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Comparative Effects of the Sorghum *bmr*-6 and *bmr*-12 Genes: II. Grain Yield, Stover Yield, and Stover Quality in Grain Sorghum

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ABSTRACT

Nearly 3 million hectares of grain sorghum [*Sorghum bicolor* (L.) Moench] are harvested in the USA each year. It may be possible to add value to crop and animal systems by enhancing the digestibility of the stover residue by the use of brown midrib (bmr) genes if grain yields can be maintained. The objectives of this study were to evaluate the effect of *bmr*-6 and *bmr*-12 genes on grain yield of sorghum and to evaluate the effect of the bmr genes on stover yield and quality in these genetic backgrounds: 'Wheatland', 'Redlan', RTx430, Tx623, Tx630, Tx631, and the hybrid AWheatland × RTx430. Plant height, maturity, grain yield and test weight, stover neutral detergent fiber (NDF), acid detergent fiber (ADF), acid detergent lignin (ADL), and in vitro NDF digestibility (IVNDFD) were measured in split-plot experiments replicated four times in each of four environments with lines being whole-plots and genotypes being subplots. Brown midrib genes reduced grain yield and residue yield in the lines; however, yield reduction was not observed in the *bmr*-12 AWheatland × RTx430 hybrid. The *bmr*-12 near-isolines generally had lowest stover lignin content and highest fiber digestibility, *bmr*-6 was intermediate, and wild-type counterparts had highest lignin content and lowest fiber digestibility. When all data are considered, the *bmr*-12 gene appears superior to the *bmr*-6 gene in terms of potentially adding value to the stover of grain sorghum for use in crop/animal systems. The variable expression of *bmr*-12 and *bmr*-6 in different lines indicates that selection of compatible genetic backgrounds will be critical in determining the realized impact on value.

Maize (*Zea mays* L.) crop residues often serve as an economical feed for ruminant animals (Klopfenstein et al., 1987). Nearly 3 million hectares of grain sorghum are harvested in the USA each year (USDA NASS, 2004), yet little research effort has been invested in the enhancement of grazing value of grain sorghum stover residue. There is less digestible organic matter found in sorghum stover than maize stover (Irlbeck et al., 1991). The DM digestibility of sorghum stover, as well as the crude protein content, is low when compared with maize stover (Osafo et al., 1997). Subsequently, when given the choice, producers choose to graze maize stalks. However, in some parts of the U.S. environmental conditions are not conducive to growing maize. Therefore, enhancing the quality of grain sorghum stover may offer an opportunity to add value to the overall system when post grain harvest stover residue is used as a forage base for livestock.

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Chemical and genetic approaches have been employed to improve forage fiber digestibility by reducing the amount of lignin or the extent of lignin cross linked with cell wall carbohydrates. Brown midrib forage genotypes usually contain less lignin and may have altered lignin chemical composition (Bucholtz et al., 1980; Cherney et al., 1991; Vogel and Jung, 2001). Activities of two separate enzymes involved in lignin synthesis are reduced as the result of the bmr mutations *bmr*-6 (reduced cinnamyl alcohol dehydrogenase downregulation) (Bucholtz et al., 1980) and the allelic (Bittinger et al., 1981) *bmr*-12 and *bmr*-18 (reduced caffeic acid O-methyl transferase activity) (Bout and Vermerris, 2003). To date, genetic control of the lignification process through use of bmr genes has offered the most direct and productive approach to reducing lignin concentration and increasing digestibility of sorghums (Gerhardt et al., 1994).

The bmr phenotype is generally associated with reduced vigor and yield. Previous research in maize has demonstrated reductions of both the grain and stover yield (Lee and Brewbaker, 1984; Miller et al., 1983) of bmr maize compared with wild-type maize. Our research with near-isogenic forage sorghum demonstrated decreased average total DM yield in bmr forage lines (Oliver et al., 2005). However, in that study significant line × gene interactions were detected, with *bmr*-6 or *bmr*-12 near-isolines being equivalent in total biomass yield to their wild-type counterpart in three of the four grain sorghum genetic backgrounds studied.

In a previous forage sorghum study we reported increased fiber digestibility associated with mature *bmr*-6 and *bmr*-12 forage sorghum (Oliver et al., 2005). The effects of bmr genes on grain yield of grain sorghum, and the effect on quality of post grain harvest stover residue are unknown. It may be possible to add value to total crop/animal systems by enhancing the digestibility of the stover residue if grain yields can be maintained at acceptable levels. Therefore, the objectives of this study were to evaluate the impact of the *bmr*-6 and *bmr*-12 genes on the grain yield of grain sorghum and to evaluate impact of the bmr genes on the yield and quality of the post grain harvest stover residue.

