Patterns of Fructose, Glucose, and Sucrose Accumulation in Snap and Dry Bean (*Phaseolus vulgaris*) Pods

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Abstract. Sugars, including fructose, glucose, and sucrose, contribute significantly to the flavor and consumer acceptance of snap beans (*Phaseolus vulgaris* L.). Little is known regarding differences in sugar content among snap bean and dry bean cultivars and the patterns of sugar accumulation with increasing pod size. Alcohol-soluble sugar concentration of five snap bean cultivars and one dry bean cultivar planted in field trials was assayed throughout pod development over 2 years using high-performance liquid chromatography. Significant differences in sugar accumulation patterns and quantity were observed among cultivars. In general, fructose and glucose content decreased, whereas sucrose increased with increasing pod size in snap beans. In contrast, fructose and glucose amounts increased, whereas sucrose concentration remained unchanged with increasing pod size in the dry bean cultivar. No year-by-genotype interactions were observed for sugar accumulation patterns or sugar amount. Results indicate that sieve size No. 3 (7.34 to 8.33 mm) or No. 4 (8.33 to 9.52 mm) pods are suitable for detecting differences in sugar concentration among genotypes.

In vegetables, taste, more than price and appearance, has an important influence on consumer food choice and is a significant predictor of consumption (Glanz et al., 1998). Taste and aroma both involve chemical sensations and make up the primary components of flavor (Reineccius, 1994). In most fruits and vegetables, taste is usually associated with fewer compounds than the wide array of volatile organic compounds

associated with aroma (Whitfield and Last, 1991). In vegetables, sourness is associated with organic acids, bitterness is often the result of phenolic compounds, saltiness is attributable to sodium or potassium, and sweetness is the result of sugars, including fructose, glucose, and sucrose (Sims and Golaszewski, 2003).

Sugars not only affect the flavor and acceptance of vegetables, but they also alter the perception of flavor sensations associated with other organic compounds (Auerswald et al., 1999). Increasing the amount of sugar in tomato (*Solanum lycopersicum* L.) while maintaining the level of organic acids increases the perceived sweetness and increases preference (Malundo et al., 1995). In broccoli (*Brassica oleracea* L.), increases in sugar concentration have been suggested as a way to mask the bitter taste of sulfur-containing glucosinolates and promote consumption (Schonhof et al., 2004). In winter squash (*Cucurbita* spp.), consumer preference depends on the ratio of sugar to starch; varieties having higher sugar-to-starch ratios are considered sweeter and are preferred (Merrow and Hopp, 1961). In general, if sweetness is perceived in a vegetable, even mildly, it may be enough to encourage consumption (Dinehart et al., 2006). Sensory panelists, who preferred

dry bean (*Phaseolus vulgaris* L.) and edamame [*Glycine max* (L.) Merr.] varieties that were classified as sweet, used sweetness as a primary characteristic to differentiate among cultivars (Mkanda et al., 2007; Wszelaki et al., 2005).

Simple sugars are the primary natural sweetener in vegetables with the most widely distributed being the monosaccharides glucose and fructose and the disaccharide sucrose (Lopez-Hernandez et al., 1994). The perceived sweetness of a vegetable varies with many factors, including pH, solids content, molarity, the presence of other sweeteners, and the type of sweeteners (Hanover and White, 1993). At equal molarity, glucose is only 74% as sweet as sucrose to the human palate. In contrast, fructose is considered 17% sweeter than sucrose and is perceived by the human palate as the sweetest of all naturally occurring carbohydrates (Joesten et al., 2007).

Although all plant tissues contain simple sugars, developmental differences in tissues consumed as vegetables, e.g., immature ovaries, mature ovaries, inflorescence, roots, tubers, and leafy vegetables, affect sugar accumulations and ratios (Hounsborne et al., 2008; Lee et al., 1970). Regardless of the tissue type, sugar concentrations are cultivar-dependent and highly variable (Nunes, 2008).

