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Broadening the Genetic Base of Upland Cotton in U.S. Cultivars – Genetic Variation for Lint Yield and Fiber Quality in Germplasm Resources

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1. Introduction

Global competition of cotton fibers has changed the U.S. cotton industry in the last decade from a mainly domestic consumer to exporter of cotton fibers in the world market. In 2012, the U.S. produced 17.3 million bales of cotton, 14.4 % of the world production. Only 3.4 million bales, 19.6 % of the total production, were used in the domestic textile industry with 13 million bales exported (USDA-FAS, 2013). Foreign customers demand stronger, longer and more uniform fibers, and less short fiber and impurity contents of raw fibers than domestic markets. Meanwhile, domestic surviving textile industries raised spinning speed by updating to modern high speed spinners in order to improve their competitive ability in the global market. Fiber quality standards were also raised in order to operate at maximum efficiency using the modern spinners. According to Estur (2004), the modern high-speed spinners require micronaire between 3.8 and 4.4, minimum 27.4 mm for 2.5% span length, 28 g/tex for strength, and 6 % for elongation, and maximum of 5 % short fiber content and 15/gram of seed coat fragments, and at least 83 % for length uniformity ratio. Currently, high yield U.S. cultivars of Upland cotton still lack sufficient fiber quality to fully meet these industry requirements. On the other hand, increasing lint yield in Upland cotton cultivars is always a top priority to keep profit for cotton growers. Increases of lint yield in U.S. cotton cultivars reached a plateau in the last two decades (Helms, 2000; Meredith, 2000; Gingle et al., 2006). Cotton yield peaked in the U.S. in 1992 and declined of an annual rate of 3.3 % in the next seven years (Helms, 2000). Furthermore, yearly fluctuation of yield increased 4 times from periods of 1960-1979 to 1980-1998 (Gingle et

al., 2006). It is a great challenge for U.S. cotton breeders to simultaneously improve lint yield and fiber quality because of negative associations between yield traits and fiber quality (Miller and Rawlings, 1967; Smith and Goyle, 1997).

It is commonly accepted that the genetic base of Upland cotton cultivars in the U.S. is narrow (Bowman et al., 1996; Van Esbroeck and Bowman, 1998). The narrowed genetic base in commercial cotton cultivars of *G. hirsutum* was caused by using only a small number of introduced wild genotypes during domestication (Van Esbroeck and Bowman, 1998; Gingle et al., 2006), breeding practices for high yield and early maturity (May et al., 1995; May, 1999), the dominance of transgenic cultivars in recent years, and insufficient utilization of exotic germplasm resources in cotton breeding. The narrowed genetic base in Upland cotton cultivars is believed to be the cause for the limited success in breakup of the negative associations between lint yield and fiber quality. Introgression from exotic germplasm resources into cultivars may be the most effective approach to broaden the genetic base of Upland cotton. The word “exotic” was defined in Google Search as “strikingly different”, “strikingly unusual”, or “introduced from other region or country”. The term exotic germplasm is defined in this chapter as the germplasm without commercial applicability before introgression of the germplasm which includes land races, wild species, and the induced mutation stocks. It is expected that the introgression of novel genes from exotic germplasm into cotton cultivars or breeding lines can increase genetic variation in the introgression populations for agronomic traits and fiber quality.

2. Genetic diversity in some cotton germplasm populations developed by public breeding programs in U.S.

Although many germplasm populations derived from interspecific crosses or race stocks have been used in cotton breeding, only a small portion of alleles in these germplasm were introgressed into the released cultivars due to the selection for regional adaption according to a survey by Van Esbroeck and Bowman (1998). Only 0.3% of the 668 released germplasm lines have been introgressed into successful cotton cultivars. However, most of the successful cultivars released between 1972 and 1996 have some exotic alleles in their pedigree according to this survey. For more successful introgression of exotic germplasm into cultivars, genetic variations of germplasm resources with exotic genetic backgrounds have to be explored.

