

BREEDING, GENETICS, AND GENOMICS

Cotton Seed Size – What is the “Fuzz” all About?

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ABSTRACT

Breeding efforts to improve lint yields in cotton may have shifted photosynthate partitioning to fibers during seed development resulting in a reduction in seed size in modern cotton cultivars. While the textile industry is the main consumer of cotton, changes in seed quality including size and composition could negatively impact other sectors of the agriculture industry that utilize cotton raw materials other than fiber. There is evidence of smaller cotton seeds impacting germination and seedling vigor as well as a reduction in oil content as seed size decreases. Moreover, downstream sectors of the cotton industry such as gins, crushers, and feedlots have been trying to draw attention to the consequences of having extremely small seeds to their operations, such as reduced ginning efficiency, seedcoat fragments, challenges in the delinting and decortication process, changes in meal nutrition, etc. This review focuses on the impacts of pursuing ever-increasing lint percent in modern cotton cultivars at the expense of seed size and attempts to highlight some of the less-known concerns of downstream cotton industry sectors.

In plant ecology, germination, seedling establishment, and vegetation dynamics within a species are often connected to seed mass and seed size (Leishman and Westoby, 1994; Leishman et al., 2000; Moles and Westoby, 2006; Silvertown, 1981). In general, larger seeds are associated with higher nutrient availability to the embryo and, therefore, faster emergence, increased seedling vigor, survival and establishment, greater competitive advantage within a population, and higher probability of recovery after environmental stress (Dalling and Hubbell, 2002; Harper, 1977; Moles and Westoby, 2004; Muller-Landau, 2010; Westoby et al., 1992, 2002). Studies

on the role of seed size in germination and seedling vigor have shown that seed size can impact seedling establishment in different agricultural crops (Bockus and Shroyer, 1996; Boyd et al., 1971; Elliott et al., 2008; Kandasamy et al., 2020; Lafond and Baker, 1986; Snider et al., 2014). In grain crops, seed size is also a significant component of the seed yield and thus, can play an important role in the economic value of the commodity. Several authors, however, describe a tradeoff between seed size and the number of seeds, indicating that one compensates for the other, not altering the final yield (Egli, 1998; Sadras, 2007).

Cotton (*Gossypium* spp.), the subject of this review, is unique among major agricultural crops in which the maternal and filial tissues in the seed, both have economic value (Ruan, 2005). Cellulose-rich fibers produced by cells of the seed coat are the main natural fiber used in the textile industry, while the cotton seed embryo is rich in oil and protein making the seed valuable not only for extraction of oil for human consumption, but also to produce protein-rich meal for feedstock (Dowd, 2015). The lint is the main and most economically valuable product of cotton, accounting for more than 80% of the crop value (Liu et al., 2012). Therefore, increasing lint yield has been a primary focus of public and private cotton breeding programs throughout the years. The seed accounts for about 15% of the cotton crop revenue from products such as feed for ruminant animals, oil, linters, and hulls (Dowd, 2015; Liu et al., 2012; Pettigrew and Dowd, 2011). Post-harvest processes in cotton include ginning (the process of separating the seed from the fiber), delinting (the process of removing linter from the seed), spinning (the process of converting fibers into thread or yarn), and crushing (the process of pressing the seed to extract oil). The average ratio of seed to fiber in modern Upland (*G. hirsutum*) cotton cultivars was about 3:2 (Dowd, 2015; Liu et al., 2012). However, breeding efforts to improve lint yield may have inadvertently altered that ratio and the size of the cotton seed (Dowd et al., 2018). Small seeds may impact cotton in different stages of its production and post-production processes. This review covers the importance of cottonseed for other sectors of the agriculture industry beyond planting seed and speculates

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on the consequences of continued breeding pressure towards higher lint percent for potential improvement in fiber yield at the expense of seed size.

The Cotton Industry. Among approximately 50 species in the cotton genus (*Gossypium* L.), four have been domesticated from wild perennial plants to an annual crop (Brubaker et al., 1999; Lee and Fang, 2015; Wendel and Cronn, 2003). *Gossypium hirsutum* (also known as Upland cotton) is the most adapted, studied, and widely cultivated cotton species representing around 95% of the world’s cotton crop production (Lee and Fang, 2015; Smith and Cothren, 1999). For that reason, *G. hirsutum* will be the main species discussed in this review, unless otherwise stated. Cotton is the top textile commodity in the world (Wakelyn, 2006) and its seed has a relevant economic impact on the industry. The U.S. produced approximately 18 million bales of cotton in the 2021/22 marketing year (USDA, 2022a), with the whole industry accounting for more than \$21 billion in products and services annually (USDA, 2022b). The U.S. cottonseed value alone was \$1.3 billion in 2021 (USDA, 2022c).

