Role of Genomic Studies in Boosting Yield

Ibrokhim Y. Abdurakhmonov

Center of Genomics and Bioinformatics, Academy of Sciences of Uzbekistan,
Ministry of Agriculture and Water Resources of Uzbekistan, "Uzpakhtasanoat" association, Uzbekistan

Abstract

Yield declines in cotton production, coming from both intrinsic and operational decreases, are a concern for producers, consumers and researchers. Yield improvement with agronomic properties such as early-maturity and superior fiber quality is the priority target of cotton breeders and cotton researchers worldwide. Contemporary cotton breeding has contributed enormously to developing high-yielding and early-maturing varieties with improved fiber quality. Other agro-technologies have also contributed to greatly improved cotton yields over the past century. The emergence of "biotech crops," adopted worldwide by cotton farmers, has further added to cotton yield gains and has brought significant economic benefits for global cotton farming. However, expanding threats from both abiotic and biotic stresses, including global warming and the narrowing genetic base of commercialized cotton cultivars, generate significant concerns and are prompting breeders to develop novel cultivars that are superior to the current (traditionally-bred or genetically engineered) ones. To address this, with the development of 21st century "omics' sciences, a considerable amount of effort has been made to develop large genetic and genomics resources for cotton through the characterization of novel genes of agronomic importance, the development of molecular marker resources and genetic mapping of complex traits, the development of better germplasm and populations, and the decoding of the entire cotton genome sequence. These efforts led to the development of novel breeding approaches, such as marker-assisted selection, genomic selection, virtual breeding and new-generation transgenomics tools such as RNAi, which are being widely applied in order to improve cotton quality and boost yields. The objective of this paper is to revisit the current and projected status of cotton yields, causes of yield declines, and efforts, successes, failures and possible future solutions with application of modern "omics" technologies that may boost cotton production worldwide. The efforts and achievements ongoing in Uzbekistan will be briefly detailed.

Key words: *Gossypium*; cotton; cotton yield status; cotton yield decline; biotech cotton; cotton genomics; marker-assisted selection; cotton genome sequencing; Uzbekistan's biotechnology.

Introduction

World agriculture, designed to supply the human diet, clothing, and pharmaceutical products, presently cultivates around 2,000 plant species (Abdurakhmonov, 2012) on around 1.55 billion ha to fulfill human needs. Despite this, product deficiencies still exist widely and will become more common with the global human population increasing to ~9 billion by 2050 (Hubert *et al.*, 2010), whereby ~1 billion people may experience product deficiencies and hunger (http://theconversation.edu.au/time-to-modify-the-gm-debate-210). This danger is prompted by 1) a gradual decrease in cultivated land because of degradation, desertification, urban sprawl, mining, toxic pollution and rising sea levels, 2) declining yields of agricultural crops due to decreased genetic diversity and increased threats of biotic and abiotic factors, and 3) reductions in yield due to climate change that will decrease soil water availability, increase heat stress of plants, and alter crop development cycles.

Soil salinity and drought stress account for large reductions in the yields of a wide variety of crops worldwide. The area affected by salinity is very large (estimated around 320 million ha), and is rapidly increasing due to increased irrigation, farming practices in arid zones, and global warming. At the same time, due to globalization and technological advances, there are urgent concerns for world agricultural production to provide bio-safety/bio-security for the world's leading crop species and safeguard them from biotic (phytopathogens, pests, and invasive species) threats (Sharma *et al.*, 2008). For example, biological threats from harmful organisms in agricultural practices cost over $1.4 trillion in crop damage, about 2% of global gross domestic product (GDP). The crop losses are even more severe in developing countries (Sharma *et al.*, 2008). This prompts researchers and scientific communities, rather than overlooking crop bio-security issues, to develop bio-secure agricultural programs and to establish an innovative strategy for regional, national and global bio-security threats (Sharma *et al.*, 2008).

Main Causes and Factors for Declining Yields

Cotton yield declines can be associated with many indirect factors such as cotton prices, food security, and other complex policy factors, which are outside of the scope of this paper. Genetic and environmental factors affecting cotton yields are discussed here. The decrease in *intrinsic* yield, which is the highest yield obtained under ideal farming situations (Gruian-Sherman, 2009), can be attributed to 1) shrinking genetic diversity of commercial cotton cultivars; 2) challenging and limited use of heterosis in cotton production (only a few

countries like India and China use it); and 3) limitations of traditional breeding to rapidly breed a productive plant architecture (e.g. with erect, compact, short internodes, more bolls and fruiting branches, etc.,) with a developed root system, short or medium vegetation, decreased photorespiration, increased photosynthesis, and nutrient utilization capacity.