In this section, the efforts on characterizing genetic diversity in the germplasm populations in a few U.S. public breeding programs were reviewed. There are different cotton breeding programs in U.S. that include both the private and public sectors. The germplasm developed in these programs constitutes the primary gene pool for breeding. Pee Dee and the New Mexico Acala germplasms are two historically important public breeding programs as highlighted by Bowman et al. (2006) in a description of U.S. cotton cultivars released between 1970 and 2005. Up to 50% of strength improvement in Upland cotton cultivars during 1980 and 2000 may have

been attributed to alleles from Pee Dee and Acala germplasm populations (Bowman and Gutiérrez, 2003).

Although there is no a single reference that fully describes the Pee Dee germplasm due to the complex nature of this breeding program, there is a series of publications that reported germplasm lines derived from the program and evaluation of genetic variation in these germplasm resources (Culp and Harrell, 1973; Culp and Harrell, 1979a; Culp and Harrell, 1979b; Bowman and Gutiérrez, 2003; Campbell and Bauer, 2007; Campbell et al. 2009a; Campbell et al., 2009b; Campbell et al., 2011). As described by Culp and Harrell (1973) and Campbell et al. (2011), Pee Dee germplasm was introgressed from triple hybrid strains (*G. arboretum* L. × *G. thurberi* Todaro × *G. hirsutum* L.) since the 1940s and followed by 50 years of intercrosses among progenitor lines and crosses with commercial Upland cotton cultivars. Based on an evaluation of 82 released Pee Dee germplasm lines (Campbell et al., 2011), genetic variation for lint yield and fiber properties has been maintained in this germplasm population. Genetic similarity among these 82 lines ranged from 0.64 to 0.96 estimated by Simple Sequence Repeat (SSR) markers (Campbell et al., 2009b). The maintenance of genetic diversity in the Pee Dee germplasm after so many years of selection in breeding may be due to multiple breeding methods including random mating, backcrossing, and composite crossing in addition to pedigree selection applied during the breeding history (Culp and Harrell, 1973; Campbell et al., 2011).

Acala germplasm populations were developed by the New Mexico State University breeding programs. The history for the development of this germplasm has been described in detail by Smith et al. (1999). The series of Acala 1517 cultivars, commonly planted in the southwestern regions of U.S., were developed in this breeding program. Similar to Pee Dee germplasm, Acala germplasm also has genetic background of triple hybrids (*G. arboretum* L. × *G. thurberi* Todaro × *G. hirsutum* L.) (Smith et al., 1999). These germplasm populations are characterized by high fiber quality and Verticillium wilt tolerance and perform well in semiarid and hot regions in the southwestern of U.S. according to Zhang et al (2005a). Genetic diversity was maintained within Acala germplasm population. Genetic similarity ranged from 0.62 to 0.94 in 30 Acala cultivars estimated by SSR markers in this study. It was also concluded in this study that divergent germplasm introgressed in the Acala breeding program has contributed to the maintenance of genetic diversity in this germplasm and the genetic gain in the Acala cultivars.

Race stocks are another germplasm resource that can be utilized for introgression breeding. There are more than 2,000 primitive accessions in the cotton germplasm collection maintained by ARS at College Station, TX (Percival, 1987). However, utilization of these accessions has been limited due to their photoperiodic sensitivity which requires short days to flower and produce bolls. A group of U.S. public breeders have converted a large number of these accessions into the day-neutral lines by incorporating day-neutral genes in the primitive accessions through backcross breeding (McCarty et al., 1979; McCarty and Jenkins, 1992). Useful genetic variations for lint yield and fiber properties have been identified by evaluation of backcrossed progenies of 14 day-neutral accessions (McCarty et al., 1995) and F₂ bulks of

crosses between 114 day-neutral accessions with Stoneville 474 and Sure-Grow 747 (McCarty et al., 2005). Twelve germplasm lines derived from converted day-neutral race stocks and introgression of wild species were evaluated and significant additive and dominant effects were identified for yield components and different fiber properties (Wu et al., 2010). Hinze et al. (2011) also identified significant variations for agronomic traits and fiber properties within four germplasm populations derived from non-photoperiodic race stocks. A study of genetic distance between four converted day-neutral lines and Delta and Pine 16 showed a wide range of genetic similarity in these germplasm lines, ranging from 0.37 to 0.65 (Zhong et al., 2002).