The stage of maturity of tissue can affect sugar accumulation and composition in vegetables. In bell pepper (*Capsicum annuum* L.), as fruit matures from green to red, total sugar increases from 2.4% to 4.2% of fresh weight. Glucose, fructose, and sucrose accumulate rapidly between the green and turning phase. As peppers mature to the red phase, glucose and fructose continue to accumulate and sucrose rapidly disappears (Luning et al., 1994). In contrast, a significant increase in the amount of sucrose during late-stage maturity has been reported in muskmelon (*Cucumis melo* L.) (Bianco and Pratt, 1977; Hughes and Yamaguchi, 1983; Lester and Dunlap, 1985; McCollum et al., 1988; Villanueva et al., 2004).

Snap beans, which are consumed as immature ovaries, are a significant source of soluble fiber, carotenoids, flavonoids, and vitamins (Anderson and Bridges, 1988; Bureau and Bushway, 1986; Favell, 1998; Granado et al., 1992; Hertog et al., 1992; Judith and Vollendorf, 1993; U.S. Department of Agriculture, Agricultural Research Services, 2010). Many important aromatic compounds that contribute to the unique flavor of snap beans have been identified, including 1-octen-3-ol, *cis*-3-hexenol, and *trans*-2-hexenal (de Lumen et al., 1978). Although sweetness is generally not considered a quality attribute in snap beans, it has been reported that sensory panelists prefer cultivars considered sweeter in both dry beans and edamame (Mkanda et al., 2007; Wszelaki et al., 2005). In snap beans, variation in total sugar ranges from 0.6% to 5.2% of fresh weight with individual ranges for glucose, fructose, and sucrose of 0.23% to 1.38%, 0.25% to 1.78%, and 0.1% to 0.78% of fresh weight, respectively (Lee et al.,

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Table 1. Descriptions for six common bean genotypes, including origin and physical attributes.

Genotype	Gene pool ^{z,y}	Origin	Market class	Growth habit ^a	Pod		
					Description ^w	Length (cm) ^{v,u}	Width ratio ^{v,t}
Black Blue Lake Pole	Mesoamerican	Rodgers Brothers Co. (1941)	Fresh market snap	I	Straight, stringless	16.3	1.1
Eagle	Andean	Asgrow Seed Co. (1972)	Processing snap	D	Long, low fiber, large sieve 5 or larger	14.8	0.97
Ferrari	Mesoamerican	Bakker Brothers	Fresh market snap	D	Small sieve 4 or smaller	13.4	1.1
Hystyle	Andean	Harris Moran Seed Co. (1985)	Processing snap	D	Long, low fiber, large sieve 5 or larger	14.5	0.97
Puebla 152	Mesoamerican	Landrace from Mexico (1942)	Dry	I	Late maturing, fibrous, flat	11.6	1.8
Roma II	Andean	Rogers Brothers Co. (1979)	Fresh market snap	D	Flat, low fiber	13.9	2.3

^aPersonal communication, Professor James Myers, Oregon State University.

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^aGrowth habit: D = determinant, I = indeterminate.

^wSieve size No. 1 (less than 5.75 mm), No. 2 (5.75 to 7.34 mm), No. 3 (7.34 to 8.33 mm), No. 4 (8.33 to 9.52 mm), and No. 5 (9.52 to 10.71 mm).

^vPersonal communication, R.F. Anuar, Plant Breeding & Plant Genetics graduate student, University of Wisconsin–Madison.

^uMeasurement from pedicel to end of the spur on sieve size 4 pods. Sieve size 3 for ‘Ferrari’ and ‘Puebla 152’.

^tCalculated as: diameter of pod on suture/diameter of pod 90° off suture. Measurements taken on sieve size 4 pods. Measurements for ‘Ferrari’ and ‘Puebla 152’ taken on sieve size 3 pods.

1970; U.S. Department of Agriculture, Agricultural Research Services, 2010).

Prior studies characterizing the simple sugars of snap bean pods have generally focused on a single cultivar at a single developmental stage (Lee et al., 1970; Muir et al., 2009; Sánchez-Mata et al., 2002). In legume crops, including *Phaseolus vulgaris*, the process of simple sugar conversion and complex polysaccharide accumulation in the seed is well understood (Górecki et al., 2001). In contrast, the accumulation of simple sugars in immature ovaries of snap bean pods is not well understood. The objective of this study was to determine sugar content of snap and Roma market classes of green beans as well as a dry bean variety and to characterize the patterns of accumulation of fructose, glucose, and sucrose during bean pod development.

