Producing Quality Cotton by Conventional Breeding, Marker Assisted Selection, and Transgenic Methods

O. Lloyd May

ABSTRACT. New cotton seeds capable of producing fiber with the properties needed by yarn and textile industries in the process of technological advance are needed to maintain market share for Nature’s renewable fiber resource. Conventional breeding, marker-assisted selection, and transgenic technologies are possible strategies to achieve improved fiber properties. Breeding has a documented record of improving fiber length and strength to benefit ring yarn manufacture. Open-end yarn manufacturing is supplanting older ring spinning systems and is demanding improved fiber strength, along with finer fiber, and less short and immature fiber. Breeding can achieve these goals, but may be supplemented by marker-assisted selection and transgenic technologies. Marker assisted selection would have particular application to the simultaneous improvement of yield and fiber quality. For modification of fiber traits with narrow sense heritability of 0.5 or higher (0-1.0 scale), marker assisted selection would likely not result in significantly greater gains than phenotypic selection. Efforts to genetically engineer modified cotton fiber properties are underway with data from a few field trials now available. Experience to date suggests that breeding value for a transgenic trait can vary even by the individual plant. Therefore, transgenic breeding may require larger population sizes to allow for simultaneous selection for expression and agronomic traits. Cotton should continue to be the World’s primary renewable textile fiber if efforts to improve its fiber properties are continued. [Article copies available for a fee from The Haworth Document Delivery Service: 1-800-342-9678. E-mail address: getinfo@haworthpressinc.com <Website: http://www.haworthpressinc.com>]

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INTRODUCTION

The properties of cotton fiber that allow it to be used as a textile fiber are genetically controlled. The brief history of the organized modification of cotton fiber properties through breeding began with the development of tools to measure these properties, and the application of genetic analysis to crop plants. Traditional breeding has been very successful in modifying fiber length and strength, two important properties of cotton fiber that allow it to be spun into yarn. However, technological advances in yarn and textile manufacture, such as rotor yarn spinning and high output weaving and knit cloth manufacture, have increased demand for ever stronger cotton fiber. These market forces are thus, incentives for cotton geneticists to develop genotypes with improved fiber characteristics. The object of this paper is to review progress from traditional breeding for fiber properties and how new tools including molecular markers and transformation can be applied to accelerate fiber property improvement.

Most of the fiber properties that condition textile performance are thought to be conditioned by two or more loci, the combined individual effects and interaction of loci produce the phenotype—so called quantitatively inherited traits. Their manipulation through phenotypic selection is a slow and tedious process indeed (Meredith, 1984). Biotechnological approaches to crop improvement are thus, attractive, because of their potential to allow direct modification of the genotype, or to speed response to traditional breeding. Before examining topics such as molecular marker facilitated and transgenic breeding, it is instructive to review the brief history of cotton fiber quality improvement through organized breeding. From such data we can draw inference as to the suitability of fiber characteristics for marker assisted selection and transformation.

Fiber Property Modification by Traditional Breeding

The Hindu peoples of India are thought to be the foundation of the World's first cotton industry, spanning nearly four thousand years from about 2000 B.C. to the present. Cotton production in the British
colonies that would become the United States can be traced to beginnings in the Virginia colonies in 1607. Organized breeding efforts at improving cotton fiber quality in the USA were not initiated until the early 1900s. Several developments combined to spur progress in this area. The properties of fiber that contribute to textile performance became better defined (Moore, 1938). Instruments, such as the fibrograph and stelometer, providing non-subjective and relatively repeatable measurements of fiber length and strength, respectively, supplanted hand measurements (Hertel, 1940; Hertel, 1953). The definition and mandatory assignment of grade and staple designations beginning in 1923 to all cotton sold elevated the status of fiber quality (Ramey, 1980). Thereafter, the study of the genetics of fiber properties became a priority.

Long staple (Pima and Sea Island, *G. barbadense* L.) and medium staple upland (*G. hirsutum* L.) cotton both have been subjected to years of breeding to improve fiber properties (Niles and Feaster, 1984). In addition to having minor production compared with upland cotton, Pima type cotton fiber has rather specific uses for fine count yarns and textile products. This chapter will concentrate on upland cotton because of its extensive production, and wider use as a textile fiber.