Species Polycross (SP) and JohnCotton (JC) germplasm populations were developed by U.S. breeders since the 1960s and 1970s. SP germplasm population was derived from multiple crosses among twelve cotton cultivars and strains of four tetraploid species: *G. barbadense* L., *G. tomentosum* Nutt., *G. mustelinum* Watt., and *G. darwinii* Watt. JC germplasm population was derived from multiple crosses between Acala 1517 type cultivars and *G. barbadense*. Both of these two germplasm populations underwent multiple generations of random mating and selfing. Significant genetic variations for lint yield and fiber properties have been identified in field evaluation of 260 SP lines (Zeng et al., 2007) and another evaluation of 200 JC lines (Zeng and Meredith, 2009a). A number of germplasm lines were selected and released from these two germplasm populations for desirable combinations between lint yield and fiber properties (Zeng and Meredith, 2009b; Zeng et al., 2010). Genetic similarity between 12 SP and JC lines and 4 Upland cultivars ranged from 0.44 to 0.99 (Zeng and Meredith, 2011).

In a few molecular studies of genetic distance among Upland cultivars (Gutiérrez et al., 2002; Rahman et al., 2002; Zhang et al., 2005b), genetic similarity ranged from 0.78 to 0.94 between pairs of cultivars in these studies. All the germplasm resources described above have larger genetic distance within the populations and from Upland cultivars. In a recent study of 193 Upland cotton cultivars collected from 26 countries using SSR markers, the pair-wise genetic similarity ranged from 0.64 to 0.99 (Fang et al., 2013). Only in this study, the genetic diversity was comparable to the germplasm populations described above. These studies are consistent with the argument that genetic diversity is maintained in the Pee Dee, New Mexico Acala, Day-neutral converted race stocks, SP, and JC germplasm.

3. Gene action and combining ability for lint yield and fiber quality in germplasm resources

Lint yield is determined by bolls per square meter, seeds per boll, and lint per seed (Worley et al., 1974; Worley et al., 1976). Although the yield component, bolls per square meter, is an inherited trait, it is highly depended on plant density, and environmental effects on this component are large (Meredith and Bridge, 1973). Lint yield is determined by seed cotton yield and lint percentage, and a number of within boll yield components contributing to lint yield including seeds per boll, lint per seed, lint weight per unit seed surface area, fibers per seed, and fibers per unit seed surface area (Worley et al., 1976; Coyle and Smith, 1997). Fiber quality

is a series of fiber properties which determine the spinnability of fibers and the efficiency of the high speed spinners in the modern textile industries. In a typical breeders' analysis, the measurements of fiber quality include micronaire, elongation, fiber strength, fiber length, short fiber content, and fineness. The neppiness traits including fiber neps, seed coat neps, and motes are getting more attention from breeders in recent years because of their severe affects in textile processing during spinning and dyeing (Jacobsen et al., 2001). While both lint yield and fiber quality are important traits to improve in Upland cotton cultivars, negative associations usually exist between them. For example, the potential of fiber productivity is highly related to fiber length and thickness of cell walls because longer fibers and thicker cell walls resulted from increased cellulose amount in the fibers (Kohel, 1999). However, the increase of fiber productivity by increasing cell wall thickness will be antagonistic with fineness, an important fiber property in fiber spinning. Determination of gene actions and combining ability for different attributes of yield and fiber quality in germplasm populations can be of help in understanding introgression and is useful information for breaking or reducing the negative associations among fiber traits.

