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BREEDING AND GENETICS

CO_2 Exchange Rate in Cotton Does Not Explain Negative Associations Between Lint Yield and Fiber Quality

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ABSTRACT

An experiment was conducted to determine if negative associations between yield and fiber quality in cotton (*Gossypium hirsutum* L.) were due to leaf CO_2 exchange rate (CER). A 3-year study evaluated six high-quality genotypes, with two high-yielding commercial control cultivars and a *G. barbadense* L.cultivar, for CER and stomatal conductance to water vapor (g) across contrasting seasons. Yield, fiber quality, and harvest index (HI) were compared with CER and g measured on the uppermost fully expanded leaf on two occasions between mid-flower and cutout. The results show no significant associations between CER and fiber-quality parameters ($p<0.05$). There was no association between CER and yield, HI, or stem weight. It was concluded that high-quality lines did not photosynthesize less than the high-yielding commercial check. There was a positive association between HI and yield ($p<0.01$). An inefficient growth habit as measured by a low HI in at least one high-fiber quality genotype was a possible reason for lower lint yield.

Improving upland cotton (*Gossypium hirsutum* L.) fiber quality has become an important objective in many breeding programs because of the need for improved efficiency in spinning mills and demand for more lightweight casual garments (Liu et al., 2010). Although lint yields have risen due to breeding efforts, corresponding increases in fiber quality have not been as successful. This is due to a proven negative relationship between yield and fiber quality (Clement et al., 2012; Meredith, 1984) assumed to be caused by genetic linkage (Culp and Harrell, 1973; Meredith and Bridge, 1971; Miller and Rawlings, 1967). However, pleiotropy (Meredith, 2005) and physiological effects (May, 2002) cannot be ruled out.

For cotton, the fiber of commercial interest is 96% cellulose (Hsieh, 1999); although the harvested fiber might only be 10 to 20% of total biomass (Yeates et al., 2010a, b). The conversion of light energy into photoassimilates dictates the resources available for cellulose production. Relationships between CER and lint yield have been previously reported (Peng and Kreig, 1991; Pettigrew and Meredith, 1994) and genotypic differences exist for CER (El-Sharkawy et al., 1965; Lopez et al., 1993; Pettigrew and Meredith, 1994; Stiller et al., 2005). Research efforts pertaining to CER and fiber-quality relationships have not been studied as extensively.

The published environmental or agronomic (not genetic) effects on the relationship between fiber quality and CER show micronaire and maturity to be positively associated during boll filling (Pettigrew and Meredith, 1994). Pettigrew (2001) reported that fiber strength was decreased by low light and increased with above average temperatures (Pettigrew, 2008), and concluded that increases in photoassimilates would help maximize fiber quality. However, in that data set the increase in strength was at the expense of lint yield due to reduced seeds per boll.

It might be accepted that there would not be an association between CER and fiber-quality parameters of length and strength, although May (2002) speculated that plant energy demands might be greater for stronger fibers. This could help explain the negative association between yield and strength, and imply that a genotype with stronger fiber might produce less fiber per unit of photosynthesis. To clarify any associations between yield and quality, this paper examines the CER of premium-quality genotypes and compares that with high-yielding control cultivars.

MATERIALS AND METHODS

Genotype Characteristics. Eight upland cotton genotypes bred by the Commonwealth Scientific and Industrial Research Organisation (CSIRO) breeding program were chosen to represent a range of fiber quality traits, particularly fiber length and

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fiber strength. These genotypes were part of large breeding populations aimed at maintaining yield while improving fiber quality, described in Clement et al. (2012). Genotypes CSX1034, CSX4026, CSX4049, CSX7008, CSX9060, and CSX9111 all have relatively high fiber length (~32 mm), high fiber strength (~320 kN m kg^{-1}), low linear density (~170 µg m^{-1}), and intermediate micronaire (~4.1). These were compared with commercial control cultivars: 'Sicot 71' (Reid, 2003), 'Sipima 280' (Stiller, 2008), and 'Sicala 340BRF' to provide benchmarks for either yield or quality. Sicot 71 has high yield but relatively short and weaker fiber with high micronaire. Sicala 340BRF is a commercial Bollgard II® Roundup Ready Flex® cultivar with fiber properties similar to the CSX breeding lines above. Sipima 280 is a different species, *Gossypium barbadense* L. (pima), and was included for comparison with higher quality upland genotypes.

