

Improving cotton productivity in arid-region agriculture

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ABSTRACT

Water deficit is the major factor limiting plant growth and crop productivity worldwide. This study was aimed to establish the physiological and genetic basis for improving productivity of cotton under arid land agriculture. Cotton cultivars, *Gossypium hirsutum* (GH), *G. barbadense* (GB) and interspecific hybrids (ISHs; *G. hirsutum* x *G. barbadense*), were examined under field and greenhouse conditions. In the field, water use efficiency (WUE = total dry matter produced / water used) was always higher in GH cultivars than in GB, while in the greenhouse the opposite ranking was observed. In both environments, however, the ISHs exhibited WUE values either similar to or larger than the largest WUE among the two species. These results suggest that the respective species have evolved different environmental adaptations with respect to WUE, and that combining genes from the two species offer the potential to improve WUE. In the second phase of this study, F₂ and F₃ (GH x GB) generations were used for genetic mapping of the crop's productivity and related physiological traits. Productivity of cotton grown under well-watered versus water-limited conditions was shown to be partially accounted for by different quantitative trait loci (QTLs), indicating that adaptation to both conditions can be combined into the same genotype. Genetic mapping clearly implicated reduced leaf osmotic potential as a major component of improved cotton productivity under arid conditions and indicated that selection for WUE alone cannot be expected to improve productivity. The finding that the GH allele is favorable at some loci and the GB allele at other loci indicates that recombination of favorable alleles from each of these species may form novel genotypes that are better-adapted to arid conditions than either of the parental species. Near-isogenic lines being made for the QTLs discovered herein will offer a powerful new tool for the identification of the underlying gene(s) and physiological mechanism(s).

Introduction

Cotton (*Gossypium hirsutum* L. and *G. barbadense* L., abbreviated hereafter as GH and GB, respectively) is usually grown during the summer in arid and semiarid regions where water availability is often limited. Regardless of whether it is irrigated or not, cotton is often exposed to drought, which adversely af-

fects both yield and lint quality. Improving the water-use efficiency (WUE, the ratio between dry matter production and water consumption at the whole-plant level, or between rates of photosynthesis and transpiration at the leaf level) could reduce the adverse effects of drought and also improve productivity under non-stressful conditions.

The cotton genus originates from wild perennial plants adapted to semi-arid, semi-tropical environments which experienced periodic drought and temperature extremes (Kohel, 1974), so adaptations to heat and drought stress are expected to exist. Modern cotton cultivars are the result of intensive selection to produce large quantities of lint suitable for mechanical harvesting and processing. This selection, traditionally emphasizing maximal productivity under high-input (irrigated) conditions, has unintentionally narrowed genetic variability for drought resistance and WUE (Rosenow *et al.*, 1983). In this study we aimed to explore the existing variation for drought adaptation and establish the physiological and genetic basis for improving productivity of cotton under arid land agriculture.

Experimental procedure

The variation in WUE among cotton cultivars, GH, GB and interspecific hybrids (GH x GB), was examined under two irrigation regimes, well watered and water-limited (50% water application of the well-watered plants) in two field trials (Saranga *et al.*, 1998). A smaller collection of genotypes was also examined in two greenhouse trials under two irrigation regimes (Saranga and Yakir, submitted). Two selected cultivars, GH cv. Siv'on with GB cv. F-177, each of which had the highest WUE among cultivars of their species in the field were crossed and their interspecific segregating progenies, F₂ and F₃, were studied in two field trials each with two irrigation regimes and used for genetic mapping (Saranga *et al.*, 2001).

Results and Discussion

Genetic variation

In the field, GH cultivars exhibited significantly greater WUE than GB cultivars (Saranga *et al.*, 1998), whereas in the greenhouse, GH cultivars revealed lower values of WUE than GB cultivars (Saranga and Yakir, submitted). The different rankings of GH vs. GB for WUE, obtained under field and greenhouse environments, suggests that the respective species have evolved different environmental adaptations. In both environments, however, the interspecific hybrids exhibited WUE values either similar to or higher than the highest WUE among the two species, suggesting that combining genes from the two species offers the potential to improve WUE. In the field, net photosynthetic rate (Pn) positively correlated with WUE (Saranga *et al.*, 1998), whereas greenhouse-grown cotton revealed negative correlation between WUE and Pn (Saranga and Yakir,