Genetic variations of quantitative traits for yield and fiber quality are the main focus in this section which discusses the differences of gene actions and combining ability among germplasm resources. For variations related to morphological phenotypes or other taxonomic characteristics, readers can refer to the reports by Percy and Kohel (1999) and Lubbers and Chee (2009). A few recent studies of gene actions in genetic populations derived from different types of germplasm resources are summarized in Table 1. The general low additive gene action for lint yield and most fiber properties in these germplasm populations except for the populations derived from crosses among tetraploid species suggests non-efficiency of early selection for lint yield in the populations. High additive gene action in yield components and fiber strength suggests early selection efficiency for these traits in these germplasm populations. In five genetic populations developed by diallel crosses among Upland cotton cultivars, as reviewed by Meredith (1984), gene actions for yield traits and fiber properties were generally partial dominant. In order to compare gene action in these five genetic populations, the degree of dominance was estimated in the same way as described by Meredith (1984) as the ratios of dominant component to additive component with values less than 1 indicating partial dominance and values equal or larger than 1 indicating complete or over-dominance. As shown in Table 1, gene action in the introgression populations was either completely dominant or over-dominant for yield traits except for lint percentage among different germplasm resources. For fiber properties, gene actions were generally partially dominant for micronaire and fiber strength while over-dominant for fiber length, short fiber content, and fineness. A reduction of heterosis values from obsolete cultivars to the modern cultivars due to increased additive genes in breeding practice has been observed previously (Campbell et al., 2008). The increase of dominance gene action in the genetic populations derived from wild cotton and interspecific crosses indicates that the adding of non-additive genes by introgression from wild cotton may be an effective approach to promote heterosis.

Traits	V_A †	V_D	$(V_D/V_A)^{1/2‡}$	Germplasm type	Sources
Lint yield	0.06**	0.25**	2.0	Primitive accession derived F2, F3	McCarty et al. (2004)
	0.08**	0.12**	1.2	Upland cotton cultivars and breeding lines	Jenkins et al. (2009)
	0.38**	0.31**	0.90	Wild tetraploid species derived F2	Zeng and Wu (2012)
	0.01	0.06**	2.5	Chromosome substitution lines of TM-1 introgressed from <i>G. barbadense</i>	Saha et al (2010)
	0.250**	0.28**	1.1	Cultivars and race stock derived F2	Cheatham et al (2003)
Lint %	0.35**	0.11**	0.56	Primitive accession derived F2, F3	McCarty et al. (2004)
	0.33**	0.22**	0.82	Upland cotton cultivars and breeding lines	Jenkins et al. (2009)
	0.54**	0.10**	0.44	Chromosome substitution lines of TM-1 introgressed from <i>G. barbadense</i>	Saha et al (2010)
	0.49**	0.32**	0.81	Wild tetraploid species derived F2	Zeng and Wu (2012)
	0.81**	0.11*	0.37	Cultivars and race stock derived F2	Cheatham et al (2003)
Boll wt	0.18**	0.34**	1.4	Primitive accession derived F2, F3	McCarty et al (2004)
	0.27**	0.32**	1.1	Upland cotton cultivars and breeding lines	Jenkins et al. (2009)
	0.17**	0.00	0.00	Chromosome substitution lines of TM-1 introgressed from <i>G. barbadense</i>	Saha et al (2010)
	0.35**	0.31**	0.94	Wild tetraploid species derived F2	Zeng and Wu (2012)
	0.23**	0.29**	1.1	Cultivars and race stock derived F2	Cheatham et al (2003)
Seed index	0.39**	0.33**	0.92	Wild tetraploid species derived F2	Zeng and Wu (2012)
Lint index	0.44**	0.32**	0.85	Wild tetraploid species derived F2	Zeng and Wu (2012)
Seeds boll ⁻¹	0.23**	0.36**	1.3	Wild tetraploid species derived F2	Zeng and Wu (2012)