In our breeding objectives and in this paper, "high fiber quality" refers to a combination of long (~32mm), strong (~320 kN m kg^{-1}), and fine (<180 µg m^{-1}) fibers. These are superior values to the base levels for marketing fiber for international export of 28.6 mm length, strength of 275 kN m kg^{-1}, and micronaire within the range 3.5 to 4.9 (note fiber fineness is a superior measure to micronaire (Montalvo, 2005)) and as such attains a premium price.

Experiments for gas exchange and harvest index (HI) measurements were grown at the Australian Cotton Research Institute (ACRI) near Narrabri, NSW, Australia (30° S; 150° E). The soil type is a heavy grey clay, Vertosol classified as Ug5.2 (Isbell, 1996) or Typic Haplustert (USDA, 2010). Field experiments were sown in early October 2010, 2011, and 2012, in rows 100 cm apart and with approximately 10 plants per meter of row. Crops were managed with full irrigation as advised by Pendergast (2010), spraying for insect pests as required, and weeds controlled by preplant herbicides such as trifluralin and fluometron followed by inter-row cultivation prior to flowering. Experiments were grown with four replications in a Latinized alpha design (Williams, 1986), with plot size 3 rows by 12 m.

Measurements. Gas exchange measurements were taken with a Li-COR® model 6400XT (Li-COR Biosciences, Lincoln, NE) infrared gas analyzer. Five uppermost fully expanded leaves per plot were measured on the center row on two occasions covering the mid-flower to cutout period each season (1100 and 1400 day degrees (base 12 °C) after sowing (Constable, 1976)). The Li-COR sample chamber was set to standard conditions: relative humidity, 50 to 70%; carbon dioxide, 380 µmol mol^{-1}; photosynthetically active radiation set to saturated light conditions (2000 µmol m^{-2} s^{-1}); and a block temperature set to ambient air temperature (Li-COR, 2004).

The center row was harvested by a plot picker at maturity on 23 May 2011, 15 May 2012, and 30 April 2013. A 250-g subsample was taken for determining lint fraction on a 20-saw laboratory gin and for fiber-quality measurements on a high-volume instrument (HVI 900 in 2011, HVI 1000 in 2012 and 2013; USTER Technologies Inc., Charlotte, NC) and Shirley Fineness Maturity Tester (FMT-3; Shirley Developments Ltd., Stockport, England). After harvest, a 1-m^2 sample of plant stems was collected from each plot, dried at 70 °C for 48 h and weighed. This weight was used in conjunction with harvested lint and seed to calculate HI: lint yield as a fraction of lint yield+seed weight+stem weight. Note this HI does not include leaves as they had been removed by defoliation prior to harvest. Studies have shown a similar ratio between leaf and stem weights based on a wide range of cotton agronomy treatments and cultivars (Constable and Hearn, 1981; Yeates et al., 2010b), therefore suggesting this measure of HI reflects differences between genotypes in the ratio of lint to other plant parts.

Analyses of variances and regression analyses were performed with Genstat 13 (Payne et al., 2009). Season-by-genotype interactions were present; however, the interaction F values were -small compared with the individual genotype main effect (range 4-200, data not shown). Significance of the genotype effect was assessed by using the season x genotype interaction as the error term in calculating F values as recommended by Cochran and Cox (1957). Pettigrew and Meredith (2012) also used this approach. Genotype means were averaged across years and measurement dates for the purpose of comparing CER with fiber-quality characteristics.

Weather and *Helicoverpa* spp. Pressure. Mean monthly temperature, total rain, solar radiation, and potential evapotranspiration (ETo) were measured at the Australian Cotton Research Institute within 1 km of the experiments. Mean monthly data from twice-weekly scouting for *Helicoverpa* spp. eggs and larvae in fields containing these experiments during November to March each season were also documented to assess pest pressure.