Measures of fiber length have long been recognized as critical predictors of yarn strength and quality (Perkins, Ethridge, and Bragg, 1984). By its very nature, not all of the fibers in a sample of lint have the same length and thus, there exist several measures of fiber length distribution. Instrument measures of fiber length include the upper half mean, defined as the mean length of the longer 50% of the fiber by weight when measured by High Volume Instrument (HVI); and the 2.5% and 50% span lengths measured on the fibrograph, respectively defined as the length of the fiber beard spanned by the indicated percentage of the fibers in the sample. Other instruments such as the Suter-Webb array provide measures of fiber length distribution, but its time-consuming nature precludes evaluation of breeding material (Brown, 1938).

The heritability of fiber length tends to be at least moderate (Table 1), and when combined with generally low genotype × environment interaction relative to genetic variance, indicates that these traits are relatively amenable to modification through breeding (Pearson, 1944; Abouh-El-Fittouh, Rawlings, and Miller, 1969). Heritability takes val-
TABLE 1. Heritability of fiber length measurements.

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2. Upper-half-mean length. Lewis (1957).
3. 2.5% length. Al-Rawi and Kohel (1970).
4. 2.5% length. May and Green (1994).
5. 2.5% length. May and Green (1994).
6. 2.5% length. May and Green (1994).

ue between zero and one, with higher values indicating that more of the phenotypic differences among candidates for selection reflect the effects of genes. Values above about 0.5 then suggest that breeding progress can be expected. The growth environment does affect the expression of genes conditioning length, but generally, the effects of environment do not prevent the separation of genetic variance from phenotypic variance (Meredith, 1984). This concept is illustrated in heritability estimates that averaged about 59% from a survey of inheritance studies (Table 1); several of these studies document gains from mass selection for one or more length parameters (Bridge, Meredith, and Chism, 1971; Bridge and Meredith, 1983; Culp and Green, 1992; May, 1999; Sasser and Shane, 1996). However, current breeding emphasis on fiber length in medium staple upland cotton is not to make the fiber longer as measured by 2.5% span length or upper half mean, but to ameliorate variation in length. The reduced emphasis on longer fiber is associated with the move from ring spinning to more productive open end spinning systems whose yarn structure is less dependent on length of the fiber to produce a strong yarn (Deussen, 1992). Additionally, high length uniformity is desired by yarn and textile manufacturers because length uniformity is associated with less fiber waste, ends down during yarn manufacture, and better yarn quality (Behery, 1993). Indirect measures of fiber length uniformity include the length uniformity index (mean length/upper half mean length) and
the uniformity ratio (50% span length/2.5% span length). Compared with length measures, these uniformity parameters have received less attention from breeders. Consistent with the data from genetic studies of length measures, length uniformity ratio and index exhibit low genotype × environment interaction relative to genetic variance; genetic variance tends to be of the fixable type (May, 1999). However, use of measures of fiber length uniformity derived from ratios of length distribution (e.g., 50% span length/2.5% span length or mean length/upper half mean length), as selection criteria to ameliorate short fiber content may not be fruitful because the correlation between fiber length uniformity and a direct measure of short fiber content was found to be \(-0.08\) (Meredith, Sasser, and Rayburn, 1992).

From a historical perspective, cotton germplasm with long fiber length dominated the U.S. cotton belt prior to the introduction of the boll weevil (Anthonomus grandis Boh.) in the late 1800s (May and Lege, 1999). Thereafter, the boll weevil made production of long fibered cottons nearly impossible because of their late maturity, with the consequence that almost all of this class of germplasm was abandoned (Culp and Harrell, 1974). Early maturing cottons with generally reduced fiber length were adopted, because they could mature some portion of a crop before boll weevil predation ruined the latest set bolls. It is interesting that the industry response to this fiber was so negative, that selection for longer fiber combined with early maturity became an important breeding objective to maintain USA market share for raw fiber (May and Lege, 1999).