Traits	V_A †	V_D	$(V_D/V_A)^{1/2‡}$	Germplasm type	Sources
MIC [§]	0.14**	0.02*	0.37	Primitive accession derived F2, F3	McCarty et al (2004)
	0.27**	0.15**	0.75	Upland cotton cultivars and breeding lines	Jenkins et al. (2009)
	0.04**	0.60**	3.9	Cultivars and race stock derived F2	Cheatham et al (2003)
	0.07**	0.33**	2.2	Wild tetraploid species derived F2	Zeng et al (2013)
T1	0.19**	0.15**	0.89	Primitive accession derived F2, F3	McCarty et al (2004)
	0.57**	0.12**	0.46	Upland cotton cultivars and breeding lines	Jenkins et al. (2009)
	0.26**	0.31**	1.1	Wild tetraploid species derived F2	Zeng et al (2013)
	0.47**	0.01**	0.14	Cultivars and race stock derived F2	Cheatham et al (2003)
SL1	0.10**	0.18**	1.3	Primitive accession derived F2, F3	McCarty et al (2004)
	0.09**	0.18**	1.4	Wild tetraploid species derived F2	Zeng et al (2013)
	0.07**	0.24**	1.8	Cultivars and race stock derived F2	Cheatham et al (2003)
Short fiber	0.06**	0.41**	2.6	Wild tetraploid species derived F2	Zeng et al (2013)
Fineness	0.12**	0.39**	1.8	Wild tetraploid species derived F2	Zeng et al (2013)

*, ** Significant at < 0.05 and 0.01, respectively.

† V_A , additive variance component; V_D , dominance variance component; V_{AE} , additive by environment; V_{DE} , dominant by environment. All components were expressed as the ratio to V_p , the phenotypic variance.

‡ $(V_D/V_A)^{1/2}$ was calculated as described by Meredith (1984): V_A was set to 100; the dominant component (V_D) was converted to $V_D/V_A \times 100$.

§MIC, micronaire; T1, fiber strength; SL1, 50% span length.

Table 1. Variance components in different germplasm resources of Upland cotton.

Determination of general combining ability for lint yield and fiber quality in germplasm lines can identify parents with potential of simultaneous improvement of lint yield and fiber quality. In reality, a parent with good general combining ability (GCA) in fiber quality usually had negative GCA in yield components or vice versa. In review of the previous studies since 1990s, a line with all desirable combinations between lint yield and fiber properties has not been reported. However, a number of studies reported by the U.S. cotton breeders have identified cultivars or germplasm lines with good lint yield and one or a few desirable fiber properties in the half diallel mating design. Green and Culp (1990) detected PD 3249 having positive GCA

for lint yield (79 kg ha^{-1}), strength (2.5 kN m kg^{-1}), and 2.5% span length (0.20 mm) in crosses among five cultivars. Coyle and Smith (1997) detected Deltapine 90 having positive GCA for lint percentage (1.1-1.2 %) and strength ($2-10 \text{ kN m kg}^{-1}$) in crosses among four cultivars and two germplasm lines. Jenkins et al (2009) reported positive predicted GCA in Acala Ultima, FM 966, and PSC 355 for lint yield ($8-84 \text{ kg ha}^{-1}$), strength ($3.6-29 \text{ kN m kg}^{-1}$), and uniformity ratio (0.32-0.71%) in crosses among 10 cultivars and one breeding line. Zeng et al. (2011) identified five germplasm lines, SP156, SP224, SP192, SP205, and JC65, having positive GCA for lint yield and favorable GCA for a few fiber properties including strength, elongation, short fiber content, and fineness in crosses among four cultivars and twelve exotic germplasm lines by a North Carolina Design II mating design. These germplasm lines can be used as parents in breeding for simultaneous improvement of lint yield and fiber quality.