Cottonseed Products. Cottonseed is used in a plethora of different sectors from the cattle and oil industry to the medical and automotive business. In 2021, the U.S. produced approximately 5.3 million tons of cottonseed, and almost half of that was sold to oil mills (USDA, 2022d). The remaining seed was distributed between feed, exports, planting seed, and other uses (USDA, 2022d). Whole cottonseed is a rich source of protein, fat, and fiber in feedstock, especially for dairy cattle. The oil industry crushes the seed to extract edible, high-quality oil for human consumption after which, the cottonseed meal can be used as a high protein supplement in animal feed (Pradyawong et al., 2018); the seed hull is used as a bulking agent in roughage to improve the digestibility of the meal (Dowd, 2015); and the linter (i.e., short, cellulose-rich fibers that remain attached to the seed coat after ginning) can be used for the production of medical pads and gauzes, upholstery fillers, cosmetics, pharmaceutical emulsions, industrial and automotive filters, laminates, toothpaste, rocket pro-

pellants and more (Dowd, 2015; NCPA, 2022). Table 1 shows all the raw materials derived from one metric ton of cottonseed and examples of their applications in various industries (Dowd, 2015; NCPA, 2022).

According to the 2021 World Markets and Trade report from USDA Foreign Agricultural Service (FAS), cottonseed ranks fifth in global oilseed production and consumption, and fourth in global protein meal consumption (USDA, 2021). Some speculate that with the advent of ultra-low gossypol cultivars, cottonseed has the potential to become one of the most important sources of plant protein (Liu et al., 2012), and could significantly contribute to meeting world protein consumption requirements in countries where malnutrition is prevalent (Kumar et al., 2021; Rathore et al., 2020).

Fiber versus Seed. Increased competition from the synthetic fiber industry has steered the cotton industry to pursue more efficient ways to produce cotton with higher fiber yields and fiber quality. Producing more lint fiber per acre by increasing resource use efficiency, for example, puts cotton in a good position to compete with other sources of fiber. A positive correlation between lint percentage and lint yield is well documented in the literature (Breux, 1954; Bridge et al., 1971; Campbell et al., 2011; Meredith Jr., 1971; Zeng and Meredith Jr, 2009), and improvements in lint percentage have been a focal point in many public and private breeding programs looking to improve lint yield (Culp and Harrell, 1975). However, lint percentage has been also reported to be negatively correlated with seed size (Campbell et al., 2011; Veeravelli, 2022). There is no doubt that improvements in lint percentages and lint yields of obsolete cultivars contributed to the rise of the modern cotton industry. Seed consequently became smaller, but within a reasonable range. The conundrum, nevertheless, arises when breeding programs, seeking ever higher fiber production, focus on lint percentage as the primary yield component without considering other traits, like seed size. That could lead to extreme results and unintended consequences that negatively impact other sectors that rely on cottonseed.

Table 1. Products derived from 1 metric ton of cottonseed

	Raw Materials	Derived Products
1 ton of cottonseed	~ 410 kg of meal	Feedstock protein supplement, bio-adhesive, fermentation media, fertilizers, etc.
	~ 245 kg of hulls	Bulking agent in roughage, growth media for mushrooms.
	~ 145 kg of crude oil	Frying/baking oil, snacks, salad dressings, shortenings, margarines, specialty soaps, lubricants, etc.
	~ 75 kg of linters	Medical pads and gauzes, upholstery fillers, industrial and automotive filters, cosmetics, etc.

In plant physiology, photosynthetic leaves are the primary carbon source responsible for the accumulation of starch, protein, oil, and cellulose in the seeds during the seed filling stage. In cotton, sucrose is transported from the leaves to maternal and filial tissues to be utilized in the development of fibers and synthesis of nutrients stored in the cotyledons (Ruan and Chourey, 2006). Therefore, during the development and maturation of the cotton boll, photosynthates are partitioned between seed and fiber (Kloth and Turley, 2010). Generally, for every 1 kg of fiber, the cotton plant produces approximately 1.6 kg of seed (Liu et al., 2012; Rathore et al., 2020). Throughout the years, selection pressure towards higher lint percentage has shifted photosynthate partitioning to fiber, increasing lint yields, and causing a reduction in seed size (Campbell et al., 2011; Kloth and Turley, 2010; Snider et al., 2016). As a result, the seed-to-lint ratio has been decreasing considerably over the years (Dowd et al., 2018; Main et al., 2013; Mitchell et al., 2007). Fig. 1 shows significant changes in seed-to-lint ratio documented in the past 45 years in commercial cotton cultivars across the U.S. based on data sourced from USDA Economic Research Service (USDA, 2022e) and USDA National Agricultural Statistics Service (USDA, 2022f) (Fig. 1).

