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Review

Solanaceae genomics: Current status of tomato (*Solanum lycopersicum*) genome sequencing and its application to pepper (*Capsicum* spp.) genome research

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Abstract Unique developmental aspects, divergent phenotypes and habitats of Solanaceae make the family an ideal model to investigate the basis of diversification and adaptation. In view of this uniqueness, a global tomato genome sequencing project designated "International Solanaceae Genome Project (SOL): Systems Approach to Diversity and Adaptation" has been launched. The goal of this initiative is to sequence the 220 Mb euchromatin that is expected to contain the majority of coding sequences, rather than 950 Mb full-length tomato genome. Given the high degree of similarity of tomato and pepper genomes, it will be particularly interesting to apply tomato genome information to pepper using a comparative genomics approach. In this review, we discuss the current progress in sequencing of tomato in Korea, genomics resources of pepper and beneficiary of the tomato sequence.

Key words: Bacterial artificial chromosome (BAC), comparative genomics, fluorescence *in situ* hybridization (FISH), genome sequencing, *Solanaceae*.

Solanaceae comprises more than 3000 species, including tuber or fruit-bearing vegetables (potato, tomato, eggplant and pepper), ornamental flowers (petunia), and medicinal plants (*Datura, Capsicum*) (Knapp 2002). The *Solanaceous* species has been extensively utilized as model plants to study various characteristics, such as fruit development and plant defense in tomato and pepper (Tanksley 2004; Giovannoni 2004; Adams-Phillips et al. 2004; Pedley and Martin 2003; Gebhardt and Volkonen 2001), tuber development in potato (Fernie and Willmitzer 2001).With regard to practical aspects, plants in the *Solanaceae* family play key roles in emerging or cutting-edge technologies, including tobacco and *Nicotiana benthamiana* for *Agrobacterium*-mediated plant transformation and virus-induced gene silencing (VIGS), respectively (Ruiz et al. 1998).

Most *Solanaceous* species are diploid with the same basic chromosome number (x=12). Furthermore, significant macro- and micro-synteny conservation and gene repertories amongst the genomes of tomato, potato, pepper and eggplant make *Solanaceae* an excellent model for comparative genomics (Knapp et al. 2004; Doganlar et al. 2002; Livingstone wt al. 1999; Tanksley et al. 1992). As the high cost of sequencing prohibits direct comparison between full *Solanaceous* genomes, we require a high quality reference full-length genome sequence to map ESTs (expressed sequence tags) or methyl-filtered sequences (Whitelaw et al. 2003; Palmer et al. 2003). To fulfill this objective, sequencing of gene-rich regions of the tomato genome is underway via SOL. All the information generated from the SOL projects will advance genomics study of not only the tomato, but also other close relative species. The characteristics of extensive sequence similarity and genome synteny between tomato and pepper definitely accelerate research trends on pepper, the most valuable vegetable crops in Korea. In this review, we summarize the current status of genome sequencing, available genomics resources in pepper, and beneficiary of the tomato sequence.

Tomato: a reference for *Solanaceae* genome sequencing

Tomato is the most intensively studied *Solanaceae* genome due to its simple diploid genetics, short generation times, routine transformation technology, and

Abbreviation: BAC; bacterial artificial chromosome, BES; BAC end sequences, ESTs; expressed sequence tags, FPC; finger print contig, FISH; fluorescence *in situ* hybridization, NOR; nucleolar organizing region, VIGS; virus-induced gene silencing.

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This article can be found at http://www.jspcmb.jp

the advantage of readily available rich genetic and genomic resources. The tomato genome size (1C amount) is generally considered as approximately 95 pg of DNA (Michaelson et al. 1991). With relatively small genome size, tomato has an excellent high-density molecular map (Tanksley et al. 1992; Broun and Tanksley 1996) and an advanced BAC (bacterial artificial chromosome)-based physical map to initiate sequencing project (http://www.sgn.cornell.edu/solanaceae-project/).

