BARD

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**Improving Productivity of Cotton (*Gossypium* spp.) in
Arid-Region Agriculture: An Integrated Physiological
Genetic Approach**

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**Improving Productivity of Cotton (*Gossypium* spp.) in Arid-Region
Agriculture: An Integrated Physiological Genetic Approach**

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Drought, Quantitative Trait Locus (QTL), Restriction Fragment Length Polymorphism (RFLP), yield, quality, carbon isotope ratio

Abbreviations used in the report, in alphabetical order: BN, BW, Chl-a, Chl-b, CT, DM, FC, FE, FF, FL, FLU, FS, GB, GH, HI, OP, QTL, RFLP, SC, $\delta^{13}\text{C}$

Publications & Patents Summary (following page)

Summary of Cooperation (following page)

Budget: IS: \$210,000

US: \$140,000

Total: \$350,000

Abstract (one page maximum, single spaced):

Objectives: We seek to establish the basis for improving cotton productivity under arid conditions, by studying the water use efficiency -- evaporative cooling interrelationship. Specifically, we will test the hypothesis that cotton productivity under arid conditions can be improved by combining high seasonal WUE with efficient evaporative cooling, evaluate whether high WUE and/or evaporative cooling are based on specific physiological factors such as diurnal flexibility in stomatal conductance, stomatal density, photosynthetic capacity, chlorophyll fluorescence, and plant water status. Genes influencing both WUE and evaporative cooling, as well as other parameters such as economic products (lint yield, quality, harvest index) of cotton will also be mapped, in order to evaluate influences of water relations on these parameters.

Approach: Carbon isotope ratio will be used to evaluate WUE, accompanied by additional parameters to elucidate the relationship between WUE, evaporative cooling, and cotton productivity. A detailed RFLP map will be used to determine the number, location, and phenotypic effects of genes underlying genetic variation in WUE between cultivated cottons, as well as test associations of these genes with traits of economic importance such as harvest index, lint yield, and lint quality.

Major Conclusions: Productivity and quality of cotton grown under well-watered versus water-limited conditions was shown to be partly accounted for by different quantitative trait loci (QTLs). Among a suite of physiological traits often found to differ between genotypes adapted to arid versus well-watered conditions, genetic mapping implicated only reduced plant osmotic potential in improved cotton productivity under arid conditions. Our findings clearly implicate OP as a major component of cotton adaptation to arid conditions. However, testing of further physiological hypotheses is clearly needed to account for additional QTL alleles conferring higher seed-cotton yield under arid conditions, such as three of the five we found. 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).

Implications: Adaptation to both arid and favorable conditions can be combined into the same genotype. We have identified diagnostic DNA markers that are being applied to creation of such desirable genotypes. Simultaneous improvement of productivity (and/or quality) for both arid and irrigated conditions will require more extensive field testing and the manipulation of larger numbers of genes, reducing the expected rate of genetic gain. These difficulties may be at least partly ameliorated by efficiencies gained through identification and use of diagnostic DNA markers. Genomic tools and approaches may expedite adaptation of crops to arid cultivation, help to test roles of additional physiological factors, and guide the isolation of the underlying genes that protect crop performance under arid conditions.

Achievements (three pages maximum, 1.5 spaced):

Results establish a framework for undertaking both practical improvement of cotton productivity under arid conditions, and for advancing understanding of the genetic/physiological basis of adaptations to arid conditions. The veracity of our results are reinforced by replication during two years, by the finding that QTLs for independently-measured phenotypes often mapped to common genomic locations, and by the finding that several sets of QTLs map to corresponding ('homoeologous') locations in the two 'subgenomes' of tetraploid cotton that are derived from different diploid ancestors (see Figs. 1&2). The favorable alleles at certain loci improve productivity under arid conditions -- study of yield and quality traits revealed that several of these QTLs appear to be free of detrimental effects, and therefore show promise for use in breeding cultivars. The discovery of favorable alleles at some loci from *Gossypium hirsutum* (hereafter GH) and at other loci from *G. barbadense* (hereafter GB) indicates that by recombining favorable alleles from each species, genotypes can be engineered with new, superior levels of arid-region productivity in each of these species that dominate world cotton commerce. The specific goals of BARD #US-2506-94R, and our results, were:

