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BARD Final Scientific Report
(Cover Page)

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Evaluating Panel: Field Crops

Project Title: Analysis of quantitative traits in pepper using molecular markers

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הספריה המרכזית
למדעי החקלאות
בית דגן

Continuation of (Related to) Previous BARD Project:

☐ Yes ☒ No Number:

Keywords *not* appearing in the title and in order of importance. Avoid abbreviations. Capsicum, cucumber mosaic virus, quantitative trait locus

Abbreviations used in the report, in alphabetical order: CMV (cucumber mosaic virus), QTL (quantitative trait locus), PCR (polymerase chain reaction)

Budget: IS: \$152,000

US: \$150,000

Total: \$302,000

Signature
Principal Investigator

Signature
Research Authority, Principal Institution

Appendix GF

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Publication Summary (numbers)

	Joint IS/US authorship	US Authors only	Israeli Authors only	Total
Refereed (published, in press, accepted)	1	6	2	9
Submitted, in review, in preparation	3	1	-	4
Invited review papers	-	-	-	-
Book chapters	-	-	-	-
Books	-	-	-	-
Master theses	-	-	3	3
Ph.D. theses	-	2	1	3
Abstracts	6	3	3	12
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	0	2	2	4
Sabbaticals	0	1	0	1
Postdoctorates	0	0	0	0

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

Our collaboration is very intensive so we could classify it as both synergistic and complementary _____

Abstract

The original objectives of this research were first, to tag and map genes controlling quantitative variation for economically important traits in pepper including fruit quality parameters and cucumber mosaic virus (CMV) resistance and to improve the molecular maps available for *Capsicum*; second, to develop breeding lines that contain QTL for these traits; and third, to test the hypothesis that at least some genes that control important traits in pepper and tomato may be orthologous. As part of effort under our first objective, we published a detailed comparative genetic map that now establishes tomato and pepper, together with potato as the broadest comparative genetic system in the dicots. Additional studies that avoid the limitations encountered in the comparative mapping population that have addressed all three research objectives were performed in a larger *C. annuum* population segregating for numerous plant and fruit characters and resistance to CMV. We analyzed and genetically mapped a number of horticulturally important traits in this population and also identified 4 QTL for CMV resistance. A total of 6 possible correspondences between QTL in pepper and tomato that affect the same traits were observed for fruit shape, color, weight, and plant height. We selected fruit color for further study because the biochemical pathway that produces fruit pigments is well characterized. We confirmed that the *y* locus for red fruit color in pepper was identical to the structural gene encoding capsanthin-capsorubin synthase and demonstrated that the gene for phytoene synthase corresponds to the fruit color gene, *C2*. When we placed clones of all 10 structural genes from the carotenoid biosynthetic pathway present in pepper fruit on our comparative genetic map, we noted possible correspondences with 3 pepper fruit color QTL, with 4 tomato QTL for fruit color reported in other studies, with two qualitative mutants in tomato for fruit color shifts, *B* and *l2*, and with the *Y* gene in potato for yellow tubers. The *C. annuum* mapping population that served as the base for the analysis of fruit characters was also segregating for polygenic resistance to cucumber mosaic virus. Four major QTL were identified together with two significant interactions. These results were confirmed by analysis of a CMV-resistant advanced breeding line. Using results from the CMV study, and other mapping studies including a collaborative study that mapped dominant resistance to tomato spotted wilt virus in pepper, we compiled map positions for all mapped available solanaceous R genes on a comparative map, the first such effort in plants. This detailed analysis of all available published and new data suggests a working hypothesis regarding the evolution of R genes. Specifically, while host R gene specificity (i.e. which pathogen taxa are controlled) may be evolving rapidly, general functions of R alleles (e.g. initiation of resistance response) may be conserved at homologous loci in related plant genera. Our work has established *Capsicum* as one of the members of the broadest comparative genetic system outside the Poaceae, and has added a large number of traits to the genetic map including a number of fruit and plant growth characters and resistance to CMV, potyviruses, and tomato spotted wilt virus. This information will allow efforts to develop and implement marker-assisted selection in pepper for a host of characters. Further, we have completed a large comparative study of genome composition in the Solanaceae, and then extended this work to provide the first comprehensive examination of the organization and evolution of resistance genes in related plant species.