Materials and Methods

Plant material. A sample of six diverse common bean genotypes with differing culinary characteristics was evaluated in the summers of 2009 and 2010 (Table 1). ‘Hystyle’ was selected as a modern large sieve commercial processing cultivar. ‘Hystyle’ was contrasted to ‘Eagle’, a large sieve commercial processing cultivar developed in the 1970s. ‘Black Blue Lake Pole’ (‘BBLP’) and ‘Roma II’ were selected based on anecdotal perceptions of superior pod flavor. ‘Ferrari’, a small sieve cultivar, was selected to contrast with the large sieve classes, Eagle and Hystyle. To contrast the snap and Roma-type bean classes, the dry bean landrace ‘Puebla 152’ was selected.

Plant culture and sampling. Twenty seeds of each genotype were sown in 91-cm rows spaced 76 cm apart at the University of Wisconsin Agricultural Research Station at West Madison, WI, using a randomized complete block design. To facilitate timely harvesting of pods of varying maturity, replicates were planted ≈1 week apart each year. A replicate consisted of all cultivars and is considered a complete block. In 2009, replicates were planted on 26 June and 3 July and

Table 2. Analysis of variance and means comparison among pods of six common bean genotypes sampled at sieve size no. 3 (7.34 to 8.33 mm).

Source ^z	df	Means square (mg·g ⁻¹ dry wt)		
		Fructose	Glucose	Sucrose
Year (Y)	1	41.9	448.7**	77.9*
Replication [Y]	2	47.8	17.2	0.5
Genotype (G)	3	765.7***	1071.4***	33.7*
Y × G	3	30.1	40.6	1.8
Error	6	21.0	14.0	6.5
Year		Means ± SD (mg·g ⁻¹ dry wt)		
2009		62.4 ± 13.6	27.6 ± 13.6	3.7 ± 2.6
2010		65.7 ± 15.4	38.2 ± 15.6	8.1 ± 3.9
Genotype				
BBLP ^y		67.9 ± 4.2	36.2 ± 4.8	3.2 ± 3.1
Eagle		73.3 ± 4.6	42.4 ± 6.6	6.0 ± 3.8
Hystyle		71.4 ± 6.5	44.3 ± 12.3	4.5 ± 2.9
Ferrari		43.6 ± 5.9	8.9 ± 3.2	9.9 ± 2.7
Puebla 152 ^x		61.8 ± 31.0	24.8 ± 14.1	3.6 ± 3.5
Roma II ^x		51.2 ± 2.8	32.3 ± 4.9	11.1 ± 2.4
LSD _{0.05} ^w		30.1	14.9	5.2

^zAnalysis of variance performed on sieve size No. 3 (7.34 to 8.33 mm) pods. Measurements taken 90° off the suture.

^yBBLP = ‘Black Blue Lake Pole’.

^x2009 data lost. Means and sds are for 2010 data only.

^wLSD based on analysis of variance for cultivars with data in both years.

*, **, ***Significance at $P \leq 0.05$, 0.01, or 0.001, respectively.

LSD = least significant difference.

2010 plantings of the replicates occurred on 25 June and 3 July. In 2009, ‘Puebla 152’ and ‘Roma II’ were lost as a result of poor germination. Standard cultural practices were followed (Bussan et al., 2012). The field was hand-weeded through harvest.

The stage of maturity of tissue is known to affect sugar accumulation and composition in vegetables (Bianco and Pratt, 1977; Hughes and Yamaguchi, 1983; Lester and Dunlap, 1985; McCollum et al., 1988; Villanueva et al., 2004). Measuring snap bean pod maturity using days after flowering or seed size as indirect criteria is problematic among the snap and dry bean cultivars used in this experiment as a result of different rates of pod and seed development. In addition, small-diameter pods do not have measurable seeds. To provide a consumer-based evaluation of sugar content relative to pod maturity, pods corresponding to sieve sizes No. 1 (less

than 5.75 mm), No. 2 (5.75 to 7.34 mm), No. 3 (7.34 to 8.33 mm), No. 4 (8.33 to 9.52 mm), and No. 5 (9.52 to 10.71 mm) were harvested (Quintana et al., 1996; Robinson et al., 1963). All measurements were done 90° off the suture at the center of the pod. A sample of five pods for each sieve size was harvested from each plot at random and bulked. All pods were harvested in the early morning and immediately placed in a cooler containing ice. Before freeze-drying, pods were stored at –80 °C.