RESULTS

Overview of Seasonal Conditions and Interactions with Genotype. The three seasons had contrasting conditions (Table 1). In 2010/11, high rainfall early in the season was followed by warm and dry conditions during flowering and boll growth. High *Helicoverpa* spp. pressure was evident, particularly during early flowering in January. In 2011/12, abundant rainfall occurred throughout the season with below normal temperatures, low radiation, and low evaporative demand until flowering ceased. *Helicoverpa* spp. activity was relatively low. In 2012/13, the growing season was hotter than in the previous seasons with low *Helicoverpa* activity.

A number of measures had significant ($p<0.05$) interactions where the relative performance or ranking of genotypes changed in response to seasonal conditions. Sicala 340BRF had relatively higher yield, CER, g, and fineness in the 2010/11 season. This was due to Bt technology in Sicala340BRF providing better protection from high *Helicoverpa* pressure (Table 1) and subsequent reduced damage from insecticide sprays on other conventional genotypes, which subsequently had delayed maturity. CSX4049 had longer fiber length; CSX1134 and CSX7008 had lower fiber strength; and CSX9060 had relatively higher strength in 2010/11 compared with other genotypes. In response, Sipima 280 had a relatively lower yield and HI to the cool, cloudy, and waterlogged conditions in 2011/12 (Table 1). Many of these interactions with season resulted in a slight change in genotype ranking or in the case of Sipima 280, no change in ranking.

Table 1. Mean monthly temperature, total rain, solar radiation, and potential evapotranspiration (ETo) measured at the Australian Cotton Research Institute within 1 km of the experiments and mean data from twice-weekly scouting for *Helicoverpa* spp. eggs and larvae in the experiments.

	Maximum Temperature	Minimum Temperature	Rain	Radiation	ETo	*Helicoverpa* eggs	*Helicoverpa* larvae
	(°C)	(°C)	(mm)	(MJ m^{-2})	(mm d^{-1})	(m^{-1})	(m^{-1})
2010-11							
October	25.2	11.7	47	21.9	4.0	-	-
November	27.9	15.1	192	21.5	4.6	2	0.4
December	29.2	17.2	161	21.7	4.6	13	1.7
January	34.9	19.6	33	27.1	6.1	20	2.5
February	34.7	20.5	41	25.3	6.0	3	1.9
March	31.3	17.3	30	19.6	4.1	3	0.9
April	28.1	10.8	25	19.0	3.3	-	-
2011-12							
October	25.6	11.1	66	22.5	4.0	-	-
November	30.9	17.2	200	22.6	5.2	1	0
December	28.4	15.6	162	24.4	4.9	3	1.6
January	31.1	17.6	148	24.5	5.3	6	1.6
February	30.0	17.4	182	22.9	4.6	8	0.9
March	30.9	15.8	6	21.3	4.3	3	1.2
April	27.3	11.8	19	16.9	3.0	-	-
2012/13							
October	28.1	9.4	7	25.1	4.8	-	-
November	32.9	16.5	32	27.7	6.4	1	0.0
December	35.0	18.3	32	30.4	6.9	2	0.2
January	37.0	20.8	109	29.7	7.0	4	0.8
February	31.3	16.8	50	25.9	5.3	2	0.2
March	30.3	15.5	119	23.8	4.5	0	0.0
April	28.4	8.8	0	20.0	3.0	-	-

Association of Properties with CER or g. CER was the highest in Sicala 340BRF, Sicot 71, CSX9060, and CSX4026 (Table 2). The lowest CER was Sipima 280 at 26.5 µmol CO_2 m^2 sec^{-1} followed by CSX1034, CSX7008, and CSX4049. Sicala 340BRF and Sicot 71 had the highest g at 0.933 and 0.931 mol m^{-2} s^{-1}, respectively. Sipima 280 had lowest g, 0.667 mol m^{-2} s^{-1}, followed by a range of 0.785 to 0.857 mol m^{-2} s^{-1} in the other breeding lines.

Lint fraction was highest in CSX4026 at 0.441, whereas Sipima 280 had the lowest at 0.328 followed by CSX4049 at 0.388 (Table 2). Yield was the highest in Sicala 340BRF, at 2188 kg ha^{-1} and the lowest in Sipima 280, 843 kg ha^{-1}, followed by CSX7008 with 1279 kg ha^{-1}. The other breeding lines did not differ for yield. Stem dry matter was greatest in CSX7008 (765 g m^{-2}) and least in Sipima 280 (546 g m^{-2}); and remaining lines were not significantly different from each other. Sicala 340BRF had the highest HI of 0.235, followed by CSX4026 with 0.209, which was similar to CSX9111, CSX9060, and CSX4026 with a range of 0.177 to 0.194. CSX7008 and Sipima 280 had the lowest HI.