Achievements

The original objectives of this research were first, to tag and map genes controlling quantitative variation for economically important traits in pepper including fruit quality parameters and CMV resistance and to improve the molecular maps available for *Capsicum*; second, to develop breeding lines that contain QTL for these traits; and third, to test the hypothesis that at least some quantitative traits in pepper and tomato may be orthologous. As part of effort under our first objective, we published a detailed comparative genetic map that now establishes tomato and pepper, together with potato as the broadest comparative genetic system in the dicots (Livingstone et al. 1999). This study conclusively establishes that the pepper and tomato genomes share significant conservation of marker order, and that the 18 homeologous genome segments comprise 98% and 95% of the tomato and pepper genomes respectively. This study was performed in an interspecific *C. annuum* x *C. chinense* F2 population that maximized polymorphism and therefore the number of common markers between tomato and pepper but was too small for QTL analysis and exhibited some sterility further limiting its utility for mapping fruit characters.

Additional studies that avoid the limitations encountered in the comparative mapping population that have addressed all three research objectives were performed in a larger *C. annuum* population derived from a cross between 'Maor', a large fruited bell-type commercial variety and 'Perennial', a small fruited pungent pepper collected in India that has served as the most important source of CMV resistance in pepper breeding. We performed a biometrical analysis of the characters segregating in this population (Ben-Chaim and Paran, 2000). Further, we have genetically mapped a number of horticulturally important traits in this population (Ben Chaim et al, in final preparation) and also we have identified several important loci for CMV resistance (Ben Chaim, submitted). Initially, we constructed a second comparative genetic map consisting of 177 RFLP, AFLP, and RAPD markers that span the pepper genome. To examine genetic control of fruit characters, 180 F3 families were grown and visually scored during 3 field seasons in Israel. From these data, a total of 55 QTL were identified by interval analysis at LOD > 3.0. One QTL located on chromosome 3 explained more than 60% of the phenotypic variability for fruit shape and affected most of the other traits evaluated in this

study. Three other QTL for multiple traits were noted on Lgs 2, 8 and 10 suggesting their importance as loci that control developmental processes with pleiotropic effects. A total of 6 possible correspondences between QTL in pepper and tomato that affect the same traits were observed for fruit shape, fruit color, fruit weight, and plant height.

To further examine the biology that might underlie these correspondences, we selected fruit color as the trait we would first pursue because the biochemical pathway that produces the pigments that determine fruit color is well characterized. We set out to test the hypothesis that the structural genes for the carotenoid biosynthetic pathway may be candidate genes for both qualitative and quantitatively inherited genes for fruit color in both tomato and pepper. We confirmed that the *y* locus for red fruit color in pepper was identical to the structural gene encoding capsanthin-capsorubin synthase (Popovsky and Paran, in press). We determined the map positions for a second enzyme in this pathway, phytoene synthase, corresponds to another gene that controls qualitative shifts in pepper fruit color, *C2*. When we placed all 10 clones of structural genes from the carotenoid biosynthetic pathway operating in pepper fruit on our comparative genetic map, we noted possible correspondences with 3 pepper fruit color QTL, 4 tomato QTL for fruit color previously reported by Bernacchi et al. 1998, 2 qualitative mutants in tomato for fruit color shifts, *B* and *l2*, and the *Y* gene in potato for yellow tubers (Thorup et al., in final preparation), in addition to the two correspondences with *Y* and *C2*.

The *C. annuum* mapping population that served as the base for the analysis of fruit characters was also segregating for polygenic resistance to cucumber mosaic virus, the most important viral pathogen of pepper causing devastating losses worldwide. Despite the importance of this disease, breeding lines with adequate levels of resistance are just now appearing and often are not suitable for type and horticultural performance due to the difficulty of phenotypically-based disease screens and unfavorable linkages with TMV susceptibility and small fruit. We have mapped QTL that account for up to 46% of the phenotypic variability associated with this trait, and have identified the genetic basis for the unfavorable linkages. These marker studies will now allow the positive identification of breeding lines where a recombination has separated the QTL for fruit size from the CMV R QTL. In addition, fingerprinting an advanced CMV resistant breeding line derived from Perennial confirmed results from this study.

