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RESEARCH

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ABSTRACT

Although heterosis is well established in grain and forage sorghum [*Sorghum bicolor* (L.) Moench], reports of heterosis in sweet sorghum are limited to results from grain sorghum × sweet sorghum hybrids. Recent development of cytoplasmic male-sterile sweet sorghum lines allows creation of sweet sorghum hybrids for research and industry. Male sterility may also affect allocation of photosynthate to plant parts, creating the potential to increase sugar content in stems by eliminating seed as a sink. The objectives of this study were to compare performance of A_3 cytoplasmic male-sterile lines and A_3 cytoplasmic male-sterile hybrids to fertile B_3 counterparts and to each other. A_3 cytoplasmic male-sterile 'Dale', 'Wray', 'Sugar Drip', and N100 were crossed in all combinations to their male-fertile counterparts, resulting in 20 genotypes including the male-fertile lines. The 20 genotypes were grown in a randomized complete block in 2004 and 2005 at Lexington, KY. Male-sterile hybrids and lines had higher brix than male-fertile lines. Hybrids produced greater stalk yield due to taller plants with greater stem diameter. Juice fraction and juice composition remained relatively unchanged. Only six hybrids showed positive heterosis for brix. The greater juice yield and higher sugar content of selected hybrids such as A_3 N100 × Dale could produce more total syrup or ethanol than current pure-line sweet sorghum varieties.

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Abbreviations: GCA, general combining ability; SCA, specific combining ability.

Sorghum [*Sorghum bicolor* (L.) Moench] is primarily a self-pollinated species with a low but measurable frequency of outcrossing (Shertz and Dalton, 1980; Pedersen et al., 1998). Sorghum exhibits hybrid vigor, and >95% of sorghum varieties grown for grain in the United States are F_1 hybrid varieties (Axtell et al., 1999). Hybrids provide a 20 to 60% grain yield advantage (Axtell et al., 1999). While most sorghum is grown in the United States for grain or for forage, sorghum also exists as sweet sorghum types. These types have juicy stems with high sugar concentration. Instead of maximizing translocation of photosynthate into grain, sweet sorghum accumulates large amounts of sugar in stem parenchyma from anthesis until physiological maturity. In the United States, sweet sorghum has historically been and is currently used for syrup production. However, interest in sweet sorghum as a feedstock for ethanol production is increasing (Rooney et al., 2007). Unlike hybrid grain sorghum, current U.S. sweet sorghum varieties are pure-line varieties.

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Table 1. Pedigrees and synonyms for 12 sweet sorghum male-sterile hybrids and their male-sterile and fertile pure-line parents (Pedersen and Toy, 1997).

Pedigree	Synonym
A_3N151 × 'Wray'	A_3 'Dale' × Wray
A_3N151 × 'Sugar Drip'	A_3 Dale × Sugar Drip
A_3N151 × N100	A_3 Dale × N100
A_3N151	A_3 Dale
Dale	Dale
A_3N153 × Dale	A_3 Wray × Dale
A_3N153 × Sugar Drip	A_3 Wray × Sugar Drip
A_3N153 × N100	A_3 Wray × N100
A_3N153	A_3 Wray
Wray	Wray
A_3N154 × Dale	A_3 Sugar Drip × Dale
A_3N154 × Wray	A_3 Sugar Drip × Wray
A_3N154 × N100	A_3 Sugar Drip × N100
A_3N154	A_3 Sugar Drip
Sugar Drip	Sugar Drip
A_3N159 × Dale	A_3 N100 × Dale
A_3N159 × Wray	A_3 N100 × Wray
A_3N159 × Sugar Drip	A_3 N100 × Sugar Drip
A_3N159	A_3 N100
N100	N100

Heterosis in sorghum is expressed by earlier blooming, increased height, larger stems, greater production of grain and biomass, and larger panicle heads with a higher threshing percentage (Quinby, 1963). Earlier flowering and greater biomass from increased height and larger stems are all sought-after traits for sweet sorghum. In comparing 24 grain sorghum hybrids with their parents, 23 had higher grain yield; however, only 16 were taller, nine bloomed earlier, and just five had greater stalk diameter than the superior parent (Kirby and Atkins, 1968). There has been little research on heterosis in sweet sorghum, although some information on characteristics valued in sweet sorghum production can be extracted from grain sorghum hybrid research. When short grain sorghum types were crossed with three tall genetically diverse sorghum accessions, midparent heterosis for grain yield was 80% with a general combining ability:specific combining ability (GCA:SCA) ratio of 3.56:1. Midparent heterosis for height was 38% with a GCA:SCA ratio of 5.88:1 (Niehaus and Pickett, 1966). The high GCA:SCA ratios suggest the likelihood of most hybrids exhibiting heterosis for these traits.