- 1) *To test the hypothesis that cotton productivity under arid conditions can be improved by combining high seasonal water use efficiency (WUE) with evaporative cooling.* **Results:** Carbon isotope ratio (an indicator of seasonal WUE) showed relationship to productivity (dry matter) only in one of the two years of field studies. Genetic differences in seed-cotton yield and/or dry matter production were associated with 3 QTLs that affected osmotic potential (water status), 2 that affected chlorophyll content (photosynthetic capacity) and 1 each that affected leaf temperature (evaporative cooling) and carbon isotope ratio. This was a particularly important finding -- although single QTLs for improved productivity did show association with carbon isotope ratio and leaf temperature (respectively), selection for these traits alone is not sufficient to realize maximal improvement of cotton productivity under arid conditions. Osmotic potential appeared to be a more useful criterion for selection, and will receive more emphasis in the future, in a continuation proposal that has been submitted.

- 2) *To evaluate whether high WUE and/or evaporative cooling are based on specific physiological factors such as diurnal flexibility in stomatal conductance, stomatal density, photosynthetic capacity, chlorophyll fluorescence, and plant water status. Results:* Seasonal WUE (carbon isotope ratio) showed phenotypic correlation with osmotic potential (water status) in each of the two years of the study, but was not related to other physiological factors. Evaporative cooling was also related to osmotic potential. We found ample genetic variation and mapped 12 QTLs for carbon isotope ratio -- several of these were associated with QTLs for chlorophyll content, boll weight or number, however not with improved seed cotton yield under either arid or well-watered conditions.
- 3) *To use the cotton RFLP map (Reinisch et al., 1994) to determine the number, location, and phenotypic effects of genes associated with seasonal WUE and heat avoidance mechanisms, as well as test associations of these genes with traits of economic importance such as harvest index, lint yield, and lint quality. Results:* As reported in detail below, we mapped a total of 165 QTLs associated with productivity (48 QTLs), quality (82 QTLs), and physiological status (35 QTLs), and identified 51 QTLs that behaved differently under well-watered versus water-limited (arid) conditions. In some cases, different traits had similar genetic control -- the 165 QTLs corresponded to only 81 non-overlapping genomic regions (Appendix a: Figs. 1, 2).
- 4) *To develop PCR-based DNA markers which can be assessed in individual cotton seeds by established techniques (Wang et al 1993), to determine the repertoire of genes associated with productivity under arid conditions. Results:* Most mapped cotton DNA probes have been sequenced, and about 100 PCR-based SSR markers have been added to the map (C. Chang and A.H.P., unpubl). An ongoing need is to identify more markers in specific regions that this work has shown to contain important QTLs, to investigate these QTLs in other populations.

Potential for application: In this study we developed a detailed genetic map of QTLs affecting cotton productivity, related physiological traits and lint quality under both irrigated and drought conditions. Further, the association between QTLs conferring

different traits provided a genetic-based evidence on the relationship between these traits. Our immediate application will be the development of near-isogenic lines for improved productivity and quality under arid conditions, toward the pyramiding of genes conferring different favorable adaptations into new genotypes to serve as cultivars and/or breeding lines (a continuation proposal on this topic has been recently submitted to BARD). Medium-term application (5-10 years) will be the cloning of specific genes that are directly responsible for adaptation to arid conditions. Cloning of these genes will provide a point of entry into the transduction pathways by which arid conditions impact plant productivity. Long-term benefit will be a better understanding of the biochemical/biophysical basis for reduced productivity under arid conditions, and new approaches to improve intrinsic genetic potential for arid-region productivity of major crops using molecular tools.

Details of Cooperation. The discoveries made to date reflect the synergies gained by combining the strengths of the US investigator, Dr. Paterson, in genetic analysis of complex traits and particularly in cotton, with the skills of the Israeli investigators in study of crop physiology under stress conditions (Dr. Saranga) and stable isotopes (Dr. Yakir). Note, that this study required a genuine collaboration with each of the three labs taking part in the same experiments. To date, this effort has resulted in 8 joint manuscripts published, submitted, or in preparation. Dr. Saranga has just spent a year of sabbatical leave (Sept. 1998 - Sept. 1999) in the lab of the US PI, further enhancing the cooperation between the two scientists. During this year the Israeli PI took a major role in the biometric analyses of the joint project and gained experience in genetic mapping technology which he will implement in the future collaboration between the two researchers.