Decreases in operational yields, which are greatly dependent on environmental influence (Gruian-Sherman, 2009), can be due to 1) again, lack of genetic diversity; 2) biotic (insect, fungal, bacterial, and viral invasions) and abiotic (salt and drought as well as heat eradications) stresses including global warming; and 3) no or limited use of commonly-practiced, efficient, standardized and widely proven agro-technologies to rapidly cope with environmental changes, and to sustain production (e.g. high density planting, drip irrigation, and integrated nutrient and pest management strategies. Of these, at least two are major global concerns for cotton researchers and producers. Firstly, the narrow genetic base of the cotton germplasm, because of a genetic bottleneck derived from historic domestication events and selection (Iqbal *et al.*, 2001), caused recent cotton yield and quality declines (Cotton Incorporated, USA). These declines were due to the vulnerability of genetically uniform cultivars to potentially new biotic and abiotic stresses, as well as to the lack of genotypic potential or existence of fewer alleles responsible for yield traits (Abdurakhmonov, 2007; Abdurakhmonov *et al.*, 2012a).

Second, global climate change caused by increases in atmospheric carbon dioxide (CO_2) is expected to negatively impact agriculture, including cotton (Hake, 2012). Climate change is a huge concern that may contribute to future cotton yield declines. Increased levels of CO_2 may increase fiber yield and water use efficiency (Hake, 2012), and the fertilization effect of increased CO_2 should increase cotton yields by 10%. However, the subsequent temperature increase, projected to be ~2-3°C by 2050, will cancel out much of the potential yield gain mentioned above (Hake, 2012). Global warming will negatively affect (i) nitrate utilization, (ii) bring more drought and heat stress, especially for rain-fed cotton, (iii) cause abnormalities in pollen development affecting fertilization of ovules and reducing boll retention, (iv) accelerate population growth and geographic expansion of cotton insects, and (v) increase extreme rain events and flooding (Hake, 2012).

Approaches to Increase Yields

The widening of the genetic diversity of currently grown cotton cultivars is very important because of the impact on both the intrinsic and operational yield of cotton. Genetic diversity can by increased through combining, introducing or pyramiding new genetic variants that provide better adaption of cultivars to environmental stresses. Wider genetic diversity has the potential to protect crops from massive new pathogens and pest epidemics or sudden environment changes, and thus create an opportunity to further improve yield potential and crop productivity (van Esbroeck *et al.*, 1998; van Esbroeck *et al.*, 1999; Abdurakhmonov, 2007, Abdurakhmonov *et al.*,

2012a). Toward this goal, the 21st century's "omics" science and innovative genomics tools are considered the most promising approaches, in combination with contemporary cotton breeding knowledge and strategies (Abdurakhmonov, 2012; Kumpatla *et al.*, 2012). These include (1) accelerated development and success of transgenic, cisgenic and intragenic biotech crop technologies (Waltz, 2012; Lusser *et al.*, 2012; Miller *et al.*, 2011) with complex effects targeted to improve the *intrinsic* yield in cotton, and (2) decoding of cotton genomes (Chen *et al.*, 2007; Wang *et al.* 2012; Paterson *et al.*, 2013), and mapping and characterization of the genetic basis of complex traits (as referred to quantitative trait loci-QTLs) that provide better exploitation of existing genetic diversity of cotton germplasm and gene pools and; widening of the genetic diversity of commercialized cotton cultivars using modern marker-assisted selection (MAS), marker-assisted backcross election (MABS) and genomic selection (GS) programs (Kumapatla *et al.*, 2012).

Transgenomics Technologies and Biotech Cotton: Its Role, Success and Perspectives in Cotton Yield Improvement

The first biotech cottons developed using transgenomic tools were the genetically engineered (GE) insect resistant (Bt-cotton) and herbicide tolerant (HT-cotton) cultivars developed to minimize weed control costs, and insect infestation that severely affected productivity. Several toxin producing *Cry* genes from the bacterium *Bacillus thuringiensis* (Bt), notably affecting the larvae of moths *Helicoverpa* ssp. and harmless to other forms of life, were genetically inserted into the cotton genome to produce insect resistant cultivars (Zhang, 2013). Similarly, HT-cottons were developed through introducing the EPSPS gene providing tolerance to the herbicide glyphosate, or with a BXN gene providing tolerance to the herbicide bromoxynil (Zhang, 2013, Saha, 2011). These two transgenic cottons have been widely commercialized over the last 17 years, and the cultivation of genetically engineered crops worldwide increased from 1.7 million hectares in 1996 to 170 million hectares in 2012 in 28 countries (ICAC, 2013). Being the third largest biotech crop, biotech cotton is currently grown on more than 66% of world cotton area (ICAC, 2012).