In a set of 28 grain sorghum × sweet sorghum hybrids, 11 hybrids showed significant high-parent heterosis for green stalk yield, only two showed high-parent heterosis for percent extractable juice, and none showed significant high-parent heterosis for juice brix (Selvi and Palanisamy, 1987). In a similar study involving hybrids from four grain sorghum A-lines crossed to 10 sweet sorghum restorer lines, overall heterosis was significant for plant height, green cane yield, and commercial cane sugar yield (Meshram et al., 2005).

Production of hybrid sorghum seed depends on cytoplasmic male sterility. Along with providing for economical seed production, male sterility may also affect the allocation of photosynthate to different plant parts. In rice (*Oryza sativa* L.), Lin and Lin (1994) concluded sterility changed the pattern of assimilate partitioning instead of reducing photosynthesis and that the stem was the most important alternative sink. Limiting seed production in sweet sorghum produces similar changes. Broadhead (1979) reported a 1-degree increase in brix following deheading before grain formation. Early deheading of sweet sorghum is recommended, as stem brix decreases from 19 degrees when deheaded at early seed stage to 15 degrees when deheaded in the hard-dough stage of seed development (Bitzer and Fox, 1994). Fortmeier and Schubert (1995) measured a constant soluble carbohydrate concentration in the stems of sweet sorghum male-sterile plants compared with a 20% decline from 34 d after anthesis until maturity in fertile sweet sorghum plants. Karper and Quinby (1963) reported an increase in stem sugar from 15 to 17% when male-sterile plants did not set seed vs. when cross-pollination and seed set was allowed. Although nonsignificant, Clark et al. (1984) reported total stem sugar at 109 when expressed as (sterile/fertile) × 100 for three sterile–fertile sorghum pairs. There is thus the potential for male sterility to positively influence brix in sweet sorghum stems.

Hybrid sorghum is produced using the A_1 cytoplasmic male-sterility system because growers and breeders are familiar with it, and numerous lines restore fertility in the A_1 system, making production of fertile hybrids possible. However, other cytoplasmic male-sterility systems are available, and one of them, A_3, could be particularly useful for production of male-sterile hybrids because few lines have been shown to restore fertility in A_3 cytoplasm (Bosques-Vega et al., 1989; Torres-Cardona et al., 1990).

The objectives of this study were to: (i) compare performance of A_3 cytoplasmic male-sterile lines to iso-cytoplasmic fertile B_3 lines, (ii) compare performance of A_3 cytoplasmic male-sterile hybrids with fertile B_3 versions of their parental lines, and (iii) compare performance of A_3 cytoplasmic male-sterile hybrids to A_3 cytoplasmic male-sterile versions of their parental lines.

MATERIALS AND METHODS

Development of Genetic Material

The sweet sorghum varieties 'Dale' (Broadhead and Coleman, 1973), 'Wray' (Broadhead et al., 1981), and 'Sugar Drip' (McCall et al., 1936), and the sweet sorghum germplasm N100 (Gorz et al., 1990) were previously male-sterilized in A_3 cytoplasm (Pedersen and Toy, 1997). The male-sterile versions of these lines were crossed in all combinations to the male-fertile versions of these same lines. All four male-fertile lines are male-sterility maintainers or B_3–lines to A_3 cytoplasm (none restore fertility), so the resulting hybrids were all male-sterile. Seed of the male-fertile lines were also produced, resulting in the 20 genotypes used in this study (Table 1).

Field Experiment

The experiment was grown on a Maury silt loam soil (fine, mixed, semiactive, mesic Typic Paleudalf) in 2004 and 2005 at the University of Kentucky research farm, Lexington, KY (lat 38° N). The 20 genotypes were planted in a randomized complete block design with four replications on 11 May both years. Plots were three rows wide, 6 m long, with 0.76-m row spacing. Planting rate was 12 seeds m^{-1}. Weeds were controlled using preplant-incorporated and postemergence-applied herbicides along with an herbicide safener seed treatment as recommended for grain sorghum in Kentucky (Martin and Green, 2003). Data were collected on the center of the three rows in a plot. Nitrogen was applied 30 d after planting at approximately growth stage 2 (Vanderlip, 1993) at 35 kg ha^{-1} as recommended for sweet sorghum for syrup (Bitzer, 1994). Before anthesis, as the flower head was emerging from the flag leaf, the flower head was bagged with a sorghum pollinating bag on 20 plants in the center row of the plot. Plants were bagged on all plots, both male-fertile and male-sterile entries, to maintain sterility and to base the comparison on bagged plants of both the sterile and fertile entries (Broadhead, 1979). All data except for lodging and disease ratings were collected from these bagged plants. Lodging and disease ratings were assigned on a whole-plot visual evaluation.