Body of the Report (10 pages maximum, 1.5 spaced, a 3 cm margin throughout):

Background: About one-third of the world's arable land suffers from chronically inadequate supplies of water for agriculture, and in virtually all agricultural regions, crop yields are periodically reduced by drought (Kramer 1980; Boyer 1982). Global climatic trends may accentuate this problem (Le Houerou, 1996). Efficient irrigation technologies help to reduce the gap between potential and actual yield -- however diminishing water supplies in many regions impel intrinsic genetic improvement of crop productivity under arid conditions (cf. Blum 1988) as a sustainable and economically-viable solution to this problem. The development of drought-tolerant crops has been hindered by low heritability of end-point measurements such as yield, and by lack of knowledge of more precise physiological parameters that reflect genetic potential for improved productivity under water deficit.

Water loss from a plant (transpiration) is an unavoidable consequence of photosynthesis (Cowan 1986), whereby the energy of solar radiation is used for carbon fixation. Carbon enters the leaves of plants as CO_2 , diffusing through epidermal pores (stomata), which also permit water vapor to diffuse out. While increased transpiration reduces 'water use efficiency' (WUE, the ratio between dry matter (DM) production and water consumption at the whole-plant level, or between rates of CO_2 fixation and transpiration at the leaf level), it also is a benefit in dissipating excess heat (Cornish et al., 1991; Radin et al., 1994). Water stress and heat stress almost invariably co-occur under arid-region field conditions. The resulting need for a balance between tolerance of heat and drought complicates strategies for manipulating plant water use to improve productivity under arid conditions. While disagreement and even confusion may characterize some discussions on what constitutes a significant and an effective mechanism of crop drought resistance, the importance of osmotic adjustment (OA) is receiving growing recognition (Zhang et al. 1999). OA, defined as the active accumulation of solutes in response to water deficit (as opposed to passive solute concentration due to water loss: Morgan, 1984) allows

the plant to maintain positive turgor pressure which is required for stomatal opening and expansion growth (Morgan, 1992).

Genetic mapping provides a powerful approach to distinguishing between casual associations and common heredity, by virtue of the inherent 'randomization' imposed by independent assortment of unlinked genes (cf. Paterson et al., 1988). Genetic mapping has been used to identify quantitative trait loci (QTLs) responsible for improved productivity under arid conditions (Agrama and Moussa, 1996; Tuinstra et al., 1996, 1997; Ribaut et al., 1997). Separately, QTLs have also been reported that confer physiological variations thought to be associated with stress tolerance, such as osmotic adjustment (Lilly et al., 1996), WUE (Martin et al., 1989), abscisic acid levels (Quarrie et al., 1994), and various measures of plant water status (Lebreton et al., 1995). However, very few (if any) prior studies mapped in the same populations QTLs conferring both productivity and physiological differences.

Cotton, *Gossypium hirsutum* (hereafter *GH*) and *G. barbadense* (*GB*), valued at about \$20 billion yearly, originates from wild perennial plants adapted to semi-arid, sub-tropical environments which experience periodic drought and temperature extremes (Kohel, 1974). Modern cotton cultivars are the result of intensive selection to produce large quantities of seed epidermal hairs ('fibers' or 'lint') suitable for mechanical harvesting and processing -- this selection has unintentionally narrowed genetic variability for drought tolerance and WUE (Rosenow et al., 1983) within each species. However, considerable variation is found between *GH* and *GB* (Saranga et al., 1998). Both *GH* and *GB* are tetraploid ($2n = 4x = 52$), comprised of 'A' and 'D' sub-genomes that appear to have diverged from a common ancestor about 4-11 million years ago then rejoined in a common nucleus about 1-2 million years ago (Wendel 1989). Virtually all genes in tetraploid cotton are represented by one or more copies in each sub-genome, in similar (albeit not identical) chromosomal orders in the two subgenomes (Reinisch et al 1994) and their diploid ancestors (Brubaker et al 1999).