The transgenic technologies, commercialized over the past several years, undoubtedly increased the income earned from cotton worldwide (FICCI report, 2012). Farmers have benefited from biotech cotton cultivation because of decreased insecticide use, reduced energy use, decreased tillage helping to reduce soil erosion, and an overall increase operational yields. For instance, the national cotton lint yield in India rose to 554 kg/ha in 2006/07,compared to pre-Bt cotton farming with yields of 300 kg/ha during 1993-2001 (Whitefield, 2003; FICCI report, 2012; Jha, 2013). Indian cotton yields have declined in recent years, but this is thought to be connected with the cultivation of cotton in non-optimal conditions (Jha, 2013) as area has expanded. Generally, the contribution of Bt cotton varieties in boosting yields in India can be questioned due to selection and cultivation biases, such as (1) selection of

successful farmers as early growers of Bt-cotton, (2) farmers taking special care of Bt-plots, and (3) short-term practices that make comparisons problematic (Stone, 2010).

A recent report compiled by Gruian-Sherman (2009), a senior scientist in the Union of Concerned Scientists (UCS) Food and Environment Program (www. ucsusa.org), based on 11,275 approved field trials for GE crops, including a large number of Bt (3,630) and HT (4,626) trials that covered more than 20 years of research and 13 years of commercialization of GE varieties, concluded that biotechnology "has done little to increase overall crop yields" with the modest aggregated success of Bt-crops. No biotech cultivars have boosted intrinsic yield of any crop with marginal operational yield gains (3-4%). The significant portion of yield increases (24-25%) observed during the 20th century was not the result of GE technologies, but the result of contemporary breeding (Gruian-Sherman 2009). According to the report, a detailed analysis of approved field trials of other transgenic traits intended to boost yields of agricultural crops such as bacterial resistance (139 trails), fungal resistance (713 trails), nematode resistance (51 trails), virus resistance (884 trails), abiotic stress tolerance (583 trails) and yield traits (652) showed limited success (Gruian-Sherman, 2009) in increasing yield components on a crop-wide basis in both national and worldwide levels.

The failure or limited success of currently available or tested GE technologies to improve yields may be due to (1) gradually loosing the 'early-stage' proven transgenic effects (in the cases of Bt and HT) because of the development of tolerance by biotic agents (resistant genotypes to Bt or herbicide tolerant weeds) resulting in more aggressive invasions in crop populations, (2) growth of secondary pests and aggressive pathogens, (3) distribution of existing management practices from "weedy volunteers" (4) non-optimal agricultural farming of GE crops that differ from conventional crops, (5) gradual loss in seed quality of GE crops due to contamination from out-crossing and off-types, and/or (6) through the generation of an epigenetic transgene silencing process that might be unrecognized and not removed in large field plots.

A decrease in the yields of GE crops in subsequent agricultural practices could also come from the introduction of transgenic traits into cultivars that are poorly adapted to local farming conditions. This is especially true with the Bt trait that must be introduced into a local cultivar background through several backcrossies. Often times, conventionally bred and approved local cotton cultivars with earlier crop maturity and desired plant architecture, i.e., more compact and erect types, have been found unsuitable for Bt introgression. Consequently, the varieties used with Bt traits have a lower yield potential but are nevertheless chosen by farmers because they require fewer pesticide applications (ICAC, 2013).

Despite these facts, transgenic technologies will play a prominent role in improving crop productivity through (1) discovery and application of more novel gene variants of transgenic traits (e.g. new variants of Bt genes or novel candidate genes for insect and disease resistance, such as protease, amylase inhibitors, etc.), (2) use of a combination of different variations for transgenes of interest (i.e., gene stacking), and (3) development of novel GE technologies with more complex genetic effects, affecting many genetic pathways and causing multiple gene interactions compared to the GE crops currently grown, and having fewer interactions with other traits in each plant genome.

The latter case is under primary consideration and focus by researchers who are working to develop GE crops with increased intrinsic and operational yields. These efforts target genes involved with complex genetic and biochemical pathways, affecting light perception and photosynthetic rate, plant architecture and organogenesis, better development of root systems, better nutrient assimilation and water use efficiency, and improved tolerance to abiotic stresses. It is not the objective of this paper to review all details of individual genes that are currently used. Nevertheless, speaking broadly, the genes being used with more complex genetic effects include 1) photosynthetic genes, 2) transcription factors, 3) light perception genes, 4) genes from cell cycle machinery, 5) signal transduction factors, 6) plant hormones, and 7) small RNA and microRNA genes (Rojas *et al.*, 2010). Table 1 summarizes some examples of complex genes used in plant biotechnology, including genes used in cotton transformation. Readers are encouraged to address Edgerton (2009), Rojas *et al.*, (2010) and Vriet *et al.*, (2012) for detailed discussion of additional genes. Novel genes that are being used for cotton biotechnology have been discussed in the recent report of the Round Table for Biotechnology in Cotton (ICAC, 2013).