Data were collected for heading date (date on which the heads of 20 plants were bagged before pollen shed), and lodging (score 5 to 1, with 5 = no lodging to 1 = >75% plants lodged). Plots were harvested when the seeds on the male-fertile pure-line varieties were at the hard-dough stage, stage 8 (Vanderlip, 1993). Twelve plants were harvested per plot. Panicles were removed. Plant height (cutting point to point of panicle removal, cm) and stem diameter (fourth internode from the cutting point, mm) were measured on two of the 12 plants, and the mean of the two measurements was analyzed. Leaves were stripped from the plant, and the weight (kg) of 12 stems was recorded. The stripped stems were crushed with a three-roller horizontal sweet sorghum mill, and the juice was collected and weighed (kg). Juice brix (% sugar + starch) was measured with a handheld manual refractometer for brix range 0 to 30%. Sugar yield was calculated as kg juice × % brix.

Statistical Analysis

The data were analyzed by Proc MIXED of SAS (Statistical Analysis System version 9.1, SAS Institute, Cary, NC) with year, replication, and year(replication) included in the RANDOM statement and type and entry(type) included in the MODEL statement, with type being B_3 line, A_3 line, or hybrid. For each trait, homogeneity of error variance across years was tested using a Levene's test, and models with heterogeneous variance were fitted by inclusion of a REPEATED statement with GROUP = year. Least squares means were estimated and single degree of freedom comparisons made among LSMEANS by inclusion of the DIFF option. Comparisons were declared significant at $P = 0.05$. Single degree of freedom comparisons of B_3 lines vs. A_3 lines, A_3 hybrids vs. A_3 lines, and A_3 hybrids vs. B_3 lines are reported. High-parent heterosis (hybrid value – value of the superior parent [either A_3 female line or B_3 male line]) was calculated for each hybrid for each trait.

Table 2. Significance levels of genotype and year plus the year means for 12 sweet sorghum male-sterile hybrids and their male-sterile and fertile pure-line parents, 2004 and 2005, Lexington, KY.

Trait	Genotype	Year	2004	2005
Stalk yield (g $plant^{-1}$)	**	NS†	556	563
Juice yield (g $plant^{-1}$)	**	**	250	216
Brix (%)	**	**	19.1	19.5
Height (cm)	**	NS	251	259
Stem diameter (mm)	*	NS	20	20
Lodging (score)‡	*	*	4.6	3.5
Maturity (d from planting to heading)	**	**	88	92

*Significant at $P \leq 0.05$.

**Significant at $P \leq 0.01$.

†NS, not significant at $P \leq 0.05$.

‡Score 5 to 1: 5 = no lodging to 1 = >75% plants lodged.

RESULTS

The genotypes (12 male-sterile hybrids, 4 male-sterile lines, and 4 male-fertile lines) exhibited significant variation for every measured trait (Table 2). The environment in 2004 produced a greater juice yield than the environment in 2005. Conversely, brix was higher in 2005 than in 2004. While plant growth (stalk height and diameter) did not differ in the 2 yr, the plants lodged significantly more in 2005 than in 2004. Although planted on 11 May in each year, the sorghum flowered 4 d earlier in 2005.

The male-sterile hybrids produced 18% more biomass and 20% more juice than the male-sterile lines as well as 17% more biomass and 9% more juice than the fertile lines (Tables 3 and 4). Compared with the male-sterile lines, the greater biomass of the hybrids resulted from both 22-cm taller plants and 1.2-mm greater stalk diameter (Table 5). The juice yield and stalk yield did not differ significantly between the fertile and sterile parental lines. The juice from the male-sterile hybrids and lines had a higher brix than the juice from the fertile lines. The hybrids produced 20% more sugar yield than the male-sterile lines and 14% more than the fertile lines. The fertile lines lodged more than the sterile lines by 0.4 unit score due to both 16-cm taller plants and the increased leverage on the stem exerted by the seed weight of the fertile panicle. While the hybrids flowered at similar dates to the A_3 female lines, the A_3 female lines flowered 2.5 d earlier than the B_3 male lines, and the A_3 hybrids flowered 3.7 d earlier than the B_3 male lines.