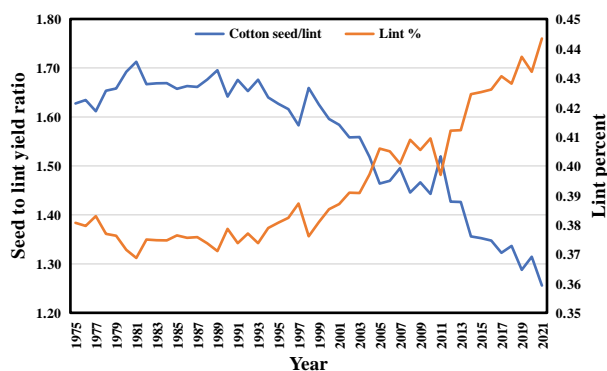


Figure 1. Historic seed to lint ratio (cotton seed to lint yield) from 1975 to 2021 (in blue, left Y axis) and lint percent (in orange, right Y axis).

The National Cotton Council (NCC) instituted a Cottonseed Quality Committee in 1994 calling on the breeding community to consider seed size during plant selections to attempt reverting the tendency of excessively smaller seeds in new varieties. The committee suggested a seed index equal to, or larger than 10 to breeding programs across the country (Bertrand et al., 2005; Herritt et al., 2020). The seed index, which is an indirect measure of the seed size, is the

weight in grams of 100 fuzzy (ginned, undelinted) cotton seeds (Groves and Bourland, 2010). Popular cotton commercial cultivars have reduced seed indices over the years (Bernard, 2003; Bertrand et al., 2005; Bridge et al., 1971; Dowd et al., 2018). As an example, Figure 2 represents a 10-year comparison of the seed index distribution by acreage of most planted cultivars in Texas. Estimated acreage of the top 10 Upland cotton cultivars planted in Texas in 2008 and 2018 (USDA, 2008, 2018) was crossed with those cultivars' seed indices collected by the cotton breeding program at the Texas A&M AgriLife Research in Lubbock in those specific years* (Dever et al., 2009, 2019). An average of seed indices collected in four locations (Lubbock, TX dryland and irrigated, and Lamesa, TX dryland and irrigated) was used. The top 10 most planted cultivars represented approximately 60% of the cotton acreage in Texas in both years and, consequently, reflect the main cultivars that reached downstream sectors of the cotton industry.

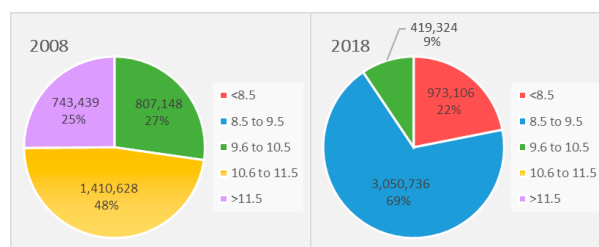


Figure 2. Seed index distribution by acreage of most planted cultivars in Texas in 2008 (left) and 2018 (right). Seed index data collected in four locations of the Texas A&M AgriLife Cotton Performance Tests. Figures show a significant shift in seed index values in acreages planted of the most popular cultivars in a 10-year period. *Seed index data from neighboring years (2007 or 2017) were used if cultivars were not planted in performance trials during 2008 or 2018.

Impacts of Seed Size. Good germination and vigorous seedling growth are paramount to establishing an early and uniform crop, which is essential in short-season agricultural regions (Lafond and Baker, 1986; Minton and Supak, 1980; Snider et al., 2016). While a correlation between final lint yield and early plant vigor has not been established in some studies (Liu et al., 2015; Snider et al., 2016), vigorous seedlings are more likely to withstand early season disease pressure and insect herbivory, outcompete weeds, maximize solar interception, and develop a larger, more adapted root system under dryland conditions (Cook and El-Zik, 1992; Liu et al., 2015; Snider and Oosterhuis, 2015). All these benefits could potentially

translate to a yield advantage, especially in environments under stress. As an example, Pettigrew and Meredith Jr. (2009) reported an increase in lint yield in larger cotton seeds due to higher seedling emergence. Wanjura et al. (1969) found that percent emergence at five days after planting correlated positively with lint yield. Lower-than-average germination and poor seedling vigor are often associated, among other factors, to small seeds (Kloth and Turley, 2010; Snider et al., 2014, 2016). In cotton, studies showed that seed size can predict seedling vigor (Liu et al., 2015; Snider et al., 2014, 2016) and a small seed could negatively impact crop establishment in regions where season length is limited and conditions at planting are often less than ideal.