Although the side effects (positive or detrimental, see Table 1) of using complex gene effects in GE crop development may prevent future commercialization of these new generation GE crops, the fundamental knowledge gained in the genomics era of the 21st century suggests the possibility of significant yield increases using these new research results and efforts. Success in future GE crop development requires (i) a better understanding of genetic interactions and physiological consequences of modification of genes with multiple effects, (ii) optimization of multiple effects of "candidate genes" in GE development with reduced side effects (with detrimental and harmful impacts), and (iii) the conduct of detailed field trails without the selection and cultivation biases (Stone, 2010) mentioned above. Future efforts also require exploiting a new generation of transgenomics (RNAi, e.g. Mao *et al.*, 2007; Saha, 2011; Fire *et al.*, 1998; Smith *et al.*, 2000; Waterhouse and Helliwell, 2003), synthetic anti-sense oligonucleotide (Higuchi *et al.*, 2009), artificial miR (Zhou *et al.*, 2013) and a new generation of genome editing such as zinc fingers (Waltz, 2012; Lusser *et al.*, 2012) and use of a transcription activator like endonuclease (TALEN; Miller *et al.*, 2011) technologies to generate more exact and conserved function of transgenic traits in GE crops.

Table 1. Examples of Candidate Genes Used in
Plant Biotechnology for Increased Crop Productivity

Genes	Effect	Side effects	References
APETALA2 (AP2)	Milder mutations increase flower production, seed size and total plant biomass	Strong mutations can cause abnormal flowers; change in seed fatty acid content; maturity of plants, change in plant phytohormone and defense gene expressions.	Jofuku *et al*., 2005; Ohto *et al*., 2005; Ogawa *et al*., 2007.
FASCIATED EAR2 (FEA2)	Controls branching and seed number		Taguchi-Shiobara *et al*., 2001.
β-subunit of farnesyltransferase (ERA1/FTA)	Increased yield through drought tolerance	Disease susceptibility, delayed growth, floral organ abnormalities	Wang *et al*., 2005; Goritschnig *et al*., 2008; Wang *et al*., 2009;
PHYTOCHROME B (Arabidopsis)	Overall yield increase (tuber and seed cotton), plant biomass and leaf index	Semi-dwarfism, decrease in apical dominance, and increase in boll size	Thiele *et al*., 1999; Rao *et al*., 2011
PHYTOCHROME A1 (Cotton)	Increased seed mass, boll number, boll size, row seed cotton yield, plant growth and biomass, root system-oriented and fiber quality	Slight lint percentage and fiber per seed decrease	Abdurakhmonov *et al*., 2012c; Abdurakhmonov *et al*., 2013 in press
Plant sterols/steroids and brassinosteroids	Improved plant biomass, vegetative growth, photosynthetic rate	Not known	Vriet *et al*., 2012 (review).
Sucrose synthase (Sus)	Improved fiber yield, seed set, leaf expansion	Not known	Xu *et al*., 2012; Jiang *et al*., 2012.
Indole-3-acetic acid (IAA)	Lint percentage	Fiber fineness	Zhang *et al*., 2011
isopentenyltransferase (IPT)	Grain yield through drought tolerance	Increased expression of brassinosteroid-related genes and repression of jasmonate-related genes	Peleg *et al*., 2011
Sucrose non-fermenting-1 (SNF1)-related protein kinases (SnRKs)	SnRKs improve yield.	Improved salinity tolerance, responses to nutritional stress and disease, and the regulation of carbon metabolism.	Coello *et al*., 2011
miR156/156b, miR319, miR396	2-fold increase in the number of flowering shoots and seed yield.	Enhanced levels of seed lutein and beta-carotene	Wei *et al*., 2010; Rojas *et al*., 2010
OsSPL14 (SQUAMOSA PROMOTER BINDING PROTEIN-LIKE 14, also known as IPA1)	Promotes panicle branching and higher grain yield.	Not known	Miura *et al*., 2010
AtNHX1 (that encodes a vacuolar sodium/proton antiporter)	Increased photosynthetic rate, plant biomass, and more fibers with superior quality.	Salt tolerance	He *et. al.,* 2005
Gossypium hirsutum casein kinase (GhCKI) gene	Increased yield through heat tolerance	Not known	Min *et al*., 2013

Marker-assisted Selection: Its Role, Success and Perspectives in Cotton Yield Improvement

As an alternative approach being developed by the genomics research community as a result of decoding entire crop genomes and the development of sufficient genomic resources during the 21st century "omics" era, is molecular breeding or so called marker-assisted selection (MAS). Being distinct from GE approaches, MAS has great potential to improve both intrinsic and operational yields of crop species (Edgerton, 2009; Gruian-Sherman, 2009) including cotton (Abdurakhmonov *et al*., 2011ab; Saha, 2011; FICCI, 2012; ICAC, 2013).