Bundle fiber strength is a key property of cotton fiber that allows it to be spun into yarn (Deussens, 1992). Yarn manufacturers today desire stronger fiber as they upgrade their spinning frames from ring to more productive open-end types (Faerber, 1995). The yarn structure of an open-end yarn when compared with that of a ring spun yarn relies less on fiber-to-fiber contact to hold together (Deussens, 1992). Fiber strength becomes more important in determining open-end yarn tenacity and textile products produced thereof as opposed to length uniformity for ring spinning. The genetic control of fiber strength has received considerable study, and can be summarized into a few key points. In populations with significant genetic variation, fiber strength tends to be moderately to highly heritable (average about 0.5) for selection units ranging from single plants to population bulks (Table 2). Genetic variance is mostly due to additive types, and genotype ×
TABLE 2. Heritability of fiber strength.

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1. Pressley measurement. Lewis (1957)

environment interactions are not of a magnitude to preclude identification of the segregates with best strength (Meredith, 1984). The greatest limitation to increasing fiber strength by conventional breeding is its inverse relationship with fiber yield (Culp, 1992). It is relatively straightforward to derive high strength segregates; the challenge lies in producing a high strength product with enough yield to satisfy producers.

Since cotton fiber is processed into yarn as a bundle of fibers, the fineness or mass per unit length affects the size and quality of yarn that can be produced (Faerber and Deussen, 1994). Finer fiber is desired for optimum efficiency and strength of rotor spun yarns. Breeders have generally not emphasized increased fineness because of its association with reduced yield (Meredith, 1984). Micronaire reading is sometimes used as a measure of fiber fineness. Micronaire reading is obtained from the micronaire instrument as the resistance to airflow of a 3.25g plug of fibers (Faerber and Deussen, 1994). Because a single measurement of airflow is taken, micronaire reading reflects the combined effects of fiber perimeter and maturity (Hake et al., 1990). Fine fiber has a low micronaire reading relative to that of more coarse fiber, because collectively fine fiber offers more resistance to airflow in the micronaire instrument. Fine fiber may result from genetically small perimeter or from incomplete secondary wall thickening. The recent
development of the Advanced Fiber Information System (AFIS) offers breeders separate estimates of fineness and maturity, that may allow these properties to become more important breeding objectives (Bragg and Shofner, 1993; Hossein, Baldwin, and Khan, 1994). The Arealo-meter is another instrument that provides separate estimates of fineness and maturity (Hertel and Craven, 1951). Fiber perimeter and other related characteristics are generally moderately heritable (Table 3) and could be modified through breeding if they become important goals.

**Fiber Properties Important to a Textile Industry Undergoing a Technological Revolution**

Today’s yarn and textile industry is demanding not only stronger fiber, but also fiber with fewer neps, and less short and immature fiber. These properties have become increasingly important as economies of scale have shrunk in the face of global competition. The AFIS allows for relatively easy quantification of previously difficult to measure fiber properties such as short and immature fiber content.

Short fiber content is a source of fiber waste to yarn manufacturers and it contributes to weaker yarns and thus textile products. Only a

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5. Short fiber content by weight from AFIS measurement. May and Jividen (1999).
8. Immature fiber content from AFIS measurement. May and Jividen (1999).
few genetic studies of short fiber content have been conducted, but they indicate that short fiber content is a heritable trait, but that heritability is low (May and Jividen, 1999). The genetic component of variation for short fiber content is large relative to the genotype × environment interaction component (Meredith, Sasser, and Rayburn, 1992). This finding is similar to that for the measures of length distribution and suggests that breeding efforts to ameliorate short fiber would be fruitful, albeit slow due to low heritability. A limitation of estimating short fiber content for breeders is that a key source of short fibers results from fiber breakage during lint cleaning (Bradow et al., 1996). Commercial ginning involves one or more lint cleaners that are employed to achieve a certain grade of cotton for marketing purposes. Breeders usually generate fiber from hand picked boll samples that are ginned on laboratory model gins not fitted with lint cleaners. The limitations of breeder fiber samples to evaluate short fiber content have been discussed (Meredith, Sasser, and Rayburn, 1992).