Sipima 280 had the longest and strongest fiber (Table 3). Upland genotypes with the longest fibers were CSX7008 and Sicala 340BRF with lengths of 33.2 mm and 32.8 mm, respectively. Sicot 71 had the shortest and weakest fiber with a length of 29.9 mm and strength 310 kN m kg^{-1}. Upland fiber strength ranges were 331 to 324 kN m kg^{-1} amongst the stronger genotypes and 316 and 317 kN m kg^{-1} in the weaker genotypes, CSX4026 and CSX9111, respectively. Micronaire was highest in Sicot 71, Sicala 340BRF, and CSX4026, whereas the remaining upland genotypes were equal. Sicala 340BRF had the highest fiber maturity ratio at 0.915. Fiber fineness ranged from 182 to 152 µg m^{-1} in Sicot 71 and Sipima 280, respectively.

Table 2. CER and stomatal conductance to water vapor (g) averaged over two sample dates in three seasons. Lint fraction, lint yield, stem weight, and harvest index for nine genotypes averaged over three seasons (2010/11, 2011/12, 2012/13).

Genotype	CER[z]	g	Lint Fraction	Yield	Stem Weight	Harvest Index[y]
	(µmol m^2 sec^{-1})	(mol m^{-2} s^{-1})		(kg ha^{-1})	(g m^{-2})	
CSX1034	**30.6 cdx**	**0.845 bc**	**0.400 d**	**1611 b**	**611 bcd**	**0.177 c**
CSX4026	**32.1 ab**	**0.857 bc**	**0.441 a**	**1735 b**	**579 cd**	**0.209 b**
CSX4049	**30.4 d**	**0.820 bc**	**0.388 e**	**1729 b**	**576 cd**	**0.194 bc**
CSX7008	**31.0 bcd**	**0.830 bc**	**0.409 c**	**1279 c**	**765 a**	**0.135 de**
CSX9060	**32.0 ab**	**0.785 c**	**0.408 cd**	**1800 b**	**660 b**	**0.188 bc**
CSX9111	**31.5 bc**	**0.837 bc**	**0.407 cd**	**1751 b**	**633 bc**	**0.187 bc**
Sicala 340BRF	**32.7 a**	**0.931 a**	**0.407 cd**	**2188 a**	**568 cd**	**0.235 a**
Sicot 71	**32.5 ab**	**0.933 a**	**0.427 b**	**1767 b**	**623 bcd**	**0.182 c**
Sipima 280	**26.5 e**	**0.667 d**	**0.328 f**	**843 d**	**546 d**	**0.115 e**
LSD	**1.07**	**0.052**	**0.008**	**207**	**79.5**	**0.025**

[z] CER- CO_2 exchange rate

[y] Harvest Index= Lint Yield/(Lint+Seed+Stem weight)

[x] Within groups, means followed by same letter do not differ at *p*=0.05

Table 3. Fiber quality means for nine genotypes averaged over three seasons (2010/11, 2011/12, 2012/13).

Genotype	Length	Strength	Micronaire	Maturity Ratio[z]	Fineness
	(mm)	(KN m kg-1)			(µg m-1)
CSX1034	**32.3 d[y]**	**331 b**	**4.11 d**	**0.890 abc**	**165 d**
CSX4026	**32.3 d**	**316 cd**	**4.30 abc**	**0.888 abc**	**176 ab**
CSX4049	**32.1 e**	**326 b**	**4.24 bcd**	**0.896 ab**	**172 b**
CSX7008	**33.2 b**	**329 b**	**4.10 d**	**0.886 bc**	**166 cd**
CSX9060	**32.6 cd**	**324 bc**	**4.14 cd**	**0.870 cd**	**170 bcd**
CSX9111	**32.4 cd**	**317 cd**	**4.14 cd**	**0.868 cd**	**171 bc**
Sicala 340BRF	**32.8 bc**	**328 b**	**4.35 ab**	**0.915 a**	**171 bc**
Sicot 71	**29.9 f**	**310 d**	**4.46 a**	**0.899 ab**	**182 a**
Sipima 280	**36.7 a**	**486 a**	**3.76 e**	**0.846 d**	**152 e**
LSD	**0.42**	**7.6**	**0.16**	**0.027**	**5.2**

[z] Maturity ratio and fineness measured by Fineness Maturity Tester (FMT).