CMV is just one of a number of pathogens that cause major economic losses in most or all the important crop species of the Solanaceae. While correspondence of genomic position has been observed for loci governing morphological and physiological characters in plants, no information was available when we began this work on the extent to which results such as our CMV study would have implications for related crops in the same family. Using results from the CMV study, and other mapping studies including a collaborative study that mapped dominant resistance to tomato spotted wilt virus in pepper (Jahn et al., in final preparation), we compiled map positions for all available solanaceous R genes on a comparative map. Resistance genes occurred at corresponding genomic positions more often than would be expected by chance, however, in only two cases, both involving *Phytophthora* species, did genes at corresponding positions have similar resistance specificities (Grube et al., accepted). This detailed analysis and synthesis of a limited data set comprising all available published and new data suggests a working hypothesis regarding the evolution of R genes. Specifically, while host R gene specificity (i.e. which pathogen taxa are controlled) may be evolving rapidly, general functions of R alleles (e.g. initiation of resistance response) may be conserved at homologous loci in related plant genera.

This project has resulted in the extension of molecular tools to *Capsicum*, and the tying together of tomato, potato and pepper to define an important resource for comparative genetics in plants, unparalleled for the analysis of disease resistance. Results from this work are already being applied at seed companies in Israel and the U.S. where use of PCR-based markers identified in these studies as linked to disease resistance or important horticultural characters such as fruit color are being tested, scaled up and implemented in commercial breeding programs. Because the costs of these activities are not public, it is not possible to estimate the economic benefits, but when the cost of using markers compared with full scale phenotypically based screens are compared, there is usually a large saving in time, effort, and cost, and often increased accuracy. The cooperation between the labs was essential to achieving this payoff because each group brought a complementary set of genetic and technical resources and capabilities to the project resulting in the wide breadth of impact.

Background

An important issue for the investment in molecular mapping in crop species is the extent to which results from one species may be relevant for another. Can the wealth of tomato genetics and the significant investment in genome research for this species provide a base to identify genes coding for qualitative and quantitative traits of economic importance in other solanaceous crops, e.g., pepper? Pepper has become a very valuable horticultural crop of still growing importance in both Israel and the USA. It has been suggested that the investment in the development of necessary tools for marker-assisted selection will yield especially high returns in valuable crops where diverse market types require the same improvements, e.g., the addition of disease resistance to a number of different market classes. This is precisely the situation with *Capsicum*, where numerous valuable specialty types exist in addition to the most important bell classes.

Variation for many of the agriculturally important traits in crop species is quantitatively inherited. Knowledge of the number of QTL that control a particular trait, their gene action, the magnitude of their effects, and their interactions with other loci and with the environment should greatly expedite the selection of these traits, at least in theory. There is, however, a great disparity between the amount of information in the scientific literature on QTL mapping and the actual utilization of this information for crop improvement. Our objectives for this grant were: first, to tag and map genes controlling quantitative variation for economically important traits in pepper including fruit quality parameters and cucumber mosaic virus (CMV) resistance and to improve the molecular maps available for *Capsicum*; second, to develop breeding lines that contain QTL for these traits; and third, to test the hypothesis that at least some genes that control important traits in pepper and tomato may be orthologous.

Methodologies and Materials

Germplasm and Genetic Populations

For the development of a comparative genetic map of *Capsicum*, an F₂ mapping population of 75 plants was developed by self-pollinating one F₁ hybrid plant of *C. annuum* cv. 'NuMex RNaky' x *C. chinense* PI 159234. The parents, F₁, and F₂ plants

were grown in the greenhouse at Cornell University, and DNA was extracted from harvested leaf tissue following the procedure of Prince *et al.* (1997).

For QTL mapping studies, an intra-specific F₂ population was constructed from a cross of the two inbred *C. annuum* lines 'Maor' and 'Perennial'. Two hundred and thirty F₂ plants, originating from a single ('Maor' x 'Perennial') F₁ were grown in the greenhouse in 1995 and selfed to obtain F₃ seeds. A subset of 180 randomly chosen F₂ and their F₃ progenies were used for the QTL analysis reported in this study.

Trait evaluation for QTL analysis

The two parents, their F₁ and 180 F₃ families were grown in the open field in Qiryat Gat, Israel, during the summers of 1996, 1997 and 1998. See Ben-Chaim *et al.* in the Appendix for details on experimental design. The plants were measured for the following traits: Ripening date, plant height, fresh fruit weight, total soluble solids concentration, fruit length, diameter, shape, and firmness, pedicel length and diameter, pericarp thickness, seed weight, degree of green (pre-mature) fruit color, measured by a Minolta chromameter (model CR-200), quantifying L (lightness), C (chroma) and H (hue) parameters, and degree of red (mature) fruit color. Narrow-sense heritability was estimated as described by Ben Chaim and Paran (2000). Correlations between traits were estimated by the QGENE program. DNA was extracted from 220 F₂ individuals and filters were prepared for Southern hybridizations. Based on the map of Livingstone *et al.* (1999), tomato and pepper cDNA and genomic clones were chosen for RFLP analysis to allow complete genome coverage. See Ben-Chaim *et al.* for details.