MATERIALS AND METHODS

Except where methods differed from Oliver et al. (2005), only a brief description is provided for the reader's conve-

Abbreviations: ADF, acid detergent fiber; ADL, acid detergent lignin; bmr, brown midrib; DM, dry matter; IVNDFD, in vitro neutral detergent fiber digestibility; NDF, neutral detergent fiber.

nience. For detailed descriptions of all materials and methods used in this study, the reader is referred to Oliver et al. (2005).

Near-isogenic versions of six common grain sorghum lines (Wheatland, Redlan, RTx430, Tx623, Tx630, Tx631) were created by crossing each to N121 (Gorz et al., 1990), a *bmr*-6 source, and F220 or F324 (donated to our project by the late Robert Kalton), *bmr*-12 sources, followed by three or four backcrosses. Near-isogenic versions of the grain sorghum hybrid AWheatland × RTx430 were also produced following male-sterilization of the *bmr*-6 and *bmr*-12 Wheatland using the A_1 cytoplasmic male-sterility system. Field trials using the recurrent parents and their counterparts near-isogenic *bmr*-6 and *bmr*-12 lines, and the near-isogenic hybrids, were conducted in 2002 and 2003 at the University of Nebraska Field Laboratory, Ithaca, NE (Sharpsburg silty clay loam; fine, smectitic, mesic Typic Argiudoll), and Lincoln, NE [Kennebec silt loam (fine-silty, mixed, superactive mesic Cumulic Hapludoll)]. Nitrogen fertilizer was applied preplant at both locations at 157 kg ha^{-1}. Individual plots consisted of two 7.6-m rows spaced 76 cm apart. Each was seeded with a precision vacuum planter calibrated to deliver 240 seeds per plot. Material was planted 20 May 2002 and 21 May 2003 in Lincoln and 22 May 2002 and 2003 in Ithaca. No supplemental irrigation was applied at Lincoln. Five centimeters of supplemental irrigation was applied at Ithaca via overhead sprinklers on 24 and 28 June and 5 and 7 August in 2002. In 2003 2.5 cm of supplemental irrigation was applied on 24 July and 14 and 28 August, and 5 cm of supplemental irrigation was applied on 4 and 7 August. Chemical application for weed and insect control was as described in Oliver et al. (2005)

Days to flowering was recorded at 50% anthesis. Height was measured to the top of the mature panicle before harvest. Panicles were hand-harvested at maturity then residue was harvested using a commercial silage cutter modified for small plot use (Pedersen and Moore, 1995). Grain and residue in the Ithaca plots were harvested 18 October 2002 and 3 to 4 October 2003. Grain and stover residue were harvested at Lincoln 6 September 2002, and 2 October 2003.

Sample Collection and Analysis

Grain samples were air dried to uniform 14% moisture, threshed, weighed, and test weight determined using a small plot combine with automated weight and test weight functions as a stationary thresher. Stover residue samples were collected and oven dried (60°C), DM content determined, ground through a Wiley mill (1-mm screen; Arthur H. Thomas Co., Philadelphia, PA), and analyzed sequentially for NDF, ADF, and ADL using an ANKOM 200 fiber analyzer (ANKOM Tech. Corp., Fairport, NY) (Vogel et al., 1999). In vitro NDF digestion (IVNDFD) was performed using ANKOM rumen fermenters (Model No: Daisy II; ANKOM Tech. Corp., Fairport, NY).

Statistical Analysis

Experimental design was a split-plot replicated four times in each of four environments with lines being whole-plots and genotypes (wild type, *bmr*-6, and *bmr*-12) being subplots. The data were analyzed using the PROC MIXED procedure of SAS (1999). The model statement included line, gene, and the line × gene effects. Environments and replication were considered random. The REPEATED function of PROC MIXED was used to account for lack of homogeniety of variance among the environments. *F*-protected least significant differences were used to determine differences among lines and genes (SAS, 1999). In the hybrid grain sorghum experiment, line was not included in the model.

RESULTS AND DISCUSSION

There was a significant effect of the environment on the measured traits as expected, but because our objective was to determine the effects of the bmr genes across multiple environments and multiple genetic backgrounds, we accounted for environment and line in our model and report the pooled gene and gene × line means. Lodging was not observed in any of the bmr grain sorghum near-isolines or the bmr near-isogenic hybrids.

