantitated FPC and tannins, respectively, in caryopses and glumes of sorghum during development. Caryopses (and glumes) of sorghums with a pigmented testa and dominant spreader gene contained more FPC and tannins than other sorghums. Stage of development affected FPC and tannins in caryopses and glumes of all sorghums. Maximum levels were observed at immature stages of development (between 5 and 22 DAA depending upon tissue and cultivar). Tannin and FPC levels in mature caryopses were a fraction of their maximum level during development. Darker pericarp and glume colors resulted in higher FPC in caryopses and glumes of sorghums.

Caryopses of sorghums with weathering resistance contained more FPC (and tannins) than susceptible cultivars. Midge resistance in type I sorghums was also related to higher FPC levels. Apparently, extractable chemicals in developing caryopses (and spikelets) affect the growth of diseases and insects. Additional analyses of developing sorghum tissues will determine which phenolic acids and flavonoids are present and biologically important for disease and insect resistance.

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