Soluble sugar extraction. A standard soluble sugar extraction procedure was followed (Bethke et al., 2009). Samples were lyophilized in a VirTis Freezemobile 25 (Virtis Co., Inc., Gardiner, NY) and ground to a fine powder in an industrial paint shaker with metal beads. Alcohol-soluble solids from 0.1 g of powdered sample were extracted twice for 24 h each using 5.0 mL of 80% ethanol at 60 °C.

Pooled extracts were brought up to a total volume of 10 mL with additional 80% ethanol. Extract samples of 1.0 or 1.5 mL were dried under vacuum without heating and resuspended in 1 mL ultrapure water. Resuspended samples were passed through a previously washed (5 mL methanol followed by 5 mL water) Sep-Pak C18 cartridge (Waters Associated, Inc., Milford, MA). Samples were then filtered through a 0.2- μ m Millipore membrane (Corning Inc., Corning, NY).

Samples (10 μ L) were analyzed by high-performance liquid chromatography (HPLC) using a Shimadzu Prominence system with Shimadzu refractive index detector and a 300 $\times$ 7.8-mm Rezex ROA-organic acid column (Phenomenex, Torrance, CA) with 0.004% HPLC-grade formic acid (pH 3.30 $\pm$ 0.02) (Sigma-Aldrich, St. Louis, MO) in water as the mobile phase at a flow rate of 0.59 mL $\cdot$ min $^{-1}$. Peaks were identified and quantified based on retention times and peak area relative to authentic standards. Standards were prepared at 0, 1, and 2 mM of fructose, glucose, and sucrose. Standards measurements were performed every 20 runs and values were averaged at each concentration level to determine the slope of the standard curve. Peaks for sucrose, glucose, and fructose were easily separated from additional peaks in the sample and concentrations were calculated based of the standard curve.

Statistical analysis. Data were analyzed using the statistical package JMP 8.0.1 (SAS Institute Inc., Cary, NC). Analysis of variance was performed on individual genotypes. Year and sieve size were treated as fixed variables. Orthogonal contrasts were used to determine the best regression fit for each genotype and sugar. In addition, analysis of variance was performed on individual sugars to compare genotype means at sieve size No. 3. In general, because no sieve size-by-year interaction was observed for genotypes sampled over both years, means used to compare genotypes were calculated using all replicates. Additionally, because genotype ranks remained unchanged over years, genotypes with data only collected in 2010 as a result of loss in 2009 were compared with genotypes with data in both years. Because of optimal market size and discriminating ability, sieve size No. 3 pods were used to compare mean sugar concentrations for glucose, fructose, and sucrose among genotypes.

Results and Discussion

Higher glucose and sucrose concentrations were observed in 2010 compared with 2009 (Table 2). Fructose concentration was not significantly different between years (Table 2). Cooler temperatures characterized the summer of 2009 with July 2009 being the coldest July on record and the seasonal growing degree-days lagging behind the 30-year average (Wisconsin State Climatology Office, 2011). The cooler temperatures of 2009 may have resulted in reduced sugar translocation between the leaves and pods (Whittle, 1964).

Significant differences among genotypes were observed for fructose, glucose, and sucrose concentrations (Table 2). Among the snap beans, the cultivars with potential for large pod diameter, 'BBLP', 'Eagle', and 'Hystyle', had higher mean fructose and glucose concentrations compared with smaller sieve and flat-pod cultivars Ferrari and Roma II, respectively (Table 2). In contrast, the highest sucrose concentrations were observed in the small sieve cultivar Ferrari and the flat-podded cultivar Roma II. Fructose and glucose concentrations were 10 to 20 times higher than sucrose in pods of all genotypes except the dry bean landrace 'Puebla 152'.

No significant genotype-by-year interactions were observed for fructose, glucose, or sucrose (Table 2). Differences in sugar concentration among genotypes were not associated with Andean or Mesoamerican origin (Tables 1 and 2).