High-parent heterosis was significant for at least one hybrid combination for each of the traits except lodging (Tables 3–5). Six of the 12 hybrids showed high-parent heterosis for stalk yield (Table 4). These six hybrids averaged 17% heterosis for stalk yield, with A_3Dale × N100 exhibiting 28% heterosis. No hybrids with A_3Sugar Drip as the female parent exhibited high-parent heterosis for stalk yield. Three hybrids showed significant high-parent heterosis for

Table 3. Comparisons of sugar traits of sweet sorghum B_3 lines, A_3 lines, and hybrids grown at Lexington, KY, in 2004 and 2005.

Group or line	Juice yield		Juice brix		Sugar yield		Differences between groups or lines†			
	Mean‡	High-parent heterosis§	Mean‡	High-parent heterosis	Mean‡	High-parent heterosis	Comparison	Juice yield	Juice brix	Sugar yield
	g plant^{-1}		%		g plant^{-1}			g plant^{-1}	%	g plant^{-1}
B_3 lines	220		19.1		42		B_3 lines–A_3 lines	14	–0.5*	2
A_3 lines	206		19.6		40		Hybrids–A_3 lines	40*	–0.1	8*
Hybrids	246		19.5		48		Hybrids–B_3 lines	20*	0.4*	6*
A_3 'Dale' × 'Wray'	227	34*	20.0	–0.06	45	5*				
A_3 Dale × 'Sugar Drip'	261	23	19.4	–0.02	51	7*				
A_3 Dale × N100	242	55*	19.1	–0.05	46	10*				
A_3 Dale	186		19.8		36					
Dale	261		18.4		48		B_3 Dale–A_3 Dale	75*	–1.4*	12*
A_3 Wray × Dale	269	8	20.2	–0.03	54	6*				
A_3 Wray × Sugar Drip	238	0	19.5	–1.0	46	2				
A_3 Wray × N100	230	24	19.3	–1.2	44	2				
A_3 Wray	206		20.5		42					
Wray	193		20.7		40		B_3 Wray–A_3 Wray	–13	0.2	–2
A_3 Sugar Drip × Dale	258	–3	19.8	0.5	51	3				
A_3 Sugar Drip × Wray	219	–30	19.5	–1.1	43	–5				
A_3 Sugar Drip × N100	251	2	19.3	0.1	48	0				
A_3 Sugar Drip	249		19.3		48					
Sugar Drip	238		18.7		44		B_3 Sugar Drip–A_3 Sugar Drip	–11	–0.6	–4
A_3 N100 × Dale	266	5	19.7	0.7*	53	5*				
A_3 N100 × Wray	219	26	19.2	–1.5	42	2				
A_3 N100 × Sugar Drip	274	38*	19.2	0.2	52	8*				
A_3 N100	185		19.0		35					
N100	187		18.6		35		B_3 N100–A_3 N100	2	–0.4	0

*Significant at $P \leq 0.05$.

†Significance determined using a two-tailed *t* test of least squares means.

‡Least squares mean.

§Significance of high-parent heterosis was determined using a one-tailed *t* test of least squares means.

juice yield, while only the hybrid A_3N100 × Dale exhibited high-parent heterosis for juice brix (Table 3). Combining these two traits produced six hybrids exhibiting high-parent heterosis for sugar yield (Table 3). Mirroring stalk yield heterosis, these six hybrids averaged 16% heterosis for sugar yield, with A_3Dale × N100 exhibiting 28% heterosis.

DISCUSSION

Sorghum with >8% brix in the juice of the stem is generally defined as sweet sorghum. The stems have to be juicy (*d* recessive to *D*) instead of dry and sweet (*x* recessive to *X*) instead of nonsweet (Rooney, 2000). Forage sorghum also has sweet, juicy stems to increase palatability for livestock, but the growth habit is different from sweet sorghum used for syrup. Sweet sorghum varieties used for syrup are tall (approximately 2 m) with thick stems (approximately 15 mm), while forage sorghum is shorter with much finer stems. While some grain sorghum varieties (e.g., Tx623) have sweet, juicy stems, the grain sorghum varieties are shorter (usually having recessive alleles at three of the four *Dw* genes) than sweet sorghum varieties (having recessive alleles at two or one *Dw* genes). Sweet sorghum varieties also differ from grain sorghum in that they have two sinks for photosynthate, the seeds and the stems, while grain sorghum has been selected as having one primary sink for photosynthate, the grain. Most hybrid research involving sweet sorghum has utilized one grain sorghum parent, the female parent with cytoplasmic male sterility (e.g., ATx623; FAO, 1994).