Tomato genome sequencing strategy

In contrast to heterochromatin, which is rich in repetitive sequences and poor in genes, euchromatin contains the majority of protein-coding genes. Since one-quarter of the tomato genome consists of euchromatin (ca. 220 Mb), sequencing a minimal tiling path of BAC clones encompassing this portion of the genome is the most plausible strategy. For this purpose, *Hin*dIII, MboI and EcoRI-digested BAC libraries were prepared from *Solanum lycopersicum* var Heinz 1706. Sequencing is based on the *S. esculentum* LA925×*S. pennellii* LA716 type F2-2000 map (http://sgn.cornell.edu) used for anchoring 1500 markers by overgo hybridization (Cai et al. 1998). At present, more than 650 available anchor points are used as "seed BAC" for sequencing. Extension is performed by walking out from the seed BAC sequence in both directions using the deep BAC end sequences (BES) and finger print contig (FPC) maps available from the *Hin*dIII and MboI libraries. FISH (fluorescence *in situ* hybridization) analysis is additionally employed to confirm chromosome mapping and delineate the euchromatin/heterochromatin boundaries (Peterson et al. 1999). General flow chart for the SOL project is shown in Figure 1. Currently, 12 chromosomes have been split between 10 countries as follows: Korea (chromosome 2), China (3), UK (4), India (5), The Netherlands (6), France (7), Japan (8), Spain (9), Italy (12) and USA (1, 10, 11). In addition, chloroplast genome sequence is available (Kahlau et al. 2006) and mitochondrial genome sequence is to be sequenced by Argentina.

Tomato chromosome 2 and current sequencing status

The Korean SOL aims to complete the sequencing of euchromatin from chromosome 2. Chromosome 2 is the third largest chromosome in tomato genome (Sherman and Stack 1995). It has not been clearly determined the physical size of chromosome 2, but it is estimated from 22 Mb to 26 Mb (Peterson 1996; Chang 2004). Pachytene chromosome 2 is easily distinguished from other chromosomes, because it is an acrocentric chromosome bears a large secondary structure, the nucleolar

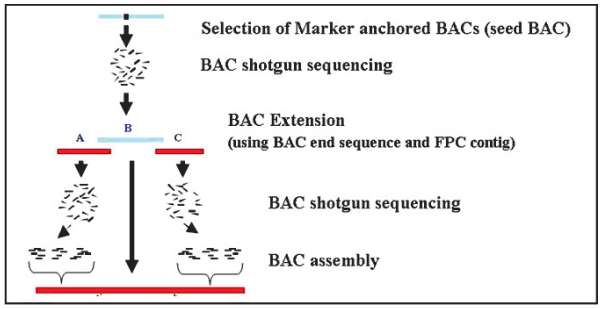

Figure 1. BAC to BAC sequencing procedure for the SOL project. At first, selections od "seed BACs" anchored to molecular markers of chromosome 2 have been tried. Extension is performed by walking out from the "seed BAC" sequence in bith directions using the deep BAC end sequences (BES) and finger print contig (FPC) maps.

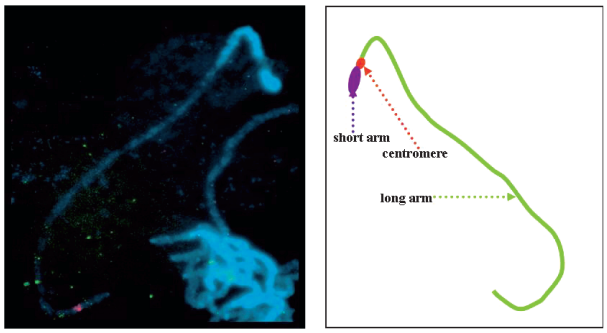

Figure 2. DAPI stained pachytene chromosome 2. Left panel indicates the image of DAPI stained pachytene chromosome 2. Brightly fluorescing heterochromtamic regions were detected at the short arm and next to centromere of long arm of chromosome 2. In contrast, weakly fluoresing euchromation was observed at the long arm of chromosome 2. The entire euchromatic block is located on distal region of the long arm of chromosome 2 that is clearly separated from remained heterochromatic block. Right panel indicates the idiogram of chromosome 2.

organizing region (NOR) at short arm (Figure 2). The acrocentromeric structure of chromosome 2 does not require additional chromosome 2 specific probe, when we try FISH for selection of chromosome 2 specific BAC clones. Since entire euchromatic block is clearly separated from the remained heterochroromatic block, it does not require accurate determination of euchromatic and heterochromatic boundaries (Figure 2). The linkage group 2 spanned 143 cM and BAC-based physical map of chromosome 2 are well defined using 308 molecular markers and 75 molecular markers anchored BAC clone, respectively.