[y] Within groups, means followed by same letter do not differ at *p*=0.05

Due to the high influence Sipima 280 places on regressions for fiber quality and yield, it has been omitted from the CER regression calculations but is present in Figs. 1 and 2, as a gray circle. The associations between yield, fiber quality, and CER in upland genotypes were not significant (p<0.05) (Fig. 1). There was a highly significant association between yield and HI (r^2=0.89, p<0.01) even when Sipima 280 was excluded (Fig. 2), but no relationship between HI and fiber-quality parameters.

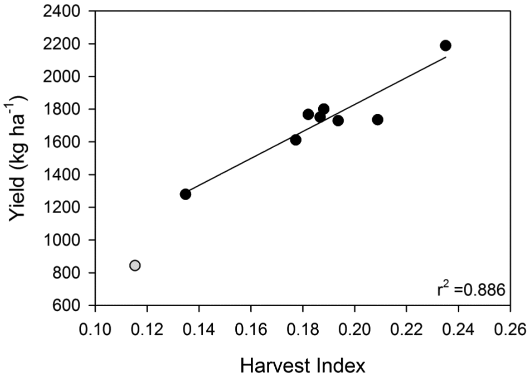

Figure 2. Association between mean yield and harvest index across three seasons (2010/11, 2011/12, 2012/13). Regression line indicate significance at p<0.05, without including Sipima 280 (gray circle).