As newer cotton cultivars reach the market, reports of post-harvest issues have also appeared (Zeng et al., 2022). Smaller seeds have reduced ginning efficiency causing equipment issues and loss of seed during the ginning process (Dowd et al., 2018; Kloth and Turley, 2010). Additionally, farmers often use cottonseed to offset ginning costs and in turn, ginners turn the seed into revenue by reselling it to feedlots and crushing plants (Dowd et al., 2018; Hudson, 1946). The reduced seed turnout in newer cultivars results in higher ginning costs to growers, possibly more seedcoat fragments, and limited revenue to ginners (Bechere et al., 2021).

Small seeds that pass through the gin ribs could be a source of lint contamination, affecting spinning performance (Bechere et al., 2021). The spacing between gin ribs is an important factor to consider when dealing with smaller cotton seed size. Commercial operators can often change gin saw thickness, but it is uncommon to change the rib gap (Funk et al., 2021). In the early 1990's, Barger and Garner (1991) published a study looking at three types of possible lint contamination: damaged seed fragments, seed chalazal cap detachment, and immature seed. They found that seeds smaller than 3.73 mm in diameter account for 73% of lint contamination. Although their study looked at immature seeds and we recognize that those seeds can be soft and easily crushed, we thought it would be interesting to measure the seed diameter of a few current commercial varieties. Two hundred fifty seeds were sampled from commercial bags of four popular cotton cultivars and measured the widest diameter of each seed (Figure 3). Out of 250 seeds, one variety had 4.4% seeds smaller than 3.73 mm, another had 6%, the other 9.6%, and the last 42%.

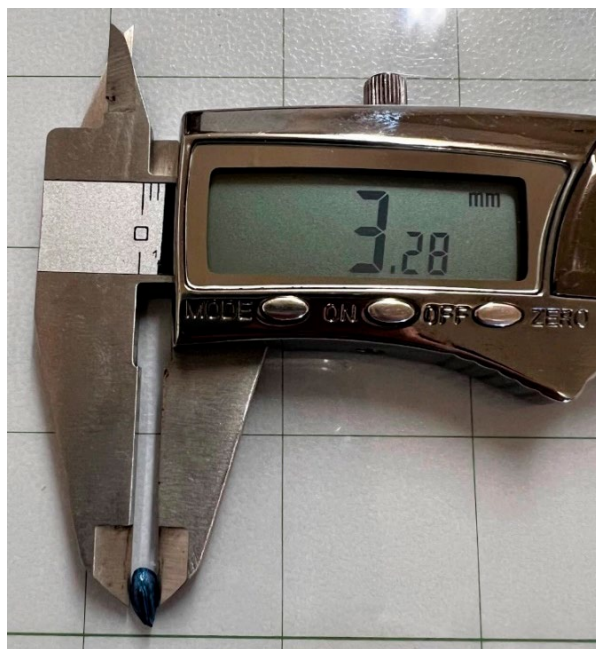


Figure 3. Measurement (mm) of seed diameter of a current commercial cultivar. A digital caliper was used to measure the widest diameter of 250 seeds sampled from commercial bags of four current and popular cotton cultivars.

Furthermore, Dowd et al. (2018) indicated that the change in compositional properties between seed and fiber due to selection pressure may have resulted in smaller seeds and weaker hulls. They reported complaints from ginners of an increase in seed and hull fragment fiber contamination. Although they have not observed, in their studies, significant changes in hull and kernel ratios, they reported a substantial decrease in seed indices and seed-to-fiber ratio when comparing old and current cotton cultivars.