Marker-assisted selection (MAS) is based on identification and tracking of genomic regions in introgression programs using DNA markers and quantitative trait loci (QTL), or association mapping results to select and further breed plant genotypes with minimal genomic fragment introgression; this allows only desirable alleles of interest to be transferred and minimizes the 'linkage' drag effects that negatively affect non-targeted but agronomically important traits (Zeven *et al*., 1983; Tanksley *et al*., 1989; Young and Tanksley, 1989; Abdurakhmonov, 2002; Abdurakhmonov *et al*., 2011ab). In this regard, DNA markers linked to the genomic regions of interest serve as an important tool, enabling breeders to conduct early-stage selection of the best plant(s) on the basis of genotype rather than phenotype (deVicente and Tanksley, 1993; Abdurakhmonov *et al*., 2011ab). MAS provides many advantages over conventional breeding, a characteristic that is widely discussed by many review papers (Collard and Mackill, 2008; Kumpatla *et al*., 2012).

The most important requirement to conduct a MAS program is the availability of a sufficient number of polymorphic marker panels evenly covering the target genome and associated with a trait of interest, mapping details with flanking loci, the extent of linkage disequilibrium blocks, donor genotypes bearing the QTL of interest, and breeders ability and capacity to use available molecular resources. User-friendly automated genotyping platforms are vital to perform large-scale MAS programs (Collard and Mackill, 2008; Abdurakhmonov *et al*., 2011ab; Kumpatla *et al*., 2012).

The MAS approach is considered to be an efficient breeding tool to improve crops. According to Google Scholar, as of September 15, 2013, there were about 42,200 articles/documents containing the keyword "marker-assisted selection" although many of them related to describing the future perspectives of MAS. MAS articles targeting improved yield traits or discussing yield traits resulted in 33,000 hits. The PubMed search resulted in 2,256 scientific publications with the keyword "marker-assisted selection." Some early successful applications of MAS were improvements in maize (Ragot *et al*., 2007) and soybeans (Cahill and Schmidt, 2004; Crosbie *et al*., 2003; Kumpatla *et al*., 2012), and MAS has been limited to the major crops for which reference sequences are available, e.g., rice and maize (Chen *et al*., 2010; Zheng *et al*., 2008; Kumpatla *et al*., 2012).

Cotton is the world's leading cash crop but lags behind other major crops for marker-assisted selection (MAS) due to limited polymorphisms and 'a genetic bottleneck' through historic domestication (Iqbal *et al*., 2001; Abdurakhmonov *et al*., 2008a). MAS programs are in their early experimental phases in cotton, and MAS platforms are being developed for fiber quality traits (Zhang *et al*., 2003; Abdurakhmonov *et al*., 2008a; Abdurakhmonov *et al*., 2009; Chen *et al*., 2009; Lacape *et al*., 2009; Lacape *et al*., 2010), early maturity (Li *et al*., 2013), yield potential (Abdurakhmonov *et al*., 2007; Qin *et al*., 2008; Wang *et al*., 2007), abiotic (Saranga *et al*., 2001; Levi *et al*., 2011) and biotic stress tolerance traits (Wang *et al*., 2006 Wang *et al*., 2009; Fang *et al*., 2010; Ulloa *et al*., 2011; Ulloa *et al*., 2013); however, there has been only limited success in utilization of MAS for complex traits in cotton (Abdurakhmonov *et al*., 2011a).

Large-scale genomics resources have been developed, and significant advances in cotton genomics have been made (Chen *et al*., 2007; Zhang *et al*., 2008; Wang *et al*., 2012; Paterson *et al*., 2013; Wang *et al*., 2013) for fostering cotton MAS programs that should facilitate better and more rapid cotton improvement programs worldwide, with the potential to raise yields. For instance, recently a researcher released a set of 17 disomic alien chromosome substitution (CS-B) lines through hypoaneuploid-based backcross chromosome substitution lines in a near-isogenic genetic background of TM-1 (Stelly *et al*., 2005). Researchers documented the chromosomal effects (Wu *et al*., 2006) on agronomic properties, including increased yield and fiber quality using these CS-B lines (Saha *et al*., 2006; Jenkins *et al*., 2006). The chromosome substitution lines serve as a new tool for both MAS and conventional breeding programs to rapidly and efficiently improve genetic diversity and yield potential in Upland cotton (Jenkins *et al*., 2006).