Grain Sorghum Lines

Brown midrib gene effects and gene × line effects were significant for maturity and height. Maturity of the *bmr*-12 near-isolines averaged 4 d later than the wild types and 3 d later than *bmr*-6 near-isolines (Table 1). In all genetic backgrounds, the *bmr*-12 near-isolines were later in maturity than the wild-type counterparts. The *bmr*-6 near-isolines were later maturing than Wheatland, Redlan, RTx430, and Tx630 wild-type counterparts, but earlier maturing than Tx623 and Tx631 wild-type counterparts. The *bmr*-6 near-isolines were consistently shorter than their *bmr*-12 or wild-type counterparts with a 9% average reduction in height. The *bmr*-12 near-isolines were equal in height to wild-type Wheatland, shorter than wild-type Tx623, Tx630, and Tx631, and taller than Redlan and RTx430 wild-type counterparts.

Line × gene interactions were not significant for grain yield. Wild-type lines averaged 6149 kg ha^{-1}, or 20% higher grain yield than their *bmr*-6 near-isoline counterparts (5135 kg ha^{-1}) and 24% more than their *bmr*-12 near-isogenic counterparts (4948 kg ha^{-1}). Individual wild-type lines yielded more than either of their bmr near-isogenic counterparts in all genetic backgrounds. These reductions in grain yield are consistent in magnitude with those observed in maize hybrids. Previous research demonstrated a decrease in grain yield due to a bmr gene in maize (Miller et al., 1983). More specifically, in 15 pairs of isogenic hybrids, the grain yield of bm_3 maize was 20% less than the wild type (Lee and Brewbaker, 1984). The *bmr*-6 near-isolines had significantly higher average grain yield than their *bmr*-12 counterparts.

Test weight of the grain was affected by the bmr genes with the wild type and their *bmr*-12 near-isoline counterparts being equivalent and averaging 731 kg m^{-3} and 735 kg m^{-3}, respectively. The *bmr*-6 near-isolines were less dense, averaging 723 kg m^{-3}. Line × gene interactions were significant. Test weights were equivalent for wild-type Wheatland, Redlan, RTx430, and Tx630 and their near-isogenic *bmr*-6 counterparts. In Wheatland, Redlan, RTx430, and Tx623 the *bmr*-12 near-isolines were denser than the wild-type counterparts. In Tx630 and Tx631, the wild type had higher test weight than the *bmr*-12 near-isoline counterparts. Although differences ($P \leq 0.05$) were statistically significant for grain test weight, the differences were of little

Table 1. Average and individual effect of brown midrib (bmr) genes on maturity, height, and grain traits in six grain sorghum lines.

		Wild type	*bmr*-6	*bmr*-12	SEM
Days to 50% anthesis (d)					
	Mean	71c†	72b	75a	3
	Wheatland	68b	70a	71a	3
	Redlan	72c	73b	75a	3
	RTx430	73c	74b	77a	3
	Tx623	69b	66c	73a	3
	Tx630	73b	77a	77a	3
	Tx631	74b	73c	79a	3
Height (cm)					
	Mean	123a	112b	124a	4
	Wheatland	101a	88b	101a	4
	Redlan	123b	119c	135a	4
	RTx430	125b	121c	137a	4
	Tx623	130a	116c	119b	4
	Tx630	130a	110c	125b	4
	Tx631	129a	121c	125b	4
Grain yield (kg ha^{-1})					
	Mean	6149a	5135b	4948c	474
	Wheatland	6068a	4860b	4498b	549
	Redlan	5922a	5715ab	5133b	553
	RTx430	6776a	5253b	4322b	549
	Tx623	6412a	5407b	6034ab	553
	Tx630	5323a	4448b	4393b	549
	Tx631	6395a	5141b	4815b	549
Grain test weight (kg m^{-3})					
	Mean	731a	723b	735a	22
	Wheatland	714b	723ab	730a	23
	Redlan	743b	741b	768a	23
	RTx430	724b	713b	740a	23
	Tx623	729b	702c	744a	23
	Tx630	731a	731a	714b	23
	Tx631	749a	727b	711b	23

† Means in rows with differing letters differ at $P = 0.05$ using an *F*-protected LSD.

practical consequence with all but one line × gene combination (Tx631 *bmr*-6) meeting standards for U.S. number 2 sorghum.