Methodologies and Materials: Two field trials were conducted in Nir-Am, located in the western Negev desert in Israel (31°31'N, 34°34'E) each with two irrigation regimes,

well-watered and water-limited. The first experiment consisted of 900 interspecific F_2 cotton plants (self fertilized progenies of a F_1 hybrid, *G. hirsutum* cv. Siv'on x *G. barbadense* cv. F-177), grown in 10 main plots (5 under each irrigation treatment). About 430 of these plants, which produced sufficient fiber to analyze for quality, were completely phenotyped and genotyped. The second experiment consisted of 214 F_3 families (self fertilized progenies of the F_2 , 107 from each treatment to eliminate any possible consequences of differential selection in the F_2) selected to represent the entire population with an emphasis on families of which parents exhibited extreme values of $\delta^{13}\text{C}$. A split-plot factorial design (irrigation regime x family) was used with irrigation in main plots, and three replicates of 5 plants per sub-plot. Average values of the three replicates were used for data analysis. Plants were sown in 1.92-m spaced rows, at a density of 4 plants/m. Water was applied twice a week using a drip system, with the well-watered treatment receiving a total of about 300 mm over the season (consistent with commercial cotton production), and the water-limited treatment receiving about 40-50% of that quantity at the same times. Other management practices were consistent with commercial cotton production for both irrigation treatments.

In year 1, both dry matter and seed-cotton yield determination were measured on each F_2 plant. At the stage of about 50% boll opening dry leaves and branches with open bolls were removed, preventing loss of DM due to defoliation. At full boll opening, the remaining seed cotton and above-ground plant parts were harvested. In year 2, however, one plant per plot was harvested for DM at 50% boll opening, while seed-cotton was harvested from a second plant at full boll opening. All plant parts were oven-dried (except seed-cotton which was air-dried) and weighed.

Physiological measurements were conducted during flowering and boll development period using the youngest fully-expanded leaf. Chlorophyll a and b contents were determined twice during the season using a spectrophotometer (Uvikon 930, Kontron Instruments, Zurich, Switzerland) according to Moran (1982). Osmotic potential of the leaf sap was assessed using a vapor-pressure osmometer (5500, Wescor, Inc., Logan, Utah). Canopy temperature was measured twice during the season at midday with an infrared thermometer (510B, Everest Interscience Inc, Tucson, Arizona). Carbon isotope ratio $\delta^{13}\text{C}$ was determined

using an elemental analyzer (Carlo Erba EA1108, Fison Inc., Milan, Italy) and an isotope ratio mass spectrometer (Opti, Micromass, Manchester, UK). Cotton fiber was separated from seed using a saw gin. Fiber span length, length uniformity, fineness, strength, elongation and color were determined with an HVI tester (Zellweger Uster Ag, Uster, Switzerland).

A total of 253 RFLP loci spaced at average intervals of 23.1 cM were detected by published procedures using DNA probes sampled from a previously-published map (Reinisch et al., 1994), supplemented with new probes to fill gaps. QTL analyses were performed using Mapmaker-QTL (Lander and Botstein, 1989), for a total of 10 data sets, including each of the four individual year x irrigation treatment combinations; 2 combined across the respective irrigation treatments, 2 combined across the respective years, 1 combined across both year and irrigation treatments, and 1 based on relative values (water-limited / well-watered) for the replicated year 2 study. A QTL that revealed a LOD difference >2 between environments was considered to show genotype x environment interaction with predominant effect under the treatment with the higher LOD. Most significant interactions showing LOD difference >2 were corroborated by single-point analysis of variance, based on genotype at the nearest single marker(s). As would be expected, single-point analysis of variance missed a few interactions that were detected using interval analysis. Crop performance under stress relative to control is a widely-accepted measure of stress adaptation, therefore QTLs derived from the relative data set were also considered to represent adaptation to water-limited conditions. Based on the length of genetic map and density of markers (above), a LOD=3 threshold (Lander and Botstein, 1989) was used to declare QTLs. Permutation tests (Churchill and Doerge, 1994) were also done for all traits, generally suggesting thresholds between 3.75 and 4.5, and indicating that LOD=3 corresponded to $\alpha \sim 0.25-0.35$. Higher thresholds were suggested for SC (LOD threshold=5.03, $\alpha=0.45$ for LOD=3) and for OP (LOD threshold=6.03, $\alpha=0.64$ for LOD=3).