Cotton Genome Sequencing and Re-sequencing Efforts

The recent completion of sequencing of a diploid cotton *Gossypium raimondii* genome with the draft (Wang *et al*., 2012) and the first "gold-standard" versions (Paterson *et al*., 2013) has provided a golden opportunity to study orthologous and paralogous genes and gene families in allotetraploid cotton. The completed genome sequencing for ancestral cotton, being the basis for near-future sequencing tetraploid genomes of commercial importance, further sequencing and re-sequencing of cotton genomes (Page *et al*., 2013; Rai *et al*., 2013) foster (1) the development of a whole genome map of DNA markers (Wang *et al*., 2013), (2) development of 'candidate' gene markers based on single nucleotide polymorphisms (SNP), (3) genome-wide association studies to identify biologically meaningful variations (Abdurakhmonov and Abdukarimov, 2008), (4) clearer understanding of transcriptome, proteome and metabolome complexes conditioning the complex traits like yield and quality, (5) allele mining efforts, and (6) understanding the genome-wide gene interactions and epigenetic regulations of agronomic traits in cotton genomes with commercial importance. These will be vital steps to enhance cotton genetic engineering as well

Como segunda limitante fisiológica en el algodón se encuentra la baja tasa de translocación de asimilados vía floema y como consecuencia acumulación de carbohidratos en las hojas, especialmente almidón (α–D–glucopiranosa polimerizada). Ashley, 1972, afirma que cerca del 43% de los fotosintatos permanecían en las hojas después de 24 horas de translocación y Brown (1973), también encontró que la retención de asimilados es de 35 a 43% de la fotosíntesis diaria en hojas maduras. En función de la retención de asimilados en las hojas, solamente se alcanza un pico máximo de exportación a los 22 días de edad y en un día de sol y con la consiguiente disminución de la fotosíntesis (Constable y Rawson, 1980).

El índice de cosecha, coeficiente efectivo o coeficiente de migración (Gardner *et al*., 1985) describe la partición de materia seca por la planta y está dado por la relación del rendimiento económico y biológico. Holifield *et al*., 2000, evaluando las características de crecimiento y desarrollo de cultivares modernos y obsoletos en sus modelos de retención de frutos, se compararon dos variedades obsoletas (Deltapaine 16 y Acala 442) con tres variedades modernas (Deltapaine Acala 90, Deltapaine 5415 y NuCotn 33b), manejadas con optima irrigación en la Universidad de Arizona y los resultados mostraron que la mayoría del rendimiento se produjo entre las ramas 10 y 18 posición 1. Para el rendimiento en fibra no se encontró diferencia significativa entre los cultivares, excepto para Acala 442 que fue el menor de todos. Los cultivares obsoletos produjeron más cantidad de fibra en las ramas vegetativas que las variedades modernas significativamente

Otro factor limitante fisiológico está en la identificación, determinación y entendimiento de la importancia de la nutrición vegetal balanceada que permita alcanzar una óptima productividad sin manifestación de deficiencias minerales. Con la introducción de nuevos cultivares (con ciclos más cortos y mayor producción de frutos), el cambio en las prácticas culturales tales como incremento en el uso de nitrógeno y utilización de reguladores de crecimiento, se ha obtenido un aumento en la aparición de la deficiencia de potasio (K) (Oosterhuis *et al*., 1990; Chang y Oosterhuis, 1995) y considerando que el algodón comparado con otras especies cultivables presenta baja eficiencia en la toma de potasio del suelo y que su deficiencia por cultivar está creciendo especialmente en suelos arenosos y con baja disponibilidad de potasio (Kerby y Adams, 1985), es importante conocer entre otras las funciones del K en la planta, las cuales están relacionadas con la activación de numerosas enzimas, en procesos de síntesis de carbohidratos, proteínas y en la activación de la ATPasa protónica; esta última no solo facilita el transporte de K^+ de la solución del suelo hacia las células de las raíces, sino que también hace del K el elemento mineral más importante para los procesos de extensión y osmorregulación celular. Igualmente, el transporte de sacarosa a través del floema es influenciado por el K (Marschner, 2002). La cápsula, incluyendo sus carpelos, son los sumideros dominantes para el K dentro de la planta (Kafkafi, 1992; Kerby y Adams, 1985; Rosolem y Mikkelsen, 1991).