In general, an inverse relationship between fructose and glucose concentration, compared with sucrose concentration, was observed for all genotypes (Fig. 1). A significant non-linear response for fructose and glucose, declining after sieve size No. 4, was observed in the snap bean cultivar BBLP (Fig. 1; Table 3). The pattern of fructose and glucose accumulation in all other snap bean cultivars, e.g., Eagle,

Fig. 1. Changes in the concentration of sucrose, glucose, and fructose with increasing pod diameter in six common bean genotypes. Sieve sizes 1, 2, 3, 4, and 5 correspond to diameters of less than 5.75 mm, 5.75 mm to 7.34 mm, 7.34 mm to 8.33 mm, 8.33 mm to 9.52 mm, and 9.52 mm to 10.71 mm, respectively. Solid lines are for illustration only and connect symbols that represent sugar concentration at each sieve size for individual replicates.

Table 3. Analysis of variance for sugar concentration changes during pod development in six common bean genotypes: (A) fructose, (B) glucose, (C) sucrose.

		BBLP	Eagle	Hystyle	Ferrari	Puebla 152 ^z	Roma II ^z
A		Fructose					
Source	df	Means square concn (mg·g ⁻¹ dry wt)					
Year (Y)	1	378.9*	116.1	788.2**	191.9	—	—
Replication [Y]	2	383.4*	43.2	63.6	171.4	65.5 ^y	72.4 ^y
Sieve (S)	4	1039.4***	1226.4***	592.5***	1138.6**	317.4	191.9 ^x
Linear	1	46.0	1800.9***	377.9*	1808.7**	1092.0	308.4
Quadratic	1	3711.8***	—	—	—	3.3	75.5
S × Y	4	147.3	256.6**	166.8*	39.5	—	—
Error	8	59.0	26.6 ^w	33.5 ^w	42.6 ^v	325.6 ^v	58.6 ^x
Year means							
	2009	53.8	64.0	51.4	58.2	—	—
	2010	60.8	70.7	65.4	67.8	69.1	62.1
B		Glucose					
Source	df	Means square concn (mg·g ⁻¹ dry wt)					
Year (Y)	1	377.4**	202.2***	579.5***	131.4*	—	—
Replication [Y]	2	28.5	128.0**	115.7**	36.5	51.0 ^y	157.9 ^y
Sieve (S)	4	295.3**	400.6***	210.3***	117.8** ^u	56.3	128.5 ^x
Linear	1	4.5	685.0***	175.9**	201.8**	194.2	187.3
Quadratic	1	1014.0***	—	—	—	0.01	69.7
S × Y	4	27.1	32.9*	33.3	11.5 ^u	—	—
Error	8	24.3	6.4 ^w	9.7 ^w	6.5 ^v	52.1 ^v	37.1 ^x
Year means							
	2009	24.7	33.8	27.2	10.7	—	—
	2010	38.3	45.5	44.7	19.6	27.5	41.6
C		Sucrose					
Source	df	Means square concn (mg·g ⁻¹ dry wt)					
Year (Y)	1	8.2	13.4**	31.4**	0.0	—	—
Replication [Y]	2	16.2	2.1	12.6**	1.3	22.2 ^y	3.5 ^y
Sieve (S)	4	123.1**	86.9***	121.1***	53.4** ^u	0.9	26.9 ^x
Linear	1	334.0***	288.7***	40.3***	98.0***	3.1	43.8 ^t
Quadratic	1	—	—	—	—	0.00	10.1
S × Y	4	29.8	2.7	18.5**	11.6 ^u	—	—
Error	8	10.3	0.8 ^w	1.2 ^w	1.0 ^v	1.3 ^v	3.7 ^x
Year means							
	2009	5.5	4.0	4.8	5.3	—	—
	2010	6.3	9.0	7.7	6.2	3.9	8.7

*, **, ***Significance at $P \leq 0.05$, 0.01, or 0.001, respectively.

^zData only collected during 2010.

^ydf = 1.

^xdf = 2.

^wdf = 7.

^vdf = 4.

^tdf = 2.

^u $P \leq 0.075$.