The conversion of four sweet sorghum varieties to cytoplasmic male-sterile lines allowed this initial investigation into the hybrid vigor for sweet sorghum characteristics in an entirely sweet sorghum background. Sweet sorghum for syrup is grown primarily in the southeastern United States, although it extends north and west to Wisconsin, Iowa, and Minnesota, with up to 12,140 ha (30,000 acres) being grown for syrup production (National Sweet Sorghum Producers and Processors Association, 2009). Sweet sorghum for ethanol can be grown in diverse and widespread areas of the United States. Desirable attributes of sweet sorghum varieties used for syrup production include a high yield of medium to large stalks, low lodging, and a high percentage of extractable juice with high total soluble solids (brix) content, mostly sugars. These attributes will also be desirable for using sweet sorghum as a bioenergy crop for ethanol production.

Hybrids will be useful for increasing biomass yields of sweet sorghum (Table 4). Hybrids produced a greater stalk yield due to taller plants with greater stem diameter. This greater stalk yield translated into a greater juice amount even though there was no hybrid vigor for juice fraction. The greater juice yield and higher brix of the hybrids will

Table 4. Stalk yield and maturity of sweet sorghum B_3 lines, A_3 lines, and hybrids grown at Lexington, KY, in 2004 and 2005.

Group or line	Stalk yield		Maturity†		Differences between groups or lines‡		
	Mean§	High-parent heterosis¶	Mean§	High-parent heterosis	Comparison	Stalk yield	Maturity
	g plant^{-1}		d			g plant^{-1}	d
B_3 lines	508		93.0		B_3 lines–A_3 lines	7	2.5*
A_3 lines	501		90.5		Hybrids–A_3 lines	94*	–1.2
Hybrids	595		89.3		Hybrids– B_3 lines	87*	–3.7*
A_3 Dale × Wray	560	60	88.4	–5.6			
A_3 Dale × Sugar Drip	607	76*	94.0	–0.6			
A_3 Dale × N100	591	131*	88.5	–5.6			
A_3 Dale	460		94.0				
Dale	576		95.2		B_3 Dale–A_3 Dale	116*	1.1
A_3 Wray × Dale	643	67*	90.4	–4.8			
A_3 Wray × Sugar Drip	623	92*	89.8	–4.8			
A_3 Wray × N100	526	27	86.8	–3.2			
A_3 Wray	499		87.2				
Wray	500		92.4		B_3 Wray–A_3 Wray	1	5.2*
A_3 Sugar Drip × Dale	618	42	95.0	0.2			
A_3 Sugar Drip × Wray	584	19	86.4	–7.7			
A_3 Sugar Drip × N100	580	15	88.0	–6.0			
A_3 Sugar Drip	565		94.1				
Sugar Drip	531		94.6		B_3 Sugar Drip–A_3 Sugar Drip	–34	0.5
A_3 N100 × Dale	661	85*	90.5	–4.7			
A_3 N100 × Wray	543	43	85.2	–7.1			
A_3 N100 × Sugar Drip	599	67*	88.8	–5.8			
A_3 N100	480		86.7				
N100	426		90.0		B_3 N100–A_3 N100	–54	3.2*

*Significant at $P \leq 0.05$.

†Days from planting to heading.

‡Significance determined using a two-tailed *t* test of least squares means.

§Least squares mean.

¶Significance of high-parent heterosis was determined using a one-tailed *t* test of least squares means.

produce more total syrup or ethanol than current pure-line sweet sorghum varieties, represented by the B_3 lines in this study (Table 3). These results from hybrid varieties have also been seen in crosses between sweet, juicy grain sorghum and sweet sorghum. For example, compared with the best performing sweet sorghum pure-line variety the Chinese hybrid Shennong No. 2 (ATx623 × 'Roma') produced 4% more biomass per hectare with no change in juice fraction or brix (FAO, 1994). Similarly Selvi and Palanisamy (1987) reported 19 of 28 grain sorghum × sweet sorghum hybrids with positive high-parent heterosis for stalk yield. For brix, however, six hybrids showed positive heterosis while 22 of the 28 hybrids showed negative heterosis. Heterosis manifests itself as greater growth and biomass production, but the juice fraction and juice composition remain relatively unchanged.