Además, la interacción entre el calcio (Ca) y K puede ser benéfica para la toma de K por la planta cuando el bajo nivel de fósforo (P) en el suelo está limitando el proceso de absorción. El efecto sinérgico de Ca^{2+} sobre la absorción de K^+ en el suelo, solo se encuentra, cuando el calcio se encuentra en baja concentración en la solución (Malavolta *et al*., 1989).

Las mejores prácticas de manejo para impedir la deficiencia de potasio son: mantener el contenido de K del suelo en la franja de disponibilidad de media a alta y el equilibrio con otros nutrientes (Ca, Mg). Debido a su relativa movilidad en los suelos arenosos, el potasio se requiere aplicar en forma fraccionada, mitad en la siembra y mitad en la fase de iniciación de los botones florales; para proceder a las aplicaciones foliares de potasio, principalmente en suelos arenosos y de bajo contenido potásico, en cultivos irrigados y de alta productividad, durante períodos de limitada humedad del suelo se debe monitorear el contenido de potasio por medio del análisis de pecíolo, para poder predecir con anterioridad de hasta dos semanas, la ocurrencia de la deficiencia y evitar pérdidas. La mejor práctica para evitar deficiencias de potasio es aplicar el fertilizante al suelo. Sólo pequeñas cantidades de potasio pueden ser suministradas por la fertilización foliar, que debe ser hecha solamente para una emergencia (Reddy *et al*., 2000).

Un caso importante de estudio actual como limitante fisiológico producto del uso del metabolismo secundario (Vía del ácido shikimico) es el efecto del glifosato en variedades genéticamente modificadas, porque se reporta por productores de algodón en Australia y el este de Estados Unidos que con la introducción del Roundup Ready® ha resurgido *Fusarium oxisporum* f. sp. vasinfectum (Harper, 2007).

Es posible aumentar el rendimiento del algodonero, a pesar de que la planta presente grandes limitaciones internas y externas, dado a que es posible manipular varios componentes hasta que el conocimiento del hombre llegue en el área de la fisiología a la fotosíntesis de laboratorio. Algunos autores como Muramoto *et al.,* 1965, afirman que una manera de mejorar el rendimiento seria aumentando el coeficiente de migración de acuerdo al máximo productivo al elevar la tasa de crecimiento foliar. A la vez una segunda opción es aumentando la longevidad de las hojas, para reducir la asincronía entre la fuente y los drenos económicos. Para Wullschleger y Oosterhuis (1990), un aumento del 20% en la longevidad de las hojas y de la tasa de fotosíntesis liquida, aumentarían en 57% el saldo de carbono para los frutos

Otro aspecto es que estos componentes están ligados a factores de control genético. La intensidad fotosintética (actividad fotoquímica de los cloroplastos) y el área de asimilación de la planta (principalmente las hojas) son características genéticas cuantitativas, con genes de efecto aditivo y dominantes, reconociendo que la sobre dominancia desempeña un papel importante para el control genético de estas características (Gaziyants, 1984), en donde la baja intensidad fotosintética es dominante sobre alta intensidad y el aumento de área foliar por planta está controlado por un grupo de genes con diferente

dirección de dominancia. También existe una alta correlación negativa entre intensidad fotosintética y área foliar

Agronómicamente las limitaciones fisiológicas del cultivo se solucionarían mediante la utilización del Monitoreo ecofisiológico, que se facilita mediante el uso de ayudas o herramientas tecnológicas como el análisis de suelo, análisis foliar, análisis de savia, predicción de clima (alertas), tiempo térmico y la zonificación de áreas óptimas entre otras, para con esta información manejar los cultivos de algodón con el fin de ser competitivos al disminuir los factores de incertidumbre o de conocimiento que afectan la productividad. También, es importante incluir la actualización y vinculación de ofertas tecnológicas disponibles no solo de entorno nacional sino del internacional.

Revisión bibliográfica.

Ashley, D. A. 1972. ^{14}C-Labeled photosynthate translocation and utilization in cotton plants. *Crop Science*. 12: 69 – 74.

Benedict, C. R., Hall, J. D. and Kohel, R. J. 1973. Incorporation of ^{14}C-photosynthate into developing cotton bolls. *Crop Science* 13: 88 –91 pp.

Black Jr., C. C. 1973. Photosynthetic carbon fixation in relation to net CO_2 uptake. *Annual Review Plant Physiology*. V 24: 253 – 286.

Brown, K. J, 1973. Factors affecting translocation of carbohydrate in cotton: Movement to the fruiting bodies. *Annals of Botany*. V, 32: 703 – 713 p.

