



# Estimating the relative effects of the endosperm traits of waxy and high protein digestibility on yield in grain sorghum

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## ABSTRACT

Sorghum (*Sorghum bicolor* L. Moench) is an important crop that is widely grown in dry climates across the world. The grain is used for food, feed and industrial purposes and the quality of the grain influences the relative utility for each specific use. In sorghum grain, both the waxy endosperm and the high protein digestibility traits have the potential to significantly alter conversion efficiencies of sorghum in several applications including production of grain ethanol and brewing. There are concerns though, that these traits may confer a reduction in the agronomic and yield performance of lines and hybrids that possess them. The objective of this study was to assess the potential impact of both the waxy and the high digestibility traits on the yield of grain sorghum lines. From an F<sub>2</sub> breeding population segregating for both waxy and highly digestible endosperm, 100 F<sub>2:4</sub> lines were derived, with equal number in each of four categories: high digestible (HD), waxy (WX), HD and waxy (HD-WX), and normal. No selection for yield was practiced during the development of these lines. The lines and checks were evaluated in two environments in Texas. Across all environments, there was no significant difference between yields. In addition, analysis by genotype revealed that several WX, HD-WX, and HD lines were among the best yielding lines. These results imply that selection of high yielding WX and HD genotypes is possible, but a significant breeding emphasis on their development and selection is required to effectively identify those genotypes.

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## 1. Introduction

Sorghum (*Sorghum bicolor* L. Moench) is an important crop grown in arid and semi-arid regions of the world. The grain is used primarily for human consumption in Asian and African countries, while in the Americas and Australia it is commonly used for animal feed and, more recently, for ethanol production. Compared to maize (*Zea mays*), sorghum grain is similar in starch content, yet has lower fat and higher protein concentrations (Dowling et al., 2002; Gualtieri and Rapaccini, 1990). Another primary difference between maize and sorghum grain is that the protein and starch in sorghum is not as readily available for enzyme degradation in many processing systems (animal, human or industrial) (Spicer et al., 1982, 1983).

The reduced protein digestibility of normal sorghum endosperm is thought to be due largely to specific endosperm storage proteins called kafirins. Sorghum kafirins form a hydrophobic matrix of protein bodies surrounding the large starch granules within

the endosperm (Taylor et al., 1984; Chankrashekar and Kirliés, 1988). Kafirins are alcohol soluble prolamins that make up about 50–73% of the endosperm matrix by volume (Paulis and Wall, 1979; Hamaker et al., 1995). Kafirins storage proteins come in three types:  $\alpha$ -,  $\beta$ - and  $\gamma$ -kafirins. The  $\alpha$ -kafirins are highly soluble and easily digested, while the latter two are less soluble and are not easily digested because they form enzyme resistant structures. Oria et al. (2000) suggested that the lower digestibility of proteins in the sorghum endosperm is due to strong disulphide bonds formed by  $\beta$ - and  $\gamma$ -kafirins that produce an enzyme resistant structure on the periphery of the protein body. Since the highly digestible  $\alpha$ -kafirins are located in the interior, the peripheral enzyme resistant layer of  $\beta$ - and  $\gamma$ -kafirins negatively influences protein hydrolysis. During starch hydrolysis, the disulphide bonds in the protein matrix also limits the access of amylases to the starch granules (Ezeogu et al., 2008).

Genetic variation for starch and protein digestibility exists in sorghum. The genotype P850029 has a higher protein digestibility compared to other normal grain sorghum lines (Weaver et al., 1998). The increased digestibility is due to structural rearrangement of  $\beta$ - and  $\gamma$ -kafirins in the endosperm and a reduction in the total amount of  $\gamma$ -kafirins in the endosperm (Tesso et al.,

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2006). Genotypes that possess these modifications produce grain that is easier to digest in any application, ranging from animal feed to ethanol production (Nyannor et al., 2007). In addition to higher protein digestibility (HD), these lines also possess 60% higher lysine content (Weaver et al., 1998; Wu et al., 2010).

In addition to the effect of sorghum endosperm proteins on bioethanol fermentation and food and feed processing; starch content and composition also influence processing characteristics. Normal sorghum genotypes produce both amylopectin and amylose in a 3:1 ratio in the endosperm. Genotypes possessing variation in the proportion of these compounds exist. For example, “waxy” endosperm sorghum types do not produce amylose, and hence, result in an endosperm in which all of the starch is amylopectin (Karper, 1933). The waxy phenotype in sorghum is conditioned by a single gene in the recessive form, designated as *wx* (Melvin and Sieglinger, 1952), which results in the absence or inactivation of granule-bound starch synthase (GBSS). Two naturally occurring waxy alleles have been identified in sorghum. The waxy GBSS-allele, designated as *wx<sup>a</sup>*, has no GBSS present, while the other allele waxy GBSS+, designated as *wx<sup>b</sup>*, has an inactive GBSS present (Pedersen et al., 2005). From a processing and utilization standpoint, amylopectin starch lowers gelatinization temperatures. As a result, processing and hydrolysis requires less energy and time to complete (Wu et al., 2010). Interestingly, there were no positive or negative effects observed on the growth and development of animals raised on waxy sorghums versus non-waxy sorghums (Shelton et al., 2004).

