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*Review paper*

# AN OVERVIEW OF MOLECULAR GENETIC LINKAGE MAPS IN *Lilium* SPP.

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Molecular genetic linkage maps are powerful tools used to identify quantitative trait loci and facilitate molecular marker-assisted breeding. A review of the molecular markers applied and genetic linkage maps constructed for *Lilium* was conducted. High-density linkage maps constructed for other plant species were also analyzed. Problems related to the construction of molecular genetic linkage maps for *Lilium* were explored. High-density linkage maps for *Lilium* may be developed on the basis of the construction strategies of several detailed linkage maps.

*Keywords:* Molecular marker, genetic linkage map, quantitative trait locus (QTL), high-density map, *Lilium*

## INTRODUCTION

Lilies are important ornamental flower plants that have become a new cut popular flower following *Dianthus caryophyllus*, *Rosa hybrida* (modern rose), *Dendranthema morifolium*, *Gladiolus hybridus*, and *Gerbera jamesonii*. Comprising more than 90 species, the genus *Lilium* is classified into seven sections—*Lilium*, *Martagon*, *Pseudolirium*, *Archelirion*, *Sinomartagon*, *Leucolirion*, and *Oxypetalum* (COMBER, 1949; ASANO, 1989). The molecular markers and genetic

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linkage maps of *Lilium* are less studied than those of other ornamental plants because of its large genome (approximately $3.6\times10^{10}$ bp; more than 300 times of *Arabidopsis* and nearly 100 times of rice) (HUO *et al.,* 2011). Molecular-assisted breeding performs better than the traditional breeding technique because of the rapid advancement of molecular marker techniques for *Lilium*. At present, nearly 10 molecular markers have been applied in studies of *Lilium* species and interspecific hybrid (YAMAGISHI *et al.,* 2002), tracing parents (HARUKI *et al.,* 1998), genetic variation (PERSSON *et al.,* 2004; AMAURY *et al.,* 2005), and markers closely linked to disease resistance (STRAATHOF *et al.,* 1996; VAN HEUSDEN *et al.,* 2002; YOSHIJI *et al.,* 2002; SHAHIN *et al.,* 2009) or carotenoid pigmentation NAKANO *et al.,* 2005).

Marker-assisted selection (MAS) can dramatically speed up the progress of linkage map construction for *Lilium.* However, the goal of this study is to construct a saturated linkage map. According to published data, the genetic linkage map for *Lilium* originated from Asiatic lily hybrid and *L. longiflorum*, wherein four linkage maps were completed using amplified fragment length polymorphisms (AFLPs), sequence-related amplified polymorphisms (SRAPs), diversity arrays technology (DArT), random amplified polymorphic DNA (RAPD), and inter-simple sequence repeats (ISSRs). Although the linkage maps for *Lilium* are not saturated, trial works have developed molecular markers and prepared an integrated map for *Lilium*. High-density linkage maps successfully constructed for several plants, such as tomato/potato, rice, Italian ryegrass, rye, lettuce, and eucalyptus, may be used as a basis to build a similar map for *Lilium* (TANKSLEY *et al.,* 1992; HARUSHIMA *et al.,* 1998; INOUE *et al.,*2004; HANNA *et al.,* 2009; TRUCO *et al.,* 2007; LEANDRO *et al.,* 2011).

## APPLICATION OF DNA MARKERs IN *Lilium*

### Identification of species and hybrids

The early identification of species and hybrids and the determination of hybridism in *Lilium* were conducted using morphological traits and isozyme markers. However, both methods have their disadvantages. Morphological traits are subjective to the environment, and isozyme markers lack enough informative markers. YAMAGISHI *et al.* (1995) first identified 13 *Lilium* species, 9 intra-section hybrids, and 7 inter-section hybrids by using RAPD markers. They found that species and hybrids can be easily distinguished by RAPD markers. RAPD markers were also applied to identify the hybrids of Oriental lilies at the seedling stage or *in vitro* stage (BEATA, 2007; WIEJACHA *et al.,* 2001).

### Analysis of genetic diversity

AMAURY *et al*. (2005) researched the genetic diversity of Miyamasukashi-yuri, an endemic and endangered species of *Lilium* at Mount Buko, Saitama, Japan, by using ISSR markers. In general, large populations show a higher level of gene diversity than small ones, and populations at high altitudes display a greater variation than those at low altitudes. Thus, populations at high altitudes experience greater annual and diurnal climatic variations than those at low altitudes. LIU *et al.* (2012) studied the genetic stability of regenerated shoots in oriental lily on the basis of ISSR marker variation. They found that direct shoot formation from explant regeneration is a safe method to multiply "true-to-type" plants. Simple sequence repeat (SSR) markers, highly polymorphic, and co-dominant characters, have been used to assay the genetic diversity of *Lilium regale* (6 species and 10 cultivars) and 84 lily cultivars (*Lilium formology*, *Lilium formosanum*, *Lilium brownii*, *Lilium longiflorum*, Asiatic hybrids, Oriental hybrids, *L. longiflorum*/Asiatic

hybrids, Oriental/Asiatic hybrids, and Oriental/Trumpet hybrids). Approximately 34.8% primer pairs show polymorphisms with 16 individuals in *L. regale*, and 47 (28%) EST–SSRs are amplified in all *Lilium* species; the polymorphism information content of these selected EST–SSRs in the former ranges from 0.111 to 0.830, with an average of 0.493, whereas that in the latter varies from 0.49 to 0.94, with an average of 0.76 (YUAN *et al.*, 2012; LEE *et al.*, 2011). NURSEL (2010) investigated the distribution of genetic variations between populations of *Lilium albanicum* and *Lilium chalcedonicum* in Greece with RAPD profiles. The researcher found that the genetic differentiation between species is 33% in 33 individuals but 17% among populations in different species and that the maximum total variance is 51%.