Reductions in cottonseed size could also impact the cattle industry (Bernard, 2003; Bertrand et al., 2005; Mullenix and Stewart, 2021). Feed is responsible for more than 70% of a dairy's operating costs (USDA, 2018b). Whole cottonseed is a valuable protein supplement for ruminants and extensively used in dairy and beef cattle diets for being high in fat and fiber (Bertrand et al., 2005; Kellogg et al., 2001; Rogers et al., 2002; Smith et al., 1981; Stewart and Rossi, 2010). The unique combination of high protein, fat, and crude fiber in one supplement is especially beneficial to high-yielding dairy cows and those with reduced appetite due to stress (Coppock et al., 1987; Rogers et al., 2002). Cotton Incorporated (2010) reports that dairy cows consume more than 50% of the U.S. whole cottonseed annual production. Although studies failed to demonstrate a strong relationship

between seed size and protein content in cotton (Dowd et al., 2018; Hinze et al., 2015; Pahlavani et al., 2008), there are reports from the dairy community that smaller cottonseed affects meal nutrition. Bernard (2003) attributed changes in whole cottonseed nutrient composition to recent commercial varieties' smaller seeds. Bertrand et al. (2005) speculated that the decrease in energy content in whole cottonseed in the past 50 years coincided with the reduction of seed size. Moreover, they also indicated that cows fed with smaller seeds may have less exposure to mastication, affecting seed digestibility.

Crushers and oil mills often report losing small seeds to the waste bin during the delinting process and difficulties in the decortication (dehulling) process (Dowd et al., 2018). Furthermore, oil processors have indicated a decrease in oil percentage, reduction in ammonia content, and more hulls per ton in smaller seed cotton cultivars. To corroborate some of the oil industry complaints, researchers report a positive correlation between seed index and oil content in cotton (Hinze et al., 2015; Pahlavani et al., 2008; Veeravelli, 2022; Zeng et al., 2015). Snider et al. (2014) also indicate a positive relationship between oil content and germination and seedling vigor going back to the discussion about seed size and plant establishment. In a panel in the ginning section at the 2019 Belt-wide conferences ("Cotton Seed Size – for Better or Worse"), it was mentioned that cotton seed size could even impact transportation logistics, such as increases in the freight rate per ton of cottonseed transported due to lower seed weight per rail car.

In cotton economics and marketing, reports on lower seed grade, due to a reduction in seed size and oil content are available in the literature. The economic impact described in those reports varies. Kinard (1993) indicated a \$10-12 loss per ton of cottonseed due to lower oil content in small-seeded cultivars grown in the 1990s. In the same period, Elam (1995) showed a \$0.83 ton⁻¹ price change for each 1 g variation of seed index. According to Elam, however, seed index does not significantly affect cottonseed grade and price. An updated economic study using current commercial varieties seed index and marketing data is needed.

CONCLUSIONS

Fiber is the primary product of the cotton crop and the main natural fiber used by the textile industry worldwide. Emphasis on increasing lint yield and fiber

quality is, and should be, one of the leading objectives in a cotton breeding program. However, Cook (1908) noted that, "too persistent attention to a single character or standard often results in the neglect of other indispensable qualities whose importance may remain unconsidered until some serious deficiency is revealed". Cotton breeding programs that use lint percent as the main yield component in early selections may inadvertently over-decrease seed size in their germplasm pool (Veeravelli, 2022). The cotton industry is extensive and comprises numerous sectors that utilize cotton raw materials other than fiber. Extreme reduction of seed size may have a broader impact than one might think. Additionally, declines in plant vigor and delays in crop establishment caused by very small planting seed could be a major problem in short-season regions like West Texas, the largest cotton-producing region in the United States. This review attempts to highlight some of the less-known concerns of downstream cotton industry sectors about the current trend in cotton seed size. More studies on the effects of smaller seeds in different scenarios of the cotton production, processing and post-processing systems are certainly needed.

PROSPECTIVE

Although cotton has great potential as an oil and feed crop, advancements in genetic improvement of its seed have been challenging. First, cottonseed represents approximately 15% of the crop economic value and second, there is concern about trading-off fiber yield and quality. With the advancement of molecular techniques, genetic improvements of the cottonseed composition and nutritional value without compromising fiber have been explored (Wu et al., 2022). These same genome-based strategies could be applied to selection for seed size in a breeding population. As an example of a genetic resource that could be used for this purpose, Wang et al. (2022) recently sequenced a multiple-parent advanced-generation inter-cross (MAGIC) population and developed a mosaic genome map to investigate genetic components and interactions controlling fiber quality. As another example, our program is using divergent selection to develop lines with the intent to isolate the effects of seed size. If successful, resultant populations could be an excellent tool for genetic mapping studies. On another note, breeding approaches for improving lint yield without impacting seed size have been proposed (Zeng et al., 2022). They investigated different strate-

gies to improve lint yield by selections of within-boll yield components and found that the combination of lint percentage and lint weight per fiber was the most successful for lint yield improvement with no changes in seed size. Fiber will probably continue to be the most important product of the cotton crop. However, continuous improvement of fiber should not have to come at the expense of seed size.

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