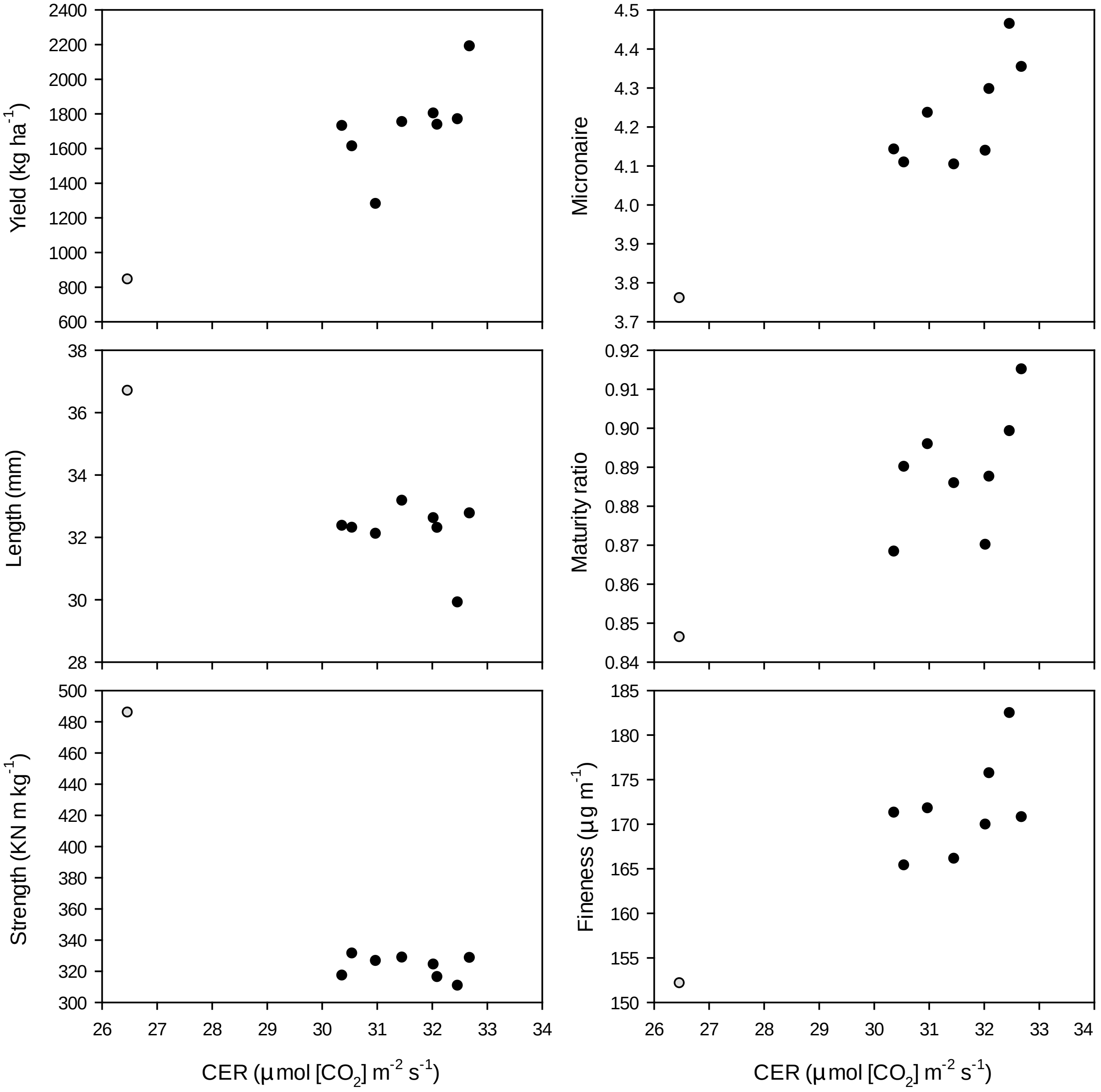

Figure 1. Associations between mean carbon exchange rate (CER) and fiber length, strength, micronaire, maturity ratio and fineness across three seasons (2010/11, 2011/12, 2012/13), Sipima 280 (gray circles).

DISCUSSION

We previously published a large dataset of US and Australian data to show a significant negative association between lint yield and fiber length, strength, and positive association with fineness (Clement et al., 2012). That association was evident in these datasets (Tables 2 and 3). These negative associations have been attributed to genetic linkage and pleiotropy (Meredith, 2005; Meredith and Bridge, 1971; Smith and Coyle, 1997) but there have been no definitive studies to determine whether stronger fibers require more energy as suggested by May (2002). Although six high fiber-quality genotypes cannot represent all breeding material in that category, the lack of association between CER and fiber length or strength in these data would indicate there are other avenues to explore to explain negative associations between yield and fiber quality, particularly given the difficulty in effectively measuring CER in large numbers.

Upland Genotypes. A positive relationship between CER and yield has been reported in upland cotton, and genotypic variation in CER rates exist (Dong et al., 2006; Pettigrew and Meredith, 1994; Pettigrew and Turley, 1998; Quisenberry et al., 1994). There was no association between CER and lint yield in this study except when Sipima 280 was included in the regression (Fig. 1). CSX7008 was influential in this association, likely due to a low HI (Table 2).

An evolving understanding of CER–fiber-quality relations is evident from previously published data. Pettigrew and Meredith (1994) and Pettigrew (1995) found significant correlations between CER and micronaire or maturity, but not with strength. In agronomic studies, Pettigrew (1995, 2001, 2004, 2008) reported low light during boll filling negatively affected fiber strength, maturity, and micronaire due to reductions in available photoassimilates. Furthermore, high temperatures reduced boll size and seed numbers but increased fiber strength. However, we found no significant association between CER and fiber-quality traits in the range of germplasm tested (Fig. 1).

In a recent study, Pettigrew and Meredith (2012) investigated the physiology that diverse genotypes use to attain yield and fiber quality with a range of attributes, including leaf shape and crop maturity. Our paper complements Pettigrew and Meredith's work in that it specifically focuses on high fiber-quality lines, including pima. It primarily concentrates on the association between yield and fiber quality, having four breeding lines with strength greater than 320 kN m kg^{-1} combined with fiber lengths greater than 32 mm. We are in agreement with Pettigrew and Meredith (2012) that there was no significant association observed between CER and fiber quality. There was significant genotypic variation in CER and g in this study (Table 2). The CER and g values followed a similar ranking across genotype, with the exception of CSX9060, which had high CER and low g, resulting in better leaf level water-use efficiency. Therefore when Sipima 280 was excluded from the regression, the average CER and g were not associated. In addition, CER and g data were collected over a limited physiological range. This was similar to Ullah et al. (2008) who reported no association under irrigated conditions.