Following grain harvest, the *bmr*-12 near-isolines had the highest stover residue DM yields (6503 kg ha^{-1}), averaging 11% more stover residue DM than the wild type (5883 kg ha^{-1}) (Table 2). The *bmr*-6 near-isolines averaged 10% less stover residue DM yield (5284 kg ha^{-1}) than the wild type. Line × gene interactions were significant. In RTx430, stover residue DM yields ranked as above. In Wheatland, Tx623, and Tx631, *bmr*-12 near-isolines and their wild-type counterparts had equivalent stover residue DM yields and all had higher stover residue DM yields than their *bmr*-6 counterparts. In Tx630 and Redlan, the *bmr*-12 near-isoline had highest stover residue yield, and the *bmr*-6 near-isoline and wild type had equivalent stover residue yield.

The literature is mixed on the effect of the bmr trait on DM yield. Previous research in maize has indicated a similar relationship in stover yield in isogenic bm_3 and the wild-type counterpart (Weller et al., 1985). In isogenic sudangrass [*Sorghum* × *drummondii* (Steud.) Millsp. & Chase], *bmr*-6 isolines counterparts had up to a 30% reduction in yield compared with the wild type (Casler et al., 2003), partially attributable to reductions in ground cover and tiller number. Dry matter yield in maize was also found to be lower in isogenic bm_3 lines by Allen et al. (1997) and Gentinetta et al. (1990). Conversely, Singh et al. (2003) reports 11 various bmr genotypes had greater yield than nine wild-type nonisogenic sorghums. The *bmr*-12 near-isolines in our study consistently yielded equivalent or more stover residue DM than wild type or *bmr*-6 counterparts.

Line × gene interactions were significant for NDF concentration of grain sorghum stover residue. Wild-type Wheatland and Tx631 had significantly higher NDF concentration than their *bmr*-6 or *bmr*-12 counterparts, which were equivalent in NDF concentration. Wild-type Tx623 had significantly more NDF concentration than its *bmr*-6 near-isogenic counterparts and was equivalent in NDF concentration to its *bmr*-12 near-isogenic counterpart. In Tx630, the *bmr*-6 near-isoline had the highest NDF concentration. In Redlan and RTx430 no differences due to bmr genes were detected. Research by Thorstensson et al. (1992) also found wild-type sorghum to have higher NDF concentration when compared to its *bmr*-6 counterpart. The same study found no differences in the NDF concentration of *bmr*-18 and its normal isogenic counterpart. Other studies have not found a difference in the NDF concentration of bmr forage sorghums and conventional forage sorghums (Aydin et al., 1999; Ruiz et al., 1995). As in our previous forage sorghum study (Oliver et al., 2005), NDF concentration appears to be quite variable in various lines and line × bmr gene combinations.

Of perhaps greater importance in predicting animal response and formulating rations, stover residue ADF content was equivalent or greater for the wild-type near-isolines than the bmr counterparts in the grain sorghum lines in the current study. Averaged across lines, the wild type had highest ADF content (379 g kg^{-1}) with *bmr*-6 near-isolines intermediate (365 g kg^{-1}), and *bmr*-12 near-isolines having lowest ADF content (354 g kg^{-1}). In Wheatland, Redlan, and Tx623, *bmr*-12 near-isolines had lower ADF content than wild type and equivalent ADF content to *bmr*-6 counterparts. Tx630

Table 2. Average and individual effect of brown midrib (bmr) genes residue traits in six grain sorghum lines.

		Wild type	*bmr*-6	*bmr*-12	SEM
Residue yield (kg ha^{-1})					
	Mean	5883b†	5284c	6503a	196
	Wheatland	4587a	4046b	4475a	241
	Redlan	6254b	5890b	7903a	245
	RTx430	6474b	5314c	7632a	241
	Tx623	5882a	5079b	5855a	245
	Tx630	6102b	6178b	6834a	241
	Tx631	6002a	5196b	6322a	241
Residue NDF‡ (g kg^{-1})					
	Mean	616a	611b	610b	31
	Wheatland	642a	612b	617b	31
	Redlan	643	628	625	31
	RTx430	631	628	631	31
	Tx623	598a	571b	588ab	31
	Tx630	567b	621a	583b	31
	Tx631	635a	610b	617b	31
Residue ADF (g kg^{-1})					
	Mean	379a	365b	354c	6
	Wheatland	394a	364b	361b	9
	Redlan	401a	378b	374b	9
	RTx430	392	377	376	9
	Tx623	363a	343b	334b	9
	Tx630	339b	360a	330b	9
	Tx631	388a	367b	350c	9
Residue ADL (g kg^{-1})					
	Mean	91a	77b	67c	4
	Wheatland	100a	83b	73c	5
	Redlan	93a	78b	72b	5
	RTx430	86a	73b	67b	5
	Tx623	87a	78b	60c	5
	Tx630	90a	67b	65b	5
	Tx631	87a	81a	64b	5
Residue IVNDFD (g kg^{-1})					
	Mean	505c	526b	556a	12
	Wheatland	477c	523b	552a	15
	Redlan	467b	501a	498a	15
	RTx430	505b	516b	554a	15
	Tx623	531c	561b	590a	15
	Tx630	550b	536b	577a	15
	Tx631	499b	518b	567a	15