4. Genetic associations among yield traits and fiber properties in different breeding programs

Negative associations between lint yield and fiber quality is the main obstacle for simultaneous genetic improvement of yield and fiber quality. Genotypic correlations between lint yield and fiber properties in different genetic populations developed by some old and modern breeding programs are summarized in Table 2. In general, unfavorable correlations were identified for lint yield vs. strength, lint yield vs. span length, and lint yield vs. fineness. The highly unfavorable association between lint yield and fineness identified in studies by Miller and Rowlings (1967) and Zeng et al. (2007) are expected since the thickness of fiber walls relates to the total amount of cellulose in fiber production. Since fineness is an important property in textile industry, the breakup of this unfavorable association would be critical in future breeding. The genetic improvement of lint yield may be achieved by selection of within-boll yield components and a balance between lint weight per unit seed surface area and fibers per unit seed surface area. In contrast, the correlations of lint yield with elongation and short fiber content were generally favorable or not significant in these germplasm resources which indicated the possibility for simultaneous improvement of these traits.

Although general negative association between lint yield and fiber strength and between lint yield and span lengths have been reported, low negative correlations were identified in studies of Percy et al. (2006), Zeng et al. (2007), and Hinze et al. (2011) compared with studies in the old breeding programs. The low correlations in these genetic populations indicated the possible recombinants with breakup of the negative associations. The genetic populations described by Percy et al. (2006) and Zeng et al. (2007) were introgressed populations from interspecific crosses. It is possible that the novel genes introgressed from wild germplasm increased recombination among parental chromosomes and therefore increased the chance to breakup negative associations.

An elaborate explanation of interrelationships among fiber traits based on phenotypes has been difficult in the previous studies. The limited success in the past was mainly due to the confounding relationships of some fiber traits with other traits. Sometimes a correlation

Lint yield vs. fiber properties	r values	Germplasm types	Sources
Strength	-0.35 (0.16) [†]	6 generations mixed intermating of	Miller and Rowlings
Elongation	0.37 (0.25)	Empire 10 × TH131-5	(1967)
Fineness	0.46 (0.19)		
Strength	-0.38 (0.19)	2 generations random mating of	Meredith and Bridge
50% span length	-0.28 (0.23)	ST7A × PD165	(1971)
2.5 % span length	-0.67 (0.19)		
Elongation	0.15 (0.20)		
Strength	0.09	Introgressed recombinant inbred	Percy et al. (2006)
50% span length	0.06	population	
2.5% span length	-0.08		
Strength	-0.19***	A mixed intermating population	Zeng et al. (2007)
Elongation	0.03	(Species Polycross, SP)	
50% span length	0.02		
2.5% span length	0.06		
Short fiber content	-0.11**		
Strength	-0.53***	A mixed intermating population	Zeng and Meredith
Elongation	-0.17*	(John Cotton, JC)	(2009a)
50% span length	-0.26**		
2.5% span length	-0.11*		
Short fiber content	-0.08		
Fineness	0.57***		
Strength	-0.19*	21 F2 populations	Hinze et al. (2011)
UHM length	-0.46***		
Elongation	0.58***		
Uniformity	0.08		

*, **, *** Significant at $P < 0.05$, $P < 0.01$, $P < 0.001$, respectively.

[†] Values of standard variation were shown in parenthesis when the significance probability was not reported.