CMV resistance evaluation

A total of three CMV inoculations were performed. Two inoculations were performed in 1997 and 1998 in The Volcani Institute, Israel using a subgroup I isolate. A third inoculation was performed in 1997 in Cornell University with a subgroup I isolate CMV-V27. For details of experimental treatments, see Ben-Chaim *et al.* in appendix.

Associations between the fruit color genes, C1, C2, and carotenoid biosynthetic enzymes

A population segregating for mature fruit color was created from a cross between *C. chinense* PI 152225 (red) and *C. annuum* 4751 (ivory-white). A total of 174 BC1 individuals were grown in the greenhouse at Bet Dagan, Israel during the summer of 1997. Five to ten fruits were selected from each plant, stored for one week, then matched to Munsell color standards. See Thorup et al., in appendix, for details. Associations between *C1* and *C2* and structural genes from the carotenoid biosynthetic pathway were tested by genotyping the BC1 population with the cloned carotenoid genes used as probes in RFLP. Genes showing RFLP segregating with only the red or white-fruited individuals were used to genotype the entire BC1 population. Map positions for the carotenoid biosynthetic enzymes were obtained as described in Thorup et al.

Comparative Genetic Analysis of Disease Resistance in the Solanaceae

The comparative maps used in this analysis are described in the manuscript by Grube et al. in the appendix. All published chromosomal locations for R genes and major QTL ($\text{LOD} > 2$ or $p < 0.01$) for tomato, potato and pepper were placed on the synteny map. Ninety R loci are listed in Table 1 with original references. For clarity, some QTL were named or renamed for ease of display. Most positions were inferred from linkage to reference markers and should be considered a best approximation. As an approximation, genetic distances were treated as constant across all molecular maps. Cross-generic gene clusters were defined by the presence of two or more genes in distinct genera within 15 cM. This interval was selected to be conservative in light of the observation that intrageneric R gene clusters vary in size from 0-30 cM, and to remain informative given the inherent imprecision of comparative mapping.

Mapping disease resistance loci in pepper:

Tsw confers resistance to tomato spotted wilt virus in pepper and a single map position was obtained in our interspecific mapping population (JAHN et al. accepted). Map positions for *Pvr4* and *Pvr7*, tightly linked potyvirus resistance genes, were obtained by analyzing DNA samples from our interspecific mapping population for a *Pvr4*-linked

sequence characterized amplified region (SCAR) marker tightly linked to *Pvr4* (GRUBE *et al.* in press).

Results and Discussion

A critical tool for comparisons across species was a well-developed comparative map thoroughly anchored in tomato. Towards this end, we published a detailed comparative genetic map that now establishes tomato and pepper, together with potato as the broadest comparative genetic system in the dicots (Livingstone *et al.* 1999). This study conclusively establishes that 18 homeologous genome segments comprise 98% and 95% of the tomato and pepper genomes respectively. Within segments, marker order is well conserved and no systematic differences in genetic distances between markers are evident. Despite the difference in genome size (pepper is about 2.5 x tomato), the genetic maps are almost identical in length. This study was performed in an interspecific *C. annuum* x *C. chinense* F2 population that maximized polymorphism and therefore maximized the number of common markers between tomato and pepper, but this population was too small for QTL analysis and exhibited some sterility further limiting its utility for mapping fruit characters.

Additional studies that avoid the limitations encountered in the comparative mapping population that have addressed all three research objectives were performed in a larger *C. annuum* population derived from a cross between 'Maor', a large fruited bell-type commercial variety and 'Perennial', a small fruited pungent pepper collected in India that has served as the most important source of CMV resistance in pepper breeding. This larger population (originally >200 individuals) was better suited for mapping the traits of interest including fruit characters and CMV resistance. We performed a biometrical analysis of the characters segregating in this population (Ben-Chaim and Paran, 2000). Further, we have genetically mapped a number of horticulturally important traits in this population (Ben Chaim *et al.*, submitted, see appendix) and also we have identified several important loci for CMV resistance (Ben Chaim *et al.*, submitted, see appendix). In this population, we constructed an intra-specific comparative genetic map consisting of 177 RFLP, AFLP, and RAPD markers that span the pepper genome. To examine genetic control of fruit characters, 180 F3 families were grown and visually