† Means in rows with differing letters differ at $P = 0.05$ using an *F*-protected LSD.
‡ NDF, neutral detergent fiber; ADF, acid detergent fiber; ADL, acid detergent lignin; IVNDFD, 30-h in vitro NDF digestibility.

bmr-6 had greater ADF content than its wild type and *bmr*-12 counterpart. Tx631 wild type had the highest ADF content, its *bmr*-6 counterpart intermediate, and its *bmr*-12 counterpart lowest ADF content. No differences in ADF content were attributable to bmr genes in RTx430. Previous research using nonisogenic forage sorghum has shown bmr genotypes to have reduced ADF concentration compared to conventional wild-type sorghum (Oliver et al., 2004) while other research has indicated similar ADF concentration among bmr and wild-type lines (Aydin et al., 1999). Initial research on the fiber content of sorghum has found it to vary greatly (Porter et al., 1978). We can surmise that the fiber content of sorghum stover residue varies greatly depending on the line as well as the genotype due to the significance of both the gene and lines.

The bmr genes are best known for their ability to reduce the amount of lignin in the stover portion of sorghum and maize. Line × gene interactions were not significant for ADL concentration of stover residue in the current study. The *bmr*-12 near-isolines had the lowest ADL concentration (67 g kg^{-1}) averaging 34% less ADL concentration than wild-type counterparts (91 g kg^{-1}) and 14% less than their *bmr*-6 counterparts (77 g kg^{-1}). These results concur with our previous research on forage hybrids (Oliver et al., 2004) and other previous research in sorghum and maize which showed a reduction in ADL concentration of bmr genotypes (Gerhardt et al., 1994; Lam et al., 1996; Miller et al., 1983; Thorstensson et al., 1992). Our results are unique, however, in comparing ADL concentration of mature-plant stover residue samples (grain fraction removed) of *bmr*-6 and *bmr*-12 near-isogenic pairs. The ADL concentration of the *bmr*-6 isolines averaged 15% higher than their *bmr*-12 counterparts, and ADL concentration of *bmr*-6 lines was intermediate to the ADL concentration of their wild type and *bmr*-12 near-isogenic counterparts.

The IVNDFD of the grain sorghum residue followed the inverse pattern as the ADL concentration. The IVNDFD of stover residue averaged across lines was 10% greater in *bmr*-12 near-isolines (556 g kg^{-1}) than in the wild-type counterparts (505 g kg^{-1}), and 6% greater than the *bmr*-6 counterparts (526 g kg^{-1}). IVNDFD line × gene effects were significant. In all the genetic backgrounds the *bmr*-12 near-isolines had IVNDFD equal to or greater than their *bmr*-6 or wild-type counterparts. In Wheatland and Tx623 the *bmr*-12 near-isolines had the highest IVNDFD, the *bmr*-6 intermediate, and wild type the lowest IVNDFD. In Redlan, no differences in IVNDFD were detected between *bmr*-6 and *bmr*-12 near-isolines, and the wild type was significantly less digestible. In Tx631, Tx630, and RTx430 the *bmr*-6 near-isolines and wild-type counterparts did not differ in IVNDFD and both had lower IVNDFD than their *bmr*-12 counterparts. These results are similar to previous studies in which bmr genotypes were shown to have increased IVDMD in sorghum silage (Akin et al., 1986; Cherney et al., 1986; Fritz et al., 1988; Porter et al., 1978). However, those prior studies did not directly compare effects bmr genes in multiple genetic backgrounds.

Grain Sorghum Hybrid

Gene effects were significant for all traits measured in the AWheatland × RTx430 grain sorghum bmr near-isogenic hybrids. The *bmr*-12 near-isogenic hybrid was 14 cm taller and 4 d later in maturity than the wild-type hybrid (Table 3). The *bmr*-6 near-isogenic hybrid was 8 cm shorter than the wild type and 1 d later in maturity. Grain test weight was highest in the *bmr*-12 near-isogenic hybrid, with the *bmr*-6 near-isogenic hybrid, and the wild type being equivalent.