Immature fiber is that with incomplete secondary wall thickening in response to environmental conditions and the genotype (Bradow et al., 1996). These fibers do not take dye uniformly, and thus contribute to dye variation in textiles. They may also contribute to weaker yarns (Faerber, 1995). Immature fiber content by AFIS measurement was found moderately heritable (Table 3), combined with non-significant genotype × year interaction (May and Jividen, 1999). The conclusion then is that selection for less immature fiber should be profitable.

Application of New Tools to Fiber Property Modification

At the same time that increasingly stringent standards are being set for fiber profiles, new tools including molecular markers and transformation are being sought to speed progress from conventional breeding. We will survey these technologies and speculate on their applicability for the improvement of fiber properties.

Marker assisted selection (MAS) has been the subject of much research, but mostly in grain crops which have high-density molecular marker maps (Austin and Lee, 1996; Bohn et al., 1997). Efforts to molecularly characterize the cotton genome lag those of other major crops. Lack of polymorphism within G. hirsutum has limited efforts to construct linkage maps and elucidate QTL in upland cotton (Reinisch et al., 1994). Mapping efforts have thus focused on interspecific populations to achieve the desired polymorphism of markers. Andy Pater-
son's lab at Texas A & M has achieved a great technological feat by the construction of a high density restriction fragment length polymorphism (RFLP) marker map in a *G. hirsutum* × *G. barbadense* F2 population (Reinisch et al., 1994). Another interspecific population has been mapped with RFLPs and randomly amplified polymorphic DNA (RAPD) by ARS, College Station, TX (Yu et al., 1997). Three putative QTLs associated with fiber strength have been mapped in this cross. Others have employed a different approach at developing markers in *G. hirsutum* (Saha et al., 1995). These researchers have used DNA probes comprised of fragments of genes of biological importance, the ACC synthase gene (ethylene precursor) and a fiber strength gene, in RFLP mapping efforts (Feng, 1996). Using such methodology, these scientists demonstrated polymorphism between *G. hirsutum* parents and among their F2 offspring. Amplified fragment length polymorphism (AFLP), with DNA bands visualized by silver staining rather than via autoradiography, may be a class of marker less tedious than RFLPs, and that finds sufficient polymorphism within *G. hirsutum* for use in MAS (Vos et al., 1995; Feng, Saha, and Soliman, 1997).

Breeding with MAS might involve monitoring markers at one or a few loci, such as the pioneering studies with isozymes in maize, or might be more complicated to involve elucidation of QTLs and their effects (Stuber, Edwards, and Wendel, 1987). In either case, the first step in employing MAS or elucidating QTLs is a molecular marker map in the target population reasonably saturated with markers (Young, 1994). The next step is to apply some statistical analysis such as single factor analysis of variance or some type of interval mapping to the phenotypes and markers to derive their association (Knapp, 1994). For the present discussion, we assume some type of segregating population in a mostly self-pollinated species such as cotton. Prior to this expensive endeavour, however, one should set goals of the MAS. As we have seen, fiber length, fiber strength, and certain of the properties measured by AFIS are at least moderately (> 0.5) heritable. Given the magnitude of heritability is MAS a useful technology to modify fiber properties? For example, to select solely for higher fiber strength MAS would not be the choice over conventional selection at the present time, given the status of the marker technology in cotton. Fiber strength introgressed from high strength germplasm, where the strength derives from the original triple hybrid source, is thought to be controlled by as few as two loci (Culp and Harrell, 1974; Meredith, 1992).
This relatively simple inheritance combined with moderate heritability and ease/cost-effectiveness of measurement suggests that MAS to increase strength would not necessarily be profitable compared with gains from conventional phenotypic selection (Stuber, 1994). The relative efficiency of MAS vs. phenotypic selection can be compared as any two selection schemes can be, given equal selection intensities. A key criterion to compare relative efficiency of MAS vs. phenotypic selection is the amount of the additive genetic variance for a trait that is explained by marker variation. Success of MAS in part is predicated on a large portion of the additive genetic variance for a trait explainable by variation for linked molecular marker loci. The additive genetic variance is the genetic variance usable by the breeder of a self-pollinated crop, where the product of the breeding is a largely inbred germplasm (Falconer, 1989). For traits with narrow-sense heritability of about 0.5 (0-1.0 scale, with heritability equal to 1.0 indicating that phenotype is same as genotype), little extra gain can be expected from MAS vs. phenotypic selection (Lande and Thompson, 1990). It would be useful, however, to apply MAS to the simultaneous improvement of fiber and agronomic properties, something long sought by breeders (Culp, 1992). This could be approached in several ways. Suppose that one had associated some type of molecular marker with the loci imparting fiber strength. Plants in F2 populations could be screened for the markers at the seedling stage, and then only those deemed to have both loci imparting strength could be phenotypically selected for advance to the F3 generation. A similar approach could be employed until the strength loci were fixed and then yield testing begun. Pollination control is an added benefit of this scheme. Even though cotton is considered primarily self-pollinated, it can experience outcrossing from pollen carried by bees (Bombus spp.). Cotton breeders often desire to maintain genetic purity for certain rather simply inherited traits such as leaf trichome density. Generally, too many F2 and F3 progeny must be screened to have a reasonable chance at simultaneous improvement of fiber and agronomic properties such that little pollination control is possible. The use of MAS would allow only those individuals to be self-pollinated to prevent genetic contamination.