scored during 3 field seasons in Israel. From these data, a total of 55 QTL were identified by interval analysis at LOD > 3.0. One QTL located on chromosome 3 explained more than 60% of the phenotypic variability for fruit shape and affected most of the other traits evaluated in this study. Three other QTL for multiple traits were noted on Lgs 2, 8 and 10 suggesting their importance as loci that control developmental processes with pleiotropic effects. A total of 6 possible correspondences between QTL in pepper and tomato that affect the same traits were observed for fruit shape, fruit color, fruit weight, and plant height.

To further examine the biology that might underlie these correspondences, we selected fruit color as the trait we would first pursue because the biochemical pathway that produces the pigments that determine fruit color is well characterized. We set out to test the hypothesis that the structural genes for the carotenoid biosynthetic pathway may be candidate genes for both qualitative and quantitatively inherited genes for fruit color in both tomato and pepper. We confirmed that the *y* locus for red fruit color in pepper was identical to the structural gene encoding capsanthin-capsorubin synthase (Popovsky and Paran, in press). We determined the map positions for a second enzyme in this pathway, phytoene synthase, corresponds to another gene that controls qualitative shifts in pepper fruit color, *C2*. When we placed all 10 structural gene clones on our comparative genetic map, in addition to the two correspondences with *Y* and *C2*, we noted possible correspondences with a pepper fruit color QTL in the Livingstone population (Livingstone 1999) and 2 others identified in Ben-Chaim et al. in preparation, 4 tomato QTL for fruit color previously reported by Bernacchi et al. 1998, two qualitative mutants in tomato for fruit color shifts, *B* and *l2*, and with the *Y* gene in potato for yellow tubers (Thorup et al., in final preparation, see appendix).

The *C. annuum* mapping population that served as the base for the analysis of fruit characters was also segregating for polygenic resistance to cucumber mosaic virus, the most important viral pathogen of pepper causing devastating losses worldwide. Despite the importance of this disease, breeding lines with adequate levels of resistance are just now appearing and often are not suitable for type and horticultural performance due to the difficulty of phenotypically-based disease screens. While the symptoms of this disease are devastating, their expression is very dependent on inoculation procedures,

host genetic background and the screening environment. F3 families from this population were scored for resistance to CMV in Ithaca, NY and Bet-Dagan Israel three times over 2 years. Four QTL were identified. The position the QTL, cmv 11.1 at TG36 corresponds to previous reports that resistance to CMV is linked to TMV susceptibility (the L locus for TMV resistance is also tightly linked to TG36). Also, the CMV resistance loci on chromosomes 3 and 4 are associated with small fruit, a problem with many of the CMV breeding lines produced to date. We now have the marker information to identify breeding lines where a recombination has separated the QTL for fruit size from the CMV R QTL. In addition, fingerprinting an advanced CMV resistant breeding line derived from Perennial indicated that the QTL identified in the F3 populations were also introgressed in this line, providing a confirmation of the QTL analysis.

CMV is just one of a number of pathogens that infect across the Solanaceae. While correspondence has been observed for morphological and physiological characters in plants, no information was available when we began this work on the extent to which results such as our CMV study would have implications for related crops in the same family. Using results from the CMV study, and other mapping studies including a collaborative study that mapped dominant resistance to tomato spotted wilt virus in pepper (Jahn et al., accepted), we compiled map positions for all available solanaceous R genes on a comparative map. Resistance genes occurred at corresponding genomic positions more often than would be expected by chance, however, in only two cases, both involving *Phytophthora* species, did genes at corresponding positions have similar resistance specificities. In contrast, resistances to *Globodera* spp., *Meloidogyne* spp., potato virus Y, tobacco mosaic virus and tomato spotted wilt virus were mapped in two or more genera and did not occur in corresponding positions. Without exception, pepper homologues of the cloned R genes *Sw-5*, *N*, *Pto*, *Prf*, and *I2* were found in syntenous positions in other solanaceous genomes, and in some cases also mapped to additional positions near phenotypically defined solanaceous R genes. This detailed analysis and synthesis of a limited data set comprising all available published and new data suggests a working hypothesis regarding the evolution of R genes. Specifically, while host R gene specificity (i.e. which pathogen taxa are controlled) may be evolving rapidly, general

functions of R alleles (e.g. initiation of resistance response) may be conserved at homologous loci in related plant genera.