Following the initial sequencing stage, 69 candidate "seed BAC" clones were selected that anchored DNA markers generated from chromosome 2. Among these, 37 were selected as "seed BAC" clones by overgo probe hybridization and FISH analysis. Subsequently, 37 BAC clones were sequenced, and their annotation is underway. We have been walking out from the seed BAC sequence to extend sequenced region of chromosome. For BAC extension, we mainly examined the BAC end sequence

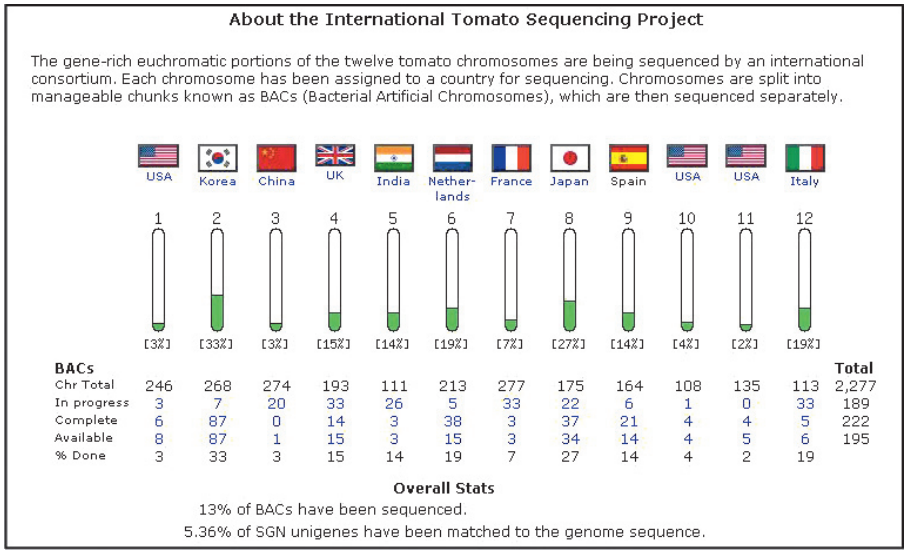

Figure 3. Current sequencing status of chromosome 2. To date (Oct. 2006), about 13% of entire euchromatic portions have been sequenced by international efforts. Over 30% euchromotaic portion of chromosome 2 has been sequenced by Korea SOL team.

(BES) database, because the size of individual contigs of FPC map is not sufficient to applicable for this project. BES searches identified next BAC clones overlapping with previously sequenced clones, recently. Result of current endeavors, we have finished total ~8 Mb sequences using 83 "seed" and "next" BAC clones. This number represents that about 30% of entire euchromatic portion of chromosome 2 were identified (Figure 3). The current status of progress in tomato sequencing is accessible on the SGN web site.

Pepper: a beneficiary of the tomato sequence

Comparative genetic molecular mapping in plants reveals a high level of conservation of gene content and order within grasses, crucifers, and legumes species (Paterson et al. 2000). Sequencing data disclose that more than 80% of the genes annotated in *Arabidopsis* are also found in rice (Bennetzen 2002). Comparative organization of the chromosomes of pepper and tomato reveals that both species are highly conserved (Tanksley et al. 1988; Linvingstone et al. 1999). Although the numbers of copies and loci of these genes are not entirely conserved, the two species share the same basic set of genes. These results indicate that the tomato sequence is applicable to pepper, similar to the relationship between the *Cruciferae* and *leguminosae* families (Paterson et al. 2001; Udvardi et al. 2005).

The economic and physiological importance of *Capsicum*

Pepper (*Capsicum* spp.), a member of the *Solanaceae* family, is widely used in the cuisine of many cultures.

Table 1. A list of *Capsicum* species based on IBPGR (1983).

Domesticated Species	*C. annuum*
	C. baccatum
	C. chinense
	C. frutescens
	C. pubescens
Wild Species	*C. buforum*
	C. campylopodium
	C. cardenasii
	C. chacoense
	C. ciliatum
	C. coccineum
	C. cornutum
	C. dimorphum
	C. dusenii
	C. eximinum
	C. galapagoense
	C. geminifolium
	C. hookerianum
	C. lanceolatum
	C. leptopodium
	C. minutiflorum
	C. mirabile
	C. paraetermissum
	C. parvifolium
	C. schottianum
	C. scolnikianum
	C. tovarii
	C. villosum

Pepper consumption is increasing worldwide, and the vegetable is an important source of vitamins and essential nutrients. In addition to its use as a food, pepper pungency (capsaicin) is employed to provide pain and long-term inflammation relief, and as topical medication for arthritis. *Capsicum* is endowed with a multitude of fruit forms, colors, and sizes. Today, the genus *Capsicum* consists of at least 25 wild and five domesticated species, as shown in Table 1. Among the five domesticated species, the majority of cultivated pepper is *C. annuum*.