Results and Discussion: Among a total of 165 QTLs (Table 1) affecting the 16 traits, 102 (62%) showed no discernible difference in their effects between well-watered and water-limited conditions. Of special interest are QTLs that showed interaction with irrigation

regime -- such interactions were clearly detected in 18 cases by ANOVA for the markers nearest the QTLs, and suggested in 34 more cases by LOD differences of >2 (100-fold) between well-watered and water-limited treatments. Thirty seven QTLs influenced plant productivity (12 QTLs), physiological traits (7 QTLs) or fiber quality (18 QTLs) 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. Fourteen QTLs (7, 4 and 3 for productivity, physiology and quality, respectively) 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. Twelve QTLs (1, 3 and 8 for productivity, physiology and quality, respectively) 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 polyploidy (genome-wide duplication) of cotton was reflected in several cases in which corresponding 'homoeologous' loci on each of the two different 'sub-genomes' appeared to account for common sets of traits (Appendix a: Figs. 1, 2). For example, the *GH* allele at a QTL on chromosome 6 (the A-subgenome) was associated with lower OP, lower CT, and higher SC than the *GB* allele in the water-limited environment (Appendix a: Fig. 1). At the homoeologous genomic location (on Chr. 25; Reinisch et al, 1994), the *GB* allele conferred both lower OP and higher SC than the *GH* allele. A second example of QTLs on homoeologous regions involved *GH* (Chr. 22) and *GB* (LGD05) alleles that each conferred higher $\delta^{13}\text{C}$ under the water-limited treatment and lower chlorophyll content under the water-limited or both treatments (Appendix a: Fig. 1). The discovery that each of two homoeologous locations account for genetic variation in the same phenotypes suggests that subsequently to polyploid formation in cotton, new functionally-significant mutations (alleles) have arisen at each of the two homoeologous loci.

Table 1: Summary of QTLs in interspecific cotton (*Gossypium hirsutum* x *G. barbadense*) population associated with dry matter yield (DM), seed-cotton yield (SC), harvest index (HI), boll weight (BW), boll number (BN), osmotic potential (OP), carbon isotope ratio ($\delta^{13}\text{C}$), canopy temperature (CT), chlorophyll a (Chl-a) and b (Chl-b) contents, and fiber

length (FL), length uniformity (FLU), strength (FS), elongation (FE), fineness (FF) and color (FC).

Trait	# QTLs LOD>3; (<.05) ^a	Range of %variation explained	Favorable genotype ^b				Environment sensitivity ^c		
			<i>GH</i>	H+	H-	<i>GB</i>	Water- limited	Well- watered	Relative value
DM	4	4.9-11.1	2	1	0	1	1	2	1
SC	14	2.9-20.5	11	2	0	1	5	2	0
HI	11	3.1-31.0	11	0	0	0	5	1	0
BW	15	4.4-18.0	13	2	0	0	1	1	0
BN	4	4.0-22.0	2	1	0	1	0	1	0
OP	12	3.6-20.2	9	2	0	1	1	0	0
13C	12	1.7-13.6	4	1	1	6	3	1	1
CT	4	3.9-15.4	1	0	1	2	2	0	1
Chl-a	3	11.0-23.7	2	1	0	0	1	1	1
Chl-b	4	3.9-13.6	3	0	0	1	0	2	0
FL	6	2.9-13.7	3	0	1	2	1	1	0
FLU	8	2.1-13.3	4	0	2	2	2	1	6
FS	23	2.8-17.4	3	0	3	17	8	0	0
FE	9	2.5- 7.3	4	0	2	3	0	0	1
FF	25	2.2-20.8	4	0	8	13	5	0	0
FC	11	2.5-14.9	6	2	1	2	2	1	1

^a Number of QTLs significant based on the traditional LOD=3 threshold.

^b Number of QTLs at which *G. hirsutum* (GH) or *G. barbadense* (GB) are favorable or the heterozygote superior (H+) or inferior (H-) to either homozygote (overdominance or underdominance, respectively).

^c Number of QTLs specifically effective under well-watered or water-limited irrigation regime, or that specifically affected relative values (water-limited / well-watered).