submitted). In the greenhouse, stomatal conductance values were generally low as compared to the field, in agreement with previous reports on cotton (Radin, 1992). This difference may have been among the factors underlying the different relationships between WUE and Pn observed under the field and greenhouse environments. Carbon isotope ratio ($d^{13}C$), previously suggested as an indirect measure of plant WUE (Farquhar *et al.*, 1982; Farquhar and Richards, 1984), was also examined in this study. In spite of the differences between field and greenhouse conditions, under both environments WUE was positively related to $d^{13}C$ (Saranga *et al.*, 1998; Saranga and Yakir, submitted), reconfirming the usefulness of the carbon isotope approach for breeding "water-efficient" cotton varieties.

Genetic mapping

A total of 82 quantitative trait loci (QTLs) were mapped for ten traits reflecting productivity (dry matter; seed-cotton yield; harvest index; boll weight; boll number) and related physiological traits (osmotic potential; carbon isotope ratio; canopy temperature, chlorophyll a, chlorophyll b) (Saranga *et al.*, in press). Among the QTLs detected, 55 showed no significant difference in their effects between well-watered and water-limited conditions. Of particular interest were 16 QTLs that influenced plant productivity or physiological traits only in the water-limited treatment, but showed no differences between *GH* and *GB* alleles in the well-watered treatment. Favorable alleles at such loci may be assembled into genotypes that incorporate adaptations to water-limited conditions, but also retain high levels of productivity under well-watered conditions. Eleven QTLs that influenced plant performance only under well-watered conditions may be useful for basic research to identify specific metabolic lesions that render some genotypes especially sensitive to water deficit. Four QTLs influenced the relative values (ratio of phenotype under water-limited to well-watered conditions) indicating differences in stability of plant performance between the two environments. The finding that partly-different sets of genetic loci account for productivity and quality under well-watered versus water-limited conditions indicates that genetic potential for productivity under arid conditions can be improved with little or no penalty under irrigated conditions.

To test the extent to which different traits were under related genetic control, we evaluated the correspondence of QTL likelihood intervals. The 82 QTLs discovered in this study were located in 45 non-overlapping genomic regions (Saranga *et al.*, submitted). While some correspondence is expected (and found) among interrelated traits such as seed-cotton yield (SC) and harvest index, or SC and yield components, we were especially interested in relationships between physiological parameters and measures of plant productivity.

A particularly strong relationship was found be-

tween QTLs for osmotic potential (OP) and QTLs reflecting plant productivity (Figure 1). An association between SC and OP occurred in three genomic regions (chromosomes [Chrs] 6 and 25, and linkage-group [LG] A02) and between boll weight and OP in one genomic region (LG A01), with the favorable allele (*GH* in LG A01, Chr 06 and LG A02, and *GB* in Chr 25) associated with both high SC (or boll weight) and low OP. The likelihood that three of 12 OP QTLs would be associated with 3 of 14 SC QTLs by chance, in a genome the size of cotton's, is about 0.5%. These results are further supported by significant correlations between OP and SC and OP and dry matter in the water-limited treatment of the second year trial. An especially important type of correspondence between OP and SC QTLs is highlighted on chromosomes 6 and 25, where the OP and SC QTLs mapped to homoeologous (corresponding) locations on the two different sub-genomes of tetraploid cotton. Such an event is highly unlikely to happen by chance and thus further supports the veracity of the association between OP and SC. These results add a new dimension to previously reported relationships between these traits, in that we have shown that there appears to exist not only a phenotypic correlation but also a partly common genetic basis of OP and productivity.

Surprisingly, $d^{13}C$ showed little clear association with productivity. QTLs conferring high $d^{13}C$ overlapped with one QTL conferring high SC (LG D01) and two QTLs conferring high boll weight (Chr 25 and LG D02). In a genome the size of cotton's, the likelihood that these associations would occur by chance is high. It worth emphasizing, however, that high WUE is not necessarily associated with productivity, since plants can modify WUE by different strategies. For example, either increased carbon assimilation rate or reduced transpiration would enhance WUE, but only the former would increase productivity. Our data indicates that selection for high $d^{13}C$ alone is not expected to neither increase nor reduce productivity; rather it can possibly reduce water consumption.