Table 2. Genetic associations between lint yield and fiber properties in the old and modern breeding programs.

between two traits appears unfavorable. However, it doesn't necessarily mean an unfavorable linkage of genes controlling the traits, but simply resulted from confounding effects from other traits. The relationships among maturity, short fiber content, and fineness in our previous studies can be an example to demonstrate how a relation between two traits is superimposed by relations among other traits. In a study of 200 germplasm lines from JohnCotton (JC) germplasm (Zeng and Meredith, 2009a), short fiber content was negatively correlated with fineness ($r=-0.41$). However, this relation was superimposed by their relations with maturity ratio, $r=-0.77$ for maturity ratio vs. short fiber content and $r=0.81$ for maturity ratio vs. fineness. This suggests that when fibers were more mature, short fiber content became less and fibers

became coarser. In another study of 45 F₂ populations derived from crosses between five cultivars and nine SP and JC germplasm lines (Zeng et al., 2013), nearly zero additive correlation was observed between short fiber content and fineness which confirmed a lack of genetic mechanism underlying the phenotypic relationships between the two traits in these populations.

5. Conclusions and perspectives

Germplasm populations with novel genes from exotic resources have been developed from different breeding programs. Molecular marker data showed genetic variation within these germplasm populations which indicated their usefulness in breeding for continuing genetic improvement of lint yield and fiber quality. Although useful genetic variations in different attributes related to lint yield and fiber quality exist in different germplasm populations, limited success has been reported in the identification of parents with desirable combination between lint yield and fiber properties. It is a challenge for U.S. cotton breeders to further broaden the genetic base of Upland cotton in the future to assist in a more successful breakup of linkages between lint yield and fiber quality.

There are a few approaches that should be considered in order to improve utilization of exotic germplasm resources and their introgression into Upland cotton cultivars for simultaneous genetic improvement of lint yield and fiber quality. (A) Genome-wide characterization of genetic diversity in different germplasm resources. There are a total of 5164 accessions of *G. hirsutum*, 1337 accessions of *G. barbadense*, and 25 accessions of *G. tomentosum*, *G. mustelinum*, and *G. darwinii* as primary gene pool, 1952 accessions for A, B, D, and F genome species as secondary gene pool, and 82 accessions for C, G, K, and E genome species as tertiary gene pool available at the National Plant Germplasm System of USDA-ARS (GRIN, 2013). These accessions have served as primary germplasm resources in cotton breeding worldwide, but most of these resources have yet to be utilized for genetic improvement of cotton cultivars. A genome-wide characterization of genetic diversity in these germplasm will undoubtedly improve their utilization in breeding. An establishment of a core set of these germplasm accessions according to the molecular characterization will definitely help their further utilization. (B) Elaboration of the complex interrelationships between yield traits and fiber properties. Because yield traits and fiber properties are often interrelated, the explanation of their interrelationships based on phenotypes would be difficult. Identification of molecular markers closely associated with these traits and determination of their genome location can help elaborate these interrelationships at the genome level and improve our understanding of the mechanisms underlying unfavorable associations between lint yield and fiber properties. (C) Use of alien chromosome substitution lines in introgression breeding. One of the major obstacles hindering utilization of exotic germplasm is the linkage between beneficial genes and unfavorable genes from the wild un-adapted germplasm during introgression. A group of U.S. scientists have developed an approach with a set of chromosome substitution lines to introgress beneficial genes from primary gene pools of *Gossypium* tetraploid species into Upland cotton (Stelly et al., 2005; Saha et al., 2011; Saha et al., 2013). The major advantage of

this approach for introgression breeding is the reduction of likelihood for undesirable associations by increasing recombination in the substituted alien chromosomes or chromosome segments (Saha et al., 2013). (D) Application of appropriate breeding methods such as random mating to maintain genetic diversity in germplasm populations or facilitate introgression of novel genes from wild germplasm resources to Upland cotton. Random mating may improve genetic variation in cotton germplasm populations and increase occurrence of recombinants and further improve opportunities to break up unfavorable associations between lint yield and fiber quality. A recent germplasm population, RMBUP-C4, was developed from crosses between three cultivars and 18 chromosome substitution lines followed by 4 cycles of random mating to introgress *G. barbadense* alleles into Upland cotton germplasm (Jenkins et al., 2013). This germplasm was released and available for cotton breeders worldwide in introgression breeding.

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