Chang, M. A. and Oosterhuis, D. M. 1995. Cotton response to foliar application of potassium compounds at different pH levels. Better Crops with Plant Food, Norcross, v. 79 (2): 20-22.

Constable, G. A. and Rawson, H. M. 1980. Carbon production and utilization in cotton: inferences from a carbon budget. Australian Journal Plant Physiology. 7: 539-553.

Elmore, C. D. 1973. Contributions of the capsule wall and bracts to the developing cotton fruit. Crop Science, v 13: 751 – 752.

Gaziyants, S.M. 1984. Diallele analysis of photosynthetic activity in cotton. Soviet Genetics, v. 19 276 – 308.

Gardner, F. P., Pearce, R. B. and MitchelL, R. L. 1985. Physiology of crop plants. Iowa University. Iowa State University Press: AMES. 327 pp.

Harper, M. 2007. The Review of the Moratorium on GM Canola. Australia. http://www.dpi.vic.gov.au/dpi/nrenfa.nsf/LinkView/5477226A88881F86CA-2572E300074EEF89E6C67B4668BD2A7CA256FB70001BAB8

Hearn, A. B. 1976. Crop physiology. In: Arnold, M. H. (ed) Agricultural research for development; The namulonge contribution. London, England: Cambridge University Press, 76-122 pp.

Hearn, A. B. and Constable, G. A. 1984. Cotton. In: Goldsworthy, P. R.; Fischer, N. M. (eds). The physiology of tropical field crops. New York: John Wiley. 495 – 527.

Holifield, C.D., Silvertooth, J.C. and Moser, H. 2000. Comparison of obsolete and modern cotton cultivars for irrigated production in arizona. This is part of the 2000 Arizona Cotton Report, The University of Arizona College of Agriculture, index athttp://cals.arizona.edu/pubs/crops/az1170/az11703f.pdf

Malavolta, E., Vitti, G. C. and Oliveira, S. A. 1989. Avaliação do estado nutricional das plantas: princípios e aplicações. Piracicaba: Associação Brasileira para Pesquisa da Potassa e do Fosfato, 201 p.

Meredith, W. R. Jr. and Bridge. R.R. 1971. Breakup of linkage blocks in cotton *Gossypium hirsutum* L. Crop. Sci. 11: 695 – 698.

Muramoto, H., Hesketh, J. and El-Sharkawy. M. 1965. Relationships among rate of leaf area development, photosynthetic rate and rate of dry mather production among american cultivated cottons and other species. Crop Science. V. 5. 163 – 166.

Oosterhuis, D. M., Wullschleger, S. D., Maples, R. L. and Miley, W. N. 1990. Foliar-feeding of potassium nitrate in cotton. Better Crops with Plant Food, Norcross, v. 74, n. 3, p. 8-9, Summer 1990.

Pettigrew, W. T. 1994. Source-to-Sink manipulations effects on cotton lint yield components. *Agron J.* 86 : 731 – 735.

Pérez, A. and Mendoza, A. 1990. Morfología y fisiología. In: Alcaraz, G. A. (ed.). Bases técnicas para el cultivo del algodón en Colombia. 4 ed. Bogotá. Federación Nacional de Algodoneros. 17 – 37 p.

Kafkafi, U. 1992. Foliar feeding of potassium nitrate in cotton. Better Crops with Plant Food, Norcross.76: 16-17.

Kerby, T. A. and Adams, F. 1985. Potassium nutrition of cotton. In: Munson, R. D. (Ed.). Potassium in agriculture. Madison: American Society of Agronomy, 1985. cap. 36, p.843-860.

Reddy, K. R., Hodges, H. F. and Varco, J. 2000. Potassium nutrition of cotton. Mississippi: Mississippi Agricultural and Forestry Experiment Station, 10p. (Bulletin, n. 1094).

Raja, R, R., Hodges, H, F., McCarty, W. H. and Mckinion, J.M. 2003. Weather and Cotton Growth: Present and Future. Published by the Office of Agricultural Communications, Division of Agriculture, Forestry, and Veterinary Medicine, Mississippi State University. Last modified: Thursday, April 3 2003. URL: http://msucares.com/pubs/bulletins/b1061.htm <Consulta: 23 Agosto 2013>.

Rosolem, C. A. and Mikkelsen, D. S. 1991. Potassium absorption and partitioning in cotton as affected by periods of potassium deficiency. *Journal of Plant Nutrition*, Athens, 14 (9): 1001-1016.

Wullschleger, S. D.; Oosterhuis, D. M. 1990. Photosynthesis carbon production and use by developing cotton leaves and bolls. *Crop Science* 30: 1259 – 1264.