There was no statistically significant difference ($P = 0.05$) in the grain yield of the *bmr*-12 near-isogenic hybrid (7549 kg ha^{-1}) and its wild-type counterpart (7629 kg ha^{-1}). Grain yield was reduced 11% in the *bmr*-6 near-isogenic hybrid (6826 kg ha^{-1}). Lee and Brewbaker (1984) stated the decrease in maize grain yield in bmr hybrids could be overcome by selection due to the significant genotype × hybrid interaction. Although our results are based on only one hybrid, these results suggest that in sorghum the effect of selective breeding and heterosis may overcome the grain yield-drag associated with bmr. It should be noted that the *bmr*-12 near-isogenic hybrid was 4 d later in maturity, and 14 cm taller than the wild-type hybrid. Increased days to maturity and height are both positively associated with grain yield, but it is doubtful that the minor changes noted in height and maturity overcame the yield reduction associated with *bmr*-12 in inbred sorghum lines. The equivalent grain yield of the AWheatland × RTx430 hybrid and its *bmr*-12 near-isogenic counterpart suggest that bmr grain sorghum hybrids can be developed with equivalent grain yield to wild-type grain sorghum hybrids.

The *bmr*-12 near-isogenic hybrid yielded 10% more stover residue DM (7039 kg ha^{-1}) than the wild type (6405 kg ha^{-1}). The *bmr*-6 near-isogenic hybrid yielded 13% less stover residue DM (5542 kg ha^{-1}) than the wild type. The *bmr*-12 and wild type near-isogenic hybrids had equivalent stover residue NDF concentration (628 g kg^{-1}, and 620 g kg^{-1}, respectively) and both had higher NDF concentration than the *bmr*-6 near-isogenic hybrid (603 g kg^{-1}). The *bmr*-6 near-isogenic hybrid had lowest stover residue ADF concentration (351 g kg^{-1}), and the *bmr*-12 and wild-type near-isogenic hybrids were equivalent in stover residue ADF content (379 g kg^{-1} and 382 g kg^{-1}, respectively). The *bmr*-12 hybrid had 33% less stover residue ADL (65 g kg^{-1}) than the wild type (96 g kg^{-1}) and 11% less ADL concentration than the *bmr*-6 near-isogenic hybrid (72 g kg^{-1}). The IVNDFD of the *bmr*-6 and *bmr*-12 near-isogenic hybrids were equivalent (544 g kg^{-1} and 537 g kg^{-1}, respectively), and 7 to 9% greater than the wild-type hybrid stover residue (501 g kg^{-1}).

Table 3. Average and individual effect of brown midrib (bmr) genes on grain and residue traits in the grain sorghum hybrid AWheatland × RTx430.

	Wild type	*bmr*-6	*bmr*-12	SEM
Days to 50% anthesis (d)	68c†	69b	72a	3
Height (cm)	123b	115c	137a	3
Grain yield (kg ha^{-1})	7629a	6826b	7549a	529
Grain test weight (kg m^{-3})	721b	716b	747a	13
Residue yield (kg ha^{-1})	6405b	5542c	7039a	372
Residue NDF‡ (g kg^{-1})	620a	603b	628a	3
Residue ADF (g kg^{-1})	382a	351b	379a	2
Residue ADL (g kg^{-1})	96a	72b	65c	6
Residue IVNDFD (g kg^{-1})	501b	544a	537a	12

† Means in rows with differing letters differ at $P = 0.05$ using an F-protected LSD.
‡ NDF, neutral detergent fiber; ADF, acid detergent fiber; ADL, acid detergent lignin; IVNDFD, 30-h in vitro NDF digestibility.

In conclusion, bmr genes have negative agronomic impact on grain yield and residue yield in grain sorghum lines. However, it appears that these negative impacts can be overcome by heterosis in sorghum as evidenced by the grain and residue yields of the AWheatland × RTx430 *bmr*-12 hybrid used in this study. Hanna et al. (1981) drew the conclusion that *bmr*-12 was the superior bmr gene in sorghum. Results from this study generally agree with that conclusion, but also demonstrate the variable expression of *bmr*-12 and *bmr*-6 in different genetic backgrounds. When all data are considered in aggregate, the *bmr*-12 gene appears superior to the *bmr*-6 gene in terms of potentially adding value to grain sorghum for use in grain production/animal forage systems.

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