Scientific implications and impact on agriculture

This body of work has established *Capsicum* as one of the members of the broadest comparative genetic system outside the Poaceae, and has added a large number of traits to the genetic map including a number of fruit and plant growth characters and resistance to CMV, potyviruses, and tomato spotted wilt virus. This information will allow efforts to develop and implement marker-assisted selection in pepper for a host of characters. Further, we have completed a large comparative study of genome composition in the Solanaceae, and then extended this work to provide the first comprehensive examination of the organization and evolution of resistance genes in related plant species. While loci for resistance to a particular pathogen are not generally found at corresponding positions, our results indicate that there do appear to be conserved positions at which resistance genes are found if specificity is disregarded. Further, results from QTL analyses in pepper indicate that loci that control quantitative traits may also correspond, suggesting that efforts to characterize these loci will have implications beyond the species of origin. Finally, for one fruit trait, fruit color, we established that the structural genes for the carotenoid biosynthetic pathway are potential candidates for loci that control both qualitative and quantitative variation in fruit color, and that results from candidate analysis in pepper may extend to loci that control organ pigmentation in both tomato and pepper.

Refereed Publications/Manuscripts in preparation that acknowledge BARD support Included in Appendix

Ben Chaim, A., R.C. Grube, M. Lapidot, M.K. Jahn and I. Paran. Identification of quantitative trait loci associated with tolerance to cucumber mosaic virus in *Capsicum annuum*. Submitted to Theor Appl Genet.

Ben-Chaim, A. and I. Paran. 2000. Genetic analysis of quantitative traits in pepper. J. Amer. Soc. Hort. Sci. 125:66-70.

Ben-Chaim, A, I. Paran, R.C. Grube, M.K. Jahn, R. van Wijk and J. Peleman. QTL mapping of fruit-related traits in pepper (*Capsicum annuum*). Submitted to Theor Appl Genet.

Grube, R.C., E.R. Radwanski and M.K. Jahn. Comparative genetics of disease resistance in the Solanaceae. Accepted Genetics.

Livingstone, K.D., V. Lackney, J.R. Blauth, R. Van Wijk and M.K. Jahn. 1999. Genome mapping in *Capsicum* and the evolution of genome structure in the Solanaceae. Genetics 152:1183-1202.

Thorup, T.A., B. Tanyolac, K.D. Livingstone, S. Popovsky, I. Paran and M.K. Jahn. The carotenoid biosynthetic pathway and the comparative genetics of quantitative and qualitative variation in fruit color in *Capsicum* and *Lycopersicon*. In final preparation.

Papers that acknowledge this grant—3 reprints have been or will be provided

Grube, R.C., J.R. Blauth, M. Arnedo, C. Caranta and MK Jahn. Identification and comparative mapping of a dominant potyvirus resistance gene cluster in *Capsicum*. Accepted Theor Appl Genet.

Grube, RC, Y Zhang, JF Murphy, F Loaiza-Figueroa, R Provvidenti and MK Jahn. A new source of resistance to *Cucumber mosaic cucumovirus* in *Capsicum frutescens*. Submitted Plant Disease 10/99

Kyle, M.M. and A. Palloix. 1997. Proposed revision of nomenclature for potyvirus resistance genes in *Capsicum*. Euphytica 97:183-188.

Jahn, M.K., I Paran, K Hoffmann, ER Radwanski, KD Livingstone, RC Grube, E Aftergroot, M Lapidot and J Moyer. Genetic mapping of the *Tsw* locus for resistance to tomato spotted wilt tospovirus in *Capsicum* and its relationship to the *Sw-5* allele for resistance to the same pathogen in tomato. accepted Molec Plant Microbe Interactions.

Murphy, J.F., J.R. Blauth, K.D. Livingstone, V.K. Lackney and M.K. Jahn. 1998. Genetic mapping of the *pvr1* locus in *Capsicum* and evidence that distinct potyvirus resistance loci control responses that differ at the cellular and whole plant level. Molecular Plant Microbe Interactions 11:943-951.

Prince, J.P., Y. Zhang, E.R. Radwanski and M.M. Kyle. 1997. A high-yielding and versatile DNA extraction protocol for *Capsicum*. HortScience 32:937-939.