Table 2. A list of pepper mapping populations from five countries.

Population	Country (PI)
C. annuum 'AG 672'×*C. chinense* 'CNPH 679'	Brazil (Leonardo Silva Boiteux)
C. annuum 'Majorca'×*C. annuum* 'CNPH 148'	Brazil (Leonardo Silva Boiteux)
C. annuum 'Azeth'×*C. annuum* 'CNPH 143'	Brazil (Leonardo Silva Boiteux)
C. annuum 'H3'×'Vania'	France (Alain Palloix)
'Perennial'×'Yolo Wonder'	France (Alain Palloix)
'Yolo Wonder'×'Criollo de Morelo's 334'	France (Alain Palloix)
Vania×*C. baccatum* 'Pen 79'	France (Alain Palloix)
C. frutescens 'BG 2816'×*C. annuum* 'Maor'	Israel (Ilan Paran)
C. annuum 'Maor'×*C. annuum* 'Perrenial'	Israel (Ilan Paran)
C. annuum '5226'×*C. chinense* 'PI 159234'	Israel (Ilan Paran)
C. chinense 'PI 152225' in background of *C. annuum*	Israel (Ilan Paran)
C. chinense 'Habanero'×*C. annuum* 'TF68'	Korea (Byung-Dong Kim)
C. annuum 'CM334'×*C. annuum* 'Chilsung'	Korea (Byung-Dong Kim)
C. annuum 'ECW123R'×*C. annuum* 'CM334'	Korea (Byung-Dong Kim)
C. annuum 'NuMex RNaky'×*C. chinense* 'PI 159234' (in progress)	USA (Molly Jahn)
C. frutescens BG2914-6×*C. annuum* RNaky F2 (in progress)	USA (Molly Jahn)
C. chinense 159234×*C. chinense* Habanero	USA (Molly Jahn)
C. frutescens BG2814-6×*C. chinense* 149234	USA (Molly Jahn)

Most of the Korean accession originates from this species, classified as sweet chili pepper. The chili pepper is widely used as raw or dried seasoning (in the form of pepper powder or paste) due to its pungency. In contrast, sweet pepper is consumed as a vegetable, since it has no pungency. In Korea, pepper is the second most valuable crop family exceeded only by rice, and the most valuable in terms of vegetable crops.

Pepper genomics resources

Three different BAC libraries, *Capsicum annuum* 'CM334' (15X haploid genome equivalent), the double haploid line 'HD208' (10X haploid genome equivalent) and *Capsicum frutescens* BG2816 (9X haploid genome equivalent), are currently available. A total of 29,580 ESTs, including 18,432 contigs and 11,148 singletons, were analyzed from 21 different libraries of pepper (S Lee, unpublished data). These are annotated in the *Solanaceae* gene index in KRIBB (Korea Research Institute of Bioscience & Biotechnology, http://www.kribb.re.kr/). In addition, a oligo-chip (followed Nimble Gene platform) containing ca. 30,000 unigenes is available to the community. Array data contained about 5000 ESTs are also available from the hot pepper microarray database (http://plant.pdrc.re.kr/array/index.html). To date, 18 mapping populations have been generated by five countries (Brazil, France, Israel, Korea, and USA) (Table 2). A number of germplasms have been collected, stored and released by the Chile Pepper Institute at New Mexico State University (http://www.nmsu.edu/), Asian Vegetable Research and Development Center (AVRDC, http://www.avrdc.org/) at Taiwan, Centro Agronómico Tropical de Investigación y Enseñanza (CATIE, http://www.catie.ac.cr/catie/) at Costa Rica, Center for Genetic Resources (CGN, http://www.cgn.wageningen-ur.nl/pgr/) at The Netherlands, and Central Institute for Genetics and Germplasm at Germany. Current metabolic profiling of the *Capsicum* species by the research group in SNU (Seoul National University) focuses on capsaicinoids and volatile compounds.