Another use of QTL analysis is the discovery of favorable genes or gene complexes in exotic germplasm that can not be discerned from phenotypic analysis (Breto, Asins, and Carbonell, 1996; Lande and Thompson, 1990; Tanksley and Nelson, 1996). For example, chromo-
some segments that impart positive yield factors under salt stress in tomato have been found that were not apparent from parental performance (Breto, Asins, and Carbonell, 1996). The genetic base of cotton cultivars is rather narrow, and thus new germplasm needs to be introgressed into ongoing cultivar development programs (Van Esbroeck et al., 1998). The race stock germplasm converted to day-neutral flowering habit is a likely source of new exons governing fiber and agronomic properties that could be of great benefit to cultivar development efforts (McCarty, Jenkins, and Parrott, 1981).

We have examined several considerations that govern the decision to employ MAS. Other limitations of MAS, given the current state of the marker technology, argue for further refinement of the technology before it will have greater impact on cotton improvement. One limitation that MAS has is recombination between the markers and exons of interest (Lande and Thompson, 1990). Linkage between the markers and chromosome segments or exons affecting a particular trait is never complete, which can result in dissociation of the marker and trait. The detection of QTLs is affected not only by the degree of linkage between the marker and QTL, but also by genetic variation at the marker locus and in the genes of interest (Sorrells and Wilson, 1997). Another issue is that once QTLs are identified and even genotyped by fine mapping, they would still need to be accumulated into the same line and their expression checked for interaction with the other QTLs and the background genotype. It would be a difficult task indeed, to accumulate many QTLs into a single genotype. Portability of mapping data among populations is another unknown. Only a few QTLs were common among two maize populations in a study of insect resistance (Bohn et al., 1997). Direct allele selection has been proposed as a further refinement of MAS (Sorrells and Wilson, 1997). This scheme relies on more detailed information about a genome, specifically knowledge of some portion of the DNA sequence within the exon so that the marker is physically located within the gene or flanking regions sufficiently close as to be indivisible from recombination. As a better understanding of the cotton genome unfolds, combined with improvements in marker technology, MAS should have more impact on cotton improvement.

Markers based on single nucleotide differences that can be resolved by denaturing gradient gel electrophoresis (DGGE; Reidel et al., 1990) or new microchip technology (Lemieux, Aharoni, and Schena,
1998) may offer an alternative where RFLP, RAPD, simple sequence repeat, or other markers fail to exhibit sufficient polymorphism for mapping and QTL elucidation. The genetic basis for the DGGE markers is nucleotide mismatch between size-fractionated single stranded DNA that is probed with another single stranded DNA fragment; relative electrophoretic mobility variations that visualize different alleles among genetic lines when screened with the same probe, arise from the properties of heteroduplex DNA. Variation in melting point of the heteroduplex DNA are related to the degree of sequence mismatch between the probe and DNA of the mapping population. Sequence mismatch as few as a single nucleotide can be visualized by DGGE or DNA microchips, increasing their potential to reveal polymorphism not apparent from restriction site based markers (Reid et al., 1990). One can envision the utility of such markers in discriminating among QTLs or exons as their expression is evaluated in various genetic backgrounds.