A notable spin-off of the basic research on sweet sorghum heterosis described above was the release of a male-sterile sweet sorghum hybrid for use in syrup production. Based on the high-parent heterosis exhibited by several of the hybrids in this experiment, in 2006 we conducted further agronomic tests of A_3 Wray × Dale, A_3 Sugar Drip × Dale, A_3 N100 × Dale, and A_3 N100 × Sugar Drip at three Kentucky locations using A_3 Dale as a check. Bagging of panicles was unnecessary since no entries produced fertile pollen. Combined across five environments in 2004, 2005, and 2006, A_3 N100 × Dale and A_3 Sugar Drip × Dale produced 24% more stalk and juice weight with equal brix, juice percentage, and lodging compared with A_3 Dale. A_3 N100 × Dale flowered 5 d earlier than A_3 Dale and A_3 Sugar Drip × Dale. In 2007 the Kentucky Agricultural Experiment Station, cooperating with the USDA at the University of Nebraska, released A_3 N100 × Dale as the male-sterile hybrid variety KN-Morris. This hybrid is intended for sweet sorghum syrup production in the primary syrup production region centered in Kentucky. It is recognized that male-sterile condition of this hybrid increases its susceptibility to sorghum ergot caused by *Claviceps africana* Frederikson, Mantle & De Milliano (Bandyopadhyay et al., 1998), but occurrence of this pathogen has not yet been documented in this region. The name KN-Morris highlights the cooperative development of the hybrid between Kentucky (K) and Nebraska (N) and recognizes Dr. Morris Bitzer, the long-term executive secretary of the National Sweet Sorghum Producers and Processors Association, a sweet sorghum production expert, and a tireless promoter of the sweet sorghum syrup industry.

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Table 5. Stalk height, diameter, and lodging of sweet sorghum B_3 lines, A_3 lines, and hybrids grown at Lexington, KY in 2004 and 2005.

Group or line	Stalk height		Stalk diameter		Lodging†		Differences between groups or lines‡			
	Mean§	High-parent heterosis¶	Mean§	High-parent heterosis	Mean§	High-parent heterosis	Comparison	Stalk height	Stalk diam.	Lodging
	cm		mm		score			cm	mm	score
B_3 lines	255		19.7		3.9		B_3 lines–A_3 lines	16*	0.5	–0.4*
A_3 lines	239		19.2		4.3		Hybrids–A_3 lines	22*	1.2*	–0.2
Hybrids	261		20.4		4.1		Hybrids–B_3 lines	6	0.7	0.2
A_3 'Dale' × 'Wray'	275	2	18.4	–1.5	3.5	–0.8				
A_3 Dale × 'Sugar Drip'	258	0	19.9	–0.7	4.1	0.2				
A_3 Dale × N100	242	0	21.6	3.0*	3.9	–0.2				
A_3 Dale	242		18.6		3.8					
Dale	278		20.1		3.3		B_3 Dale–A_3 Dale	36*	1.5	–0.5
A_3 Wray × Dale	283	5	20.3	0.2	3.4	–1.0				
A_3 Wray × Sugar Drip	277	14	20.8	0.2	4.1	–0.3				
A_3 Wray × N100	261	–2	18.9	–0.8	4.3	–0.1				
A_3 Wray	263		19.8		4.4					
Wray	273		19.9		4.3		B_3 Wray–A_3 Wray	10	0.2	0.1
A_3 Sugar Drip × Dale	266	–12	20.5	0.4	4.5	0.2				
A_3 Sugar Drip × Wray	264	–9	20.1	0.1	4.1	–0.2				
A_3 Sugar Drip × N100	248	1	21.1	2.2*	4.4	0.1				
A_3 Sugar Drip	247		18.9		4.3					
Sugar Drip	258		20.6		3.9		B_3 Sugar Drip–A_3 Sugar Drip	11	1.7	–0.4
A_3 N100 × Dale	257	–21*	21.4	1.3	3.9	–0.7				
A_3 N100 × Wray	260	–13	20.3	0.4	4.1	–0.5				
A_3 N100 × Sugar Drip	241	–17	21.5	0.9	4.5	–0.1				
A_3 N100	205		19.7		4.6					
N100	212		18.2		4.1		B_3 N100–A_3 N100	7	–1.5	–0.5

*Significant at $P \leq 0.05$.

†Score 5 to 1: 5, no lodging to 1, >75% plants lodged.

‡Significance determined using a two-tailed *t* test of least squares means.

§Least squares mean.

¶Significance of high-parent heterosis was determined using a one-tailed *t* test of least squares means.

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