Pima. Although this Narrabri site is not a pima production area, Sipima 280 was included in this study to provide a comparison with higher fiber-quality upland genotypes. Sipima 280 demonstrated all the characteristics of a *G. barbadense* cultivar with lower yield (Table 2) and high fiber quality (Table 3), compared with upland types.

Literature shows pima to have lower CER and g compared with upland. Lu et al. (1997) showed that upland cotton had 25 to 35% higher g values than pima, similar to our measurements of 22 to 31.7% (Table 2). This is in agreement with the difference in photosynthetic parameters between the two species. Pima having 60% less stomata per unit area (Wise et al., 2000) and a 20% increase in CER was reported when removing the stomatal limitation (Lawson et al., 2012). CER in pima is also limited by photosynthetic electron transport and ribulose-1,5-bisphosphate (RuBP) regeneration capacity (Wise et al., 2004). Breeding efforts for increased yield in pima have occurred simultaneously with increases in stomatal conductance and improved heat resistance (Cornish et al., 1991; Radin et al., 1994).

Harvest Index. Regardless of the inclusion of Sipima 280, there was a significant (p<0.01) and positive association between yield and HI in this study (Fig. 2) and there was no significant association between CER and HI. Although there is autocorrelation in plotting yield against HI (Fig. 2), other measures of HI, such as yield relative to seed plus stem weight, or yield relative to stem weight, gave the same ranking across genotypes. Because lint yield is a low fraction of total biomass in cotton (Yeates et al., 2010a, b), the autocorrelation is less of an issue compared with grains, which might have

HIs >0.6 (Hay, 1995). The positive association between yield and HI indicates that in some genotypes, more resources were allocated to vegetative growth instead of cotton lint, resulting in lower yields. One high-quality line, CSX7008, was the extreme example in this data.

Wells and Meredith (1984) found that modern higher yielding cultivars produced less vegetative dry matter with an earlier peak compared with old cultivars. They concluded that partitioning of assimilates was more important than total dry-weight production—high HI was desirable. Low HI reflects a more indeterminate growth habit and in our study might be associated with the original genetic sources of better fiber quality. Breeding lines were chosen from the data set reported by Clement et al. (2012) to represent CSIRO genetic material with a yield penalty associated with improved fiber length and strength. The lines were derived from high-quality genotypes crossed with high-yielding locally adapted cultivars or breeding lines over a number of generations. Although a wide source of germplasm has been used for fiber-quality improvement, the six lines chosen have been developed from breeding with US Acala types such as Acala 1517-70 (Davis et al., 1978), which has better adaptation to Australian conditions than other sources of improved fiber quality (Constable et al., 2001). The proportion of Acala 1517-70 in the pedigree of the breeding lines in this study ranged from 1.6% in CSX4026 to 15.6% in CSX4049. One parent line derived from Acala 1517-70 was CSX118, and has been shown in earlier studies to have low HI (Bange and Milroy, 2004). However, the proportion of high-quality background in the pedigree was not associated with the HI in our study, indicating that breeding selection for fiber quality has not necessarily carried low HI in all lines. HI is an important aspect to consider in breeding for improved fiber quality while maintaining yield. As a screening procedure during breeding with high fiber-quality types, we suggest eliminating undesirable plant types (i.e., low HI) in early generation screening, using visual scores for HI or growth habit. To take account of seasonal differences, using a control cultivar as reference for growth habit is advisable. Within the remaining lines with more desirable growth habit (i.e., high HI) for the climate and system of interest, breeding resources in later generations can then be more efficiently utilized to select for improved yield and fiber quality combinations.

CONCLUSION

In this study, we examined the possibility that the negative association between fiber yield and quality was due to a source limitation. As there were no significant negative associations between CER and fiber-quality parameters; we cannot conclude that a lower CER would be the reason for a negative association. However, there was an indication that a more vegetative growth habit, measured as low HI, was involved in the negative association of yield and fiber quality by placing a limitation on yield. Future research into negative yield and fiber-quality associations would be better invested in studies of assimilate distribution as well as metabolic requirements for high fiber strength genotypes to determine if the lint chemical composition differs with increased fiber strength.

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