A revolution in molecular biology, however, may soon obviate existing DNA marker assay technologies that employ gels or filters as media to visualize markers. Molecular biology assays conducted with microchip technology offer the promise of industrial-pace throughput on a scale unimaginable with current gel-based DNA, RNA, and protein assays (Lemieux, Aharoni, and Schena, 1998). The DNA chip technology is expected to accelerate the discovery of expressed sequences in many genera and should facilitate marker-based and transgenic breeding to develop improved germplasm. The acceleration in the discovery of expressed sequences with this technology may allow greater exploitation of transformation in crop improvement, possibly supplanting marker assisted conventional breeding.

Transformation of cotton to incorporate value-added traits is now a reality, as about 45% of the hectarage in cotton in 1998 was planted to transgenic cultivars (USDA-AMS, 1998). Herbicide- and insect-tolerance genes are being inserted into cotton along with those conferring improved fiber properties (John, 1996; Perlak et al., 1990; Rajasekaran et al., 1996). Most of the commercial insect and herbicide tolerant cultivars are, however, backcrossed derived, in that a line of the cultivar Coker 312 that will regenerate plants from callus is first transformed by a strain of Agrobacterium. Other than lines selected out of Coker 312, most cotton cultivars are quite recalcitrant to regeneration from callus. The transformed line of Coker 312 is then crossed with
the recurrent parent to produce an F1. Then, backcrossing to the desired recurrent parent is accomplished one or more times, followed by selfing and selection for expression of the transgene and phenotypic performance of the parent cultivar. A recent report on regeneration and transformation of several elite lines of cotton including Acala cultivars offers the promise of extending this technology to a broader range of germplasm (Rajasekaran et al., 1996). An alternative approach involves direct transformation of the desired variety by biolistic methods (John, 1996). The advantage here is that any cultivar can be transformed and evaluated as a potential new product, without the time consuming task of backcrossing. Linkage drag from the Coker 312 line is eliminated in this scheme. The current disadvantage of biolistic transformation is the low frequency of germline transformants.

Essential to the success of transformation is obtaining consistent expression of the transgene. What has been found so far in the limited field testing of transgenic cotton, is that the expression of the transgene may vary by transformation event and can be affected by the genetic line into which the transgene was inserted (Jenkins et al., 1997; Sachs et al., 1998). A multitude of other factors affecting expression of a transgene have recently been enumerated to include: position in the genome where the transgene is incorporated, composition of the transgenic construct, interaction with native genes, and growth environment (Sachs et al., 1998). Non-mendelian segregation is another possibility that the breeder of transgenic cotton should be prepared for. My experience in working with transgenic cotton, is that the male gamete is very sensitive to the presence of the transgene, something noted long ago from classical cotton genetics when dealing with chromosomal abnormalities (Endrizzi, Turcotte, and Kohel, 1984). Therefore, heritability of the transgene should be considered in breeding efforts. Larger segregating populations may be necessary to have a reasonable chance at simultaneously selecting for the desired expression of the transgene and agronomic qualities. Close cooperation between the molecular biologist and plant breeder are thus, necessary to realize success from transformation.

CONCLUSION

Molecular genetics will likely never supplant breeding as a means of cotton improvement. Instead, the two disciplines must work togeth-
er to achieve a greater common goal, than could be realized from separate efforts. Further refinement of MAS, greater knowledge about the organization and regulation of the cotton genome, and ultimately transformation will have positive impacts on cotton improvement efforts. Herbicide- and insect-tolerance, that can earn an immediate monetary return to the biotechnology-company, have been the most successful efforts, to date, to engineer cotton. Modernization in our textile industry demands that efforts to enhance cotton fiber properties receive attention also. The history of the cotton industry clearly shows that when fiber properties have not matched industry needs, then cotton’s share of the fiber market has declined. I am hopeful, however, that the combined efforts of molecular biology and breeding can produce better fiber properties.

REFERENCES


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