In theory, combining the high digestible and waxy traits should yield grain sorghum that has an endosperm with reduced energy gelatinization requirements and improved enzymatic hydrolysis. These traits are valued in the ethanol industry as they reduce energy requirements, yield faster conversion and turnover, and increase profit margins. The addition of the high digestibility trait, which confers 60% higher lysine, improves the animal feed value of the dried distillers grain solubles (DDGS). What is not known, is whether combining the waxy grain trait and high lysine/digestibility grain traits will confer lower grain yield potential and increase susceptibility to grain weathering, both of which would limit the potential value of these two traits in combination.

The maize high lysine trait, referred to as quality protein maize (QPM), is conferred by the recessively inherited *opaque-2* (*o2*) allele. This trait has functional similarity to the HD trait found in sorghum, where the high lysine HD trait is thought to be due to a mutation in the prolamin storage protein  $\gamma$ -kafirin and a redistribution of amino acids pools from low lysine kafirins to higher lysine globulin storage proteins (Tesso et al., 2006). In maize endosperm, the most abundant storage proteins are zeins and  $\alpha$ -zeins in particular, both of which share the low lysine and tryptophan content of kafirin and other prolamins (Gibbons and Larkins, 1990). The *opaque-2* allele has been shown to encode a transcription factor regulator of zein expression (Schmidt et al., 1990). Similar to the HD trait in sorghum, the homozygous recessive form of *o2* results in a shift from a lower expression of low lysine zeins to an increased expression of naturally higher lysine globulin pools (Gibbons and Larkins, 1990). Studies have suggested that both the waxy and the QPM traits are linked to lower grain yields.

While no yield data has been reported for the HD trait of sorghum, lower yields have been reported for QPM versus wildtype maize. The dedicated efforts of the CIMMYT program to introduce high yield QPM maize provides a good example that the limiting factor in lower yield is not linkage drag or pleiotropy, but simply the need for a focused breeding effort (Krivanek et al., 2007; Vivek et al., 2008). Current results have demonstrated the grain yield competitiveness of QPM with the best normal maize cultivars (Bjarnason and Vasal, 1992; Pixley and Bjarnason, 1993).

Similarly, studies have reported reduced yield resulting from the waxy endosperm trait in several cultivated cereals. For instance, Rooney et al. (2005) reported a 17% reduction in yield between waxy and non-waxy sorghums derived from the same population. Other studies have reported similar results in sorghum (Tover et al., 1977) as well as wheat (Graybosch, 1998), maize (Ferguson, 2001) and barley (Oscarsson et al., 1998). In maize, the yield of waxy hybrids averages 95% of non-waxy hybrids. As such, waxy maize is only grown for specific food and industrial applications. The lower yields in waxy maize and sorghum are likely the product of several factors such as pleiotropy, potential genetic linkage, and because breeding efforts to improve the yield of waxy inbreds and hybrids have lagged behind the extensive efforts made in traditional maize and sorghum types. As an example, Rooney et al. (2005) did find several high-yielding waxy lines among the highest yielding non-waxy lines in the population. As such, it appears that the potential to enhance and improve the yield of the waxy endosperm sorghums exists similar to that observed in waxy maize. The objective of this study is to determine the relative effect on agronomic performance of the high digestible trait, both independently and in combination with the waxy endosperm trait.

## 2. Materials and methods

### 2.1. Parental lines and population development

A set of 100 F<sub>2:4</sub> derived recombinant inbred lines (RIL) was developed from an F<sub>2</sub> population of the cross between Tx2907/P850029. Tx2907 is a waxy endosperm sorghum parental line that was released from the Texas AgriLife Research sorghum-breeding program (Miller et al., 1996). Tx2907 has protein digestibility similar to wildtype sorghum lines since it is wildtype at the HD locus described below and thus has a protein digestibility that performs equivalent to flour of wildtype grain sorghum (Yan et al., 2011). The normal or wildtype protein digestibility of the waxy trait is based on our unreported phenotypic data comparisons between the waxy, HD, HD-*wx* and wildtype sorghum lines phenotyped in this study. P850029 is a sorghum line with normal (non-waxy) starch endosperm and high digestible protein (HD), which was developed at Purdue University from a population derived from P721Q (Weaver et al., 1998; Mohan, 1975).

To develop the RILs, 200 randomly chosen F<sub>2</sub> panicles were self-pollinated. From these, F<sub>2:3</sub> progeny were self-pollinated to produce the F<sub>2:4</sub> seed. Because the two parental lines do not segregate for major height (*Dw*) and maturity (*Ma*) genes, differences in maturity and/or height are limited to segregation in smaller effect genes. At the F<sub>4</sub> generation, all of the RILs were phenotyped for the high digestible and waxy traits. Lines homozygous for the high digestible trait were identified by visual observation and chemical analysis. Under visual observation, 25 seed from each RIL were halved and observed on a light box. Seed from lines with wildtype endosperm have a small oval floury center and flinty outer layer surrounding the floury center, while seed from lines with the high digestible endosperm (HD) have a completely floury endosperm (Fig. 1). For the chemical analysis verification of the HD trait, protein digestibility was measured using the in vitro pepsin digestibility assay of Mertz et al. (1984) was used as described in Yan et al. (2011).

Lines were screened for waxy endosperm using the iodine staining technique described by Pedersen et al. (2004). The seed from each entry was crushed and placed in each well of a 96 well plate. Water was added to each well, and the mixture was heated to 95 °C for 1 h. Later, after the plates were cooled, iodine stain solution was added to each well, and the wells were color scored after 60 s. The wildtype seed stained purple due to the presence of amylose, while the waxy lines stained reddish brown or magenta because of the presence of amylopectin.

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