BBLP = 'Black Blue Lake Pole'.

Hystyle, Ferrari, and Roma II, was similar to that observed in 'BBLP' (Fig. 1); however, the best-fit regression for fructose and glucose was linear (Table 3). In all snap bean cultivars, fructose and glucose concentration decreased with increasing sieve size (Fig. 1). In contrast to the snap bean cultivars, a significant linear increase in fructose and glucose concentration with increasing pod diameter was observed in the dry bean landrace 'Puebla 152' (Fig. 1; Table 3). Although these data are from 1 year only, in other cultivars sampled in both years, patterns of sugar accumulation were, in general, the same between years (data not shown) and cultivars did not change rank between years. These observations suggest that the replicated data for 'Puebla 152' in 2010 can be considered when making comparisons among cultivars.

In contrast to the monosaccharides, the disaccharide sucrose increased in 'BBLP',

'Eagle', 'Hystyle', 'Ferrari', and 'Roma II' with increasing pod diameter (Fig. 1). Unlike the snap beans, no significant change in sucrose concentration was observed with increasing pod diameter in the dry bean 'Puebla 152' (Fig. 1; Table 3). Significant sieve size-by-year interactions were observed in cultivars Eagle and Hystyle for fructose, in 'Eagle' for glucose, and in 'Ferrari' and 'Hystyle' for sucrose; however, the interactions were not the result of a change in rank (data not shown).

Sucrose transported into the bean pod through the phloem is the primary source of carbon and metabolic energy during development (Weber et al., 1997). During the early stages of development, pods undergo rapid dry weight accumulation. During this period, activity of acid invertase peaks, which breaks sucrose into the monomers fructose and glucose (Sturm, 1999). When snap bean pods

reach intermediate stages of growth (≈ 10 to 14 d post-anthesis), acid invertase activity rapidly decreases (Sung et al., 1994). The patterns observed in sugar development in the snap bean cultivars, e.g., BBLP, Eagle, Ferrari, Hystyle, and Roma II, are consistent with the pattern of acid invertase activity (Sung et al., 1994). During early stages of pod development, sucrose concentrations remain low as acid invertase actively cleaves the disaccharide into fructose and glucose. As rapid dry weight accumulation begins, the monosaccharides are used for cell growth and respiration more rapidly than they are produced and concentrations begin to decrease. Acid invertase activity decreases in intermediate stages of snap bean pod development resulting in a decrease of available fructose and glucose. Simultaneously, as acid invertase activity decreases, sucrose concentration increases as assimilate is transported through the phloem and produced in the photosynthetic pod (Crookston et al., 1974; Sung et al., 1994). The rapid decline of fructose and glucose and the simultaneous increase in sucrose in the snap bean cultivars at large pod diameters likely corresponds to the rapid decrease in acid invertase activity reported by Sung et al. (1994), suggesting that acid invertase may be the primary enzyme responsible for available monosaccharides in snap beans.

The contrasting pattern of sugar development in the dry bean landrace 'Puebla 152' compared with snap bean cultivars suggests that the amount or activity of acid invertase may differ between these market classes. The increase in fructose and glucose concentration at late stages of pod development suggests that either acid invertase remains active or another sucrose-cleaving enzyme replaces the activity of acid invertase, e.g., sucrose synthase or sucrose phosphate synthase. Because sucrose concentration remained constant with increasing sieve size in the dry bean, whereas fructose and glucose concentrations increased, it is likely that an active process of either assimilate transport through the phloem or internal photosynthetic production of sucrose is occurring in the developing pod of the dry bean landrace 'Puebla 152'.

Although neither snap beans nor dry beans are traditionally thought of as a sweet dessert vegetable, the significant difference in sugar concentrations among genotypes and among sieve sizes within genotypes suggests that both cultivar and stage of pod development affect the taste of snap beans. Because the presence and concentrations of sugars often alter the perception of flavor, including the perceived taste associated with organic compounds, any significant increase or decrease in sugar concentration may change the taste and, ultimately, the consumer preference for a particular snap bean pod. The differences among cultivars suggest that genetic variation in both patterns and concentration of sugars might be exploited to develop cultivars with increased amounts of sugars and enhanced consumer demand.

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