Conclusion

The merger of genetics and physiology promises to yield better understanding, and more effective improvement, of plant response to arid conditions. While our data clearly implicate OP in adaptation to arid conditions, testing of further traits is needed to account for QTL alleles that have not yet been linked to their physiological basis. The finding that the *GH* allele is favorable at some loci and the *GB* allele at other loci indicate that recombination of favorable alleles from each of these species may form novel genotypes that are better-adapted to arid conditions than either of the parental species. A genetic map of lint quality traits constructed for the same population (Paterson *et al.*, 2003) shows that QTLs for improved drought resistance have neither positive nor negative association with QTLs

for lint quality. Near-isogenic lines being made for QTLs discovered herein will offer a powerful new tool useful toward identification of the underlying gene(s) by using fine-scale mapping approaches (Paterson *et al.*, 1990). The prevalence and possible spread of arid lands worldwide impel further efforts to dissect the molecular and physiological basis of adaptations to arid conditions in the world's leading crops.

References

- Farquhar, G.D., O'Leary, M.H. and Berry, J.A. (1982). On the relationship between carbon isotope discrimination and intercellular carbon dioxide concentration in leaves. *Aust J Plant Physiol.*, **9**: 121-137.
- Farquhar, G.D. and Richards, R.A. (1984). Isotopic composition of plant carbon correlates with water-use efficiency of wheat genotypes. *Aust. J. Plant Physiol.*, **11**: 539-552.
- Kohel, R.J. (1974). Influence of certain morphological characters on yield. *Cotton Gro., Rev.*, **51**: 281-292.
- Paterson, A.H., DeVerna, J., Lanini, B. and Tanksley, S.D. (1990). Fine mapping of quantitative trait loci using selected overlapping recombinant chromosomes, from an interspecies cross of tomato. *Ge-*

netics, **124**: 735-742.

- Paterson, A.H., Saranga, Y., Menz, M., Jiang, C. and Wright, R. (2002). QTL Analysis of genotype x environment interactions affecting cotton fiber quality. *Theor. Appl. Genet.*, **106**: 384-396.
- Radin, J.W. (1992). Reconciling water-use efficiencies of cotton in field and laboratory. *Crop Sci.*, **32**: 13-18.
- Rosenow, D.T., Quisenberry, J.E., Wendt, C.W. and Clark, L.E. (1983). Drought tolerant sorghum and cotton germplasm. *Agric. Water Management*, **7**: 207-222.
- Saranga, Y., Flash, I. and Yakir, D. (1998). Variation in water-use efficiency and its relation to carbon isotope ratio in cotton. *Crop Sci.*, **38**: 782-787.
- Saranga, Y. and Yakir, D. (200#). Variation in water-use efficiency in greenhouse-grown cotton. (submitted).
- Saranga, Y., Menz, M., Jiang, C., Wright, R., Yakir, D. and Paterson, A.H. (2001). Genomic dissection of genotype x environment interactions conferring adaptation of cotton to arid conditions. *Genome Res.*, **11**: 1988-1995.
- Saranga, Y., Menz M., Jiang, C.X., Wright, R.J., Yakir, D. and Paterson, A.H. (200#). Genetic dissection of cotton productivity and related physiological traits under well-watered and water-limited conditions. (submitted).

Figure 1.

Genetic map of selected regions (circled) showing an association between QTLs for seed cotton yield (SC) and QTLs for osmotic potential (OP) in interspecific cotton (*Gossypium hirsutum* x *G. barbadense*) population. Other mapped traits are: dry matter, DM; harvest index, HI; boll weight, BW; boll number, BN; carbon isotope ratio, $\delta^{13}C$; canopy temperature, CT; chlorophyll a content, Chl a; chlorophyll b content, Chl b. Traits and environment-specificity are indicated in the legend. Bars and whiskers indicate 1-LOD and 2-LOD QTL likelihood intervals, respectively. Homoeologous chromosome pairs are indicated by lines joining duplicated DNA loci detected by common probes, with the A-subgenome chromosome to the left. Loci indicated by arrows did not segregate for DNA polymorphisms in this population, but are inferred from the primary reference population, in order to clarify homoeologous alignments.