Pepper genome structure

The nuclear DNA content of various *Capsicum* species ranges from 3.34 to 3.43 pg (3273–3361 Mb) in *C. chacoense* and *C. annuum* to 5.77 pg (5655 Mb) in *C. parvifolium* (Morscone et al. 2003). This is approximately more than three-fold larger than the tomato genome. Most pepper species are diploid with 24 chromosomes (2n=2x=24). Comparative organization of the chromosomes of pepper and tomato has been reported by several researchers (Tanksley et al. 1998; Livingstone et al. 1999). Tanksley et al. (1998) showed that the gene repertoire of these two species is highly conserved, yet the linear order of the genes on the chromosomes is greatly modified. Furthermore, the numbers of copies and loci of these genes is not entirely conserved, due to extensive rearrangement (Tanksley et al. 1998). In addition, hybridization of all tomato-derived probes onto the pepper genetic map by Livingstone group reveals that no major losses occur during the divergence of these genomes, 18 homologous linkage blocks cover 98.1% of the tomato genome and 95% of the pepper genome, and the overall genetic lengths of pepper and tomato are approximately equal, despite different genome sizes (Livingstone et al. 1999). As a result, significant macro- and micro-synteny conservation and gene repertories between the genomes of tomato and pepper may be useful in the analysis of orthologous gene functions.

Pepper functional genomics

VIGS (virus induced gene silencing) is an attractive approach that involves rapid assessment of gene function, prior to stable transformation. VIGS has been successfully applied to *Solanaceae*, including *Nicotiana* species (Baulcombe 1999), *Solanum* species (Brigneti et al. 2004) and tomato (Liu et al. 2002). We have recently established a TRV (tobacco rattle virus)-based VIGS system in pepper (Chung et al. 2004). Although gain-of-function studies were performed using *Agrobacterium*-mediated transformation in pepper, a successful and reproducible transformation method is yet to be established. In addition to our efforts, a number of investigators have explored the methodology of *Agrobacterium*-mediated transformation in pepper (Kim et al. 2001; Cai et al. 2000; Li et al. 2003: Lee et al. 2004). To date, agrobacterium-mediated transformation in pepper is extremely inefficient (0.5–1% success rate) the main obstacle of functional genomics in pepper (Jung et al. 2005). To overcome this difficulty, we plan to use heterologous systems for gain-of-function studies. A miniature tomato cultivar Micro-Tom is possibly the best candidate for this purpose, since it has several advantages for functional genomics analysis on a laboratory scale, including short life cycle (70–90 days), easy growth conditions, occupation of small density, and routine genetic transformation (Meissner et al. 1997).

Expected data from comparative pepper-tomato genomes

In recent years, particular emphasis has been placed on tomato as an exceptionally tractable system for the molecular genetic analysis of fleshy fruit development and ripening. Fleshy fruits undergo distinctive ripening processes in which the biochemistry, physiology and structure of the organ are developmentally altered to influence appearance, texture, flavor and aroma in ways designed to attract seed-dispersing organisms. The major difference between tomato and pepper is that the former follows climacteric, while the latter displays non-climacteric fruit ripening. Recent cloning of *LeMADS-Rin* in tomato revealed a global developmental regulator of ripening potentially shared among climacteric and non-climacteric species (Vrebalov et al. 2002). Through comparative genomics approaches, it should be possible to determine the evolutionary changes/conservations that enable disparate/converse ripening mechanisms between both types of fruit.

The comparative genomics approach has advanced the discovery and understanding of conserved genes. However, most sequencing projects have additionally revealed many rapidly evolving 'orphan' genes of unknown function and evolutionary history (Paterson et al. 2001). A BLAST sequence comparison between pepper ESTs and other *Solanaceae* plants, including eggplant, *N. bentamiana*, *N. tabacum*, tomato and potato, disclosed the putative pepper specific genes (Lee et al., unpublished data). Although appropriate approaches are required for the accurate estimation of pepper-specific genes, this preliminary information indicates the possible importance of these genes in accounting for key differences between pepper and other *Solanaceous* species.

The abundance of information and resources related to diverse plant defense responses and the numerous R genes cloned from *Solanaceae*s (Martin et al. 2003) should facilitate characterization of the tomato genome sequence to improve our understanding of plant disease resistance and susceptibility. Furthermore, it is important to note that pepper is susceptible to many of the same pathogens as tomato. Comparative genomics approaches will be beneficial in the study of plant defense responses in pepper. The recent isolation of late blight resistance genes in potato using comparative genomics is a good example of these approaches (Huang et al. 2005).

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