The finding that the *GH* allele is favorable at some loci and the *GB* allele at other loci support our postulate (above) 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. The phenotypic effect of most QTL alleles for most traits was consistent with the expectation based on parental phenotypes, but a number of exceptions were noted (Table 1). The 'genomic exploration' of other accessions of these species, or other wild tetraploid cottons (*G. tomentosum*, *G. darwinii*, *G. mustelinum*) may yield still additional valuable alleles.

The finding (both herein and elsewhere: Tuinstra et al., 1996) that partly-different sets of genetic loci account for productivity and quality under well-watered versus water-limited conditions (Table 1) indicates that genetic potential for productivity under arid conditions can be improved with little or no penalty under irrigated conditions. These results contradict the notion that selection for stress tolerance will generally result in reduced productivity under favorable environments and a decrease in average overall production (Rosielle and Hamblin, 1981). However, simultaneous improvement of productivity (and/or quality) for both arid and irrigated conditions will require more extensive field testing and the manipulation of larger numbers of genes, reducing the expected rate of genetic gain (Falconer, 1982). These difficulties may be at least partly ameliorated by efficiencies gained through identification and use of diagnostic DNA markers (cf. Paterson, 1997).

Scientific implications: Our findings clearly implicate OP as a major component of cotton adaptation to arid conditions. However, testing of further physiological hypotheses is clearly needed to account for additional QTL alleles conferring higher seed-cotton yield under arid conditions. Near-isogenic lines 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 availability of detailed BAC libraries (C. Abbey, D. Rana, B. Zehr, A.H.P., in prep; D. Peterson, J. Tomkins, R. Wing, A.H.P., in prep.) and established transformation methods for cotton (Bayley et al., 1992), together with the possibility of using comparative approaches (Paterson et al 1996) to exploit complete sequence data from botanical models such as *Arabidopsis*, may help to address the complexities of cloning QTLs. The prevalence (Kramer 1980; Boyer 1982), and possible spread (Le Houerou, 1996) 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.

Potential impact: Cotton is the leading textile fiber in the world, and the second most important oilseed. In recent years, cotton has been grown on about 12 million acres per year in the U.S.A., with an annual crop value of about \$5 billion. This represents an

average value of about \$400 per acre, higher than the per-acre value of most agronomic crops. Finally, cotton is important not only as a crop, but also as an employer -- it is the basis of the \$60 billion/yr textile industry which employs 300,000 Americans (Wilcher 1991).

Cotton is among the leading herbaceous warm-season crops in Israel. Virtually all of Israel's cotton is irrigated, consuming much of the water used for agriculture. Cotton production in Israel has declined from 150,000 acres in the mid 1980's to 45,000-65,000 acres in recent years, due to water limitations and low prices. However, it remains one of Israel's major irrigated field crops. This project may provide the Israeli cotton industry with new cultivars, well adapted to arid conditions. It undoubtedly will provide basic information and possibly candidate genes as an important foundation for scientific improvement of plant productivity under arid conditions.

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Publication Summary (numbers)

	Joint IS/US authorship	US Authors only	Israeli Authors only	Total
Refereed (published, in press, accepted)	1			
Submitted, in review, in preparation			1	
Invited review papers				
Book chapters				
Books				
Master theses			2	
Ph.D. theses				
Abstracts				
Not refereed (proceedings, reports, etc.)				

Patent Summary (numbers)

	Israeli inventor only	US inventor only	Joint IS/US inventors	Total
Submitted				
Issued (allowed)				
Licensed				

Cooperation Summary (numbers)

	From US to Israel	From Israel to US	Together, elsewhere	Total
Visits/Meetings		2		2
Sabbaticals		1		1
Postdoctorates				

- **Cooperation**, briefly explain whether synergistic, complementary or supportive.

Synergistic (see page 4)

APPENDICES

Appendix A: Manuscripts published.

Appendix B: Manuscript submitted; Genetic mapping implicates osmotic potential as a major component of crop adaptation to arid conditions.

Appendix C: Complete documentation of biometrical parameters for all QTLs found in the study (in tabular format). Quantitative genetic parameters are as described in Appendix A.

Appendix D: Complete genetic maps for all QTLs found from populations studied in this work. These maps are the basis for the additional publications that are in progress (as listed above).

- Figure 1: QTLs associated with productivity and physiological traits
- Figure 2: QTLs associated with fiber quality traits