**EST analysis of generative Cells and development of EST-SSR Markers**

TAKASHI *et al.* (2006) studied the gene expression profile of generative cells from *L. longiflorum* by sequencing expressed sequence tags (ESTs). A total of 637 unique ESTs contain all 886 ESTs derived from the generative cell DNA library, of which 168 are significantly similar to maize sperm cell ESTs, 129 to Arabidopsis male gametophyte-specific genes, and 55 to both maize sperm cell ESTs and Arabidopsis male gametophyte-specific genes. This finding suggests that these male gamete-specific genes are common across different plant species. LEE *et al.* (2011) and YUAN *et al.* (2012) used sequencing EST information to develop EST-SSR markers and research the genetic characters of cultivars (species and hybrids) in *Lilium*. Yuan found 1716 SSR sites in 1606 UniGene sequences and evaluated 59,046 UniGene sequences by data mining. Lee found that 754 unique ESTs (total of 2235 unique ESTs) include SSR motifs.

**Fingerprint**

YAMAGISHI *et al.* (2002) examined RAPD and ISSP markers in Asiatic hybrid lily 'Montrecux' and 'Connecticut.' In RAPD markers, random primers with four lengths (10-, 12-, 15-, and 20-base) generated 17 (12%), 4 (17%), 33 (54%), and 14 (67%) polymorphic fragments, respectively. The efficiency of the RAPD reaction increased with increasing primer length. Meanwhile, 33 out of 63 (52%) 3′-anchored simple sequence repeat primers amplified polymorphic bands. Examination of the $F_1$ hybrids with these polymorphic primers revealed that the RAPD and ISSR markers are highly reproducible and genetically stable.

**Molecular genetic linkage Maps in *Lilium***

VAN HEUSDEN *et al.* (2002) is one of the earliest reporters of a genetic linkage map in *Lilium*; they constructed a map with 100 descendants of Asiatic hybrid lily by using AFLP markers. In the same year, Abe *et al.* constructed a genetic linkage map for *Lilium* and utilized this map with 96 $F_1$ progenies of Asiatic lily by using a double pseudo-testcross strategy and RAPD and ISSR markers. KHAN *et al.* (2009) completed a genetic linkage map in an $F_1$ population of *Longiflorum* × Asiatic lily hybrids by using DArT markers. We constructed a genetic linkage map for a recombinant inbred line (RIL) population of Raizan No.1 (Formolongo) × Gelria (*Longiflorum*) cultivars by using SRAP markers (data unpublished). Information on the four maps is presented in Table 1.

Several problems can be found from the data in Table 1: (1) the polymorphisms of the AFLP and SRAP markers (both 89.7%) are higher than that of the DArT marker and RAPD and ISSR markers (55.6%, 62%, respectively), but the average interval of the AFLP marker is much better than that of the SRAP marker because the former generates more polymorphic markers than the latter; (2) the size of these populations has a small distinction, but the total genome length varies

distinctively (867.5–2135.5 cM); and (3) the number of linkage groups does not equal to the haploid chromosomes (n=12), which implicates that they are not integrated maps.

Using the same strategy in RAPD–ISSR mapping, CHEN *et al.* (2010) finished the first intra-specific genetic linkage map of winter sweet by using AFLP and ISSR markers; this map is still not saturated, and the average distance of both markers is 20 cM. Gao *et al.* (2008) described a genetic linkage mapping of Chinese hedychium by using an SRAP marker, wherein the percentage of unlinked markers is 11.6%, which is similar to that in the study by LIU *et al.* (2012). However, the mean marker gap (8.0 cM) is smaller than that in the study by LIU *et al.* (2012) (27.4 cM).

*Table 1. Characters of molecular linkage maps in lily*

| Marker systeam | Type of population | Size of population | No. of markers | Morphisms | Total of genome | Average interval | Linkage groups |
|---|---|---|---|---|---|---|---|
| | | | | | cM | cM | |
| AFLP | $F_1$ | 100 | 399 | 251 | 1367 | 5.4 | 24 |
| SRAP | RIL | 180 | 87 | 78 | 2135.5 | 27.4 | 16 |
| DArT | $F_1$ | 88 | 687 | 382 | 1329 | 3.5 | 14 |
| RAPD,ISSR | $F_1$ | 96 | 345 | 95 | 867.5 | 14.1±7.4 | 26 *1 |
| | | | | 119 | 1114.8 | 14.0±8.6 | 24 *2 |

*1: represents the genetic information of parent 'Montreux' using a double pseudo-testcross strategy;*2: represents the genetic information of parent 'Connecticut King' using a double pseudo-testcross strategy

**QTLs of molecular genetic linkage map in *Lilium***

**QTLs on disease resistance**

In 1996, *Fusarium* resistance in Asiatic hybrid lilies has been found by linkage of RAPD markers (STRAATHOF *et al.*, 1996). VAN HEUSDEN *et al.* (2002) mapped four QTLs for Fusarium resistance on linkage groups 1, 5, 13, and 16 of the 'Connecticut King' AFLP map. After 7 years, the research team constructed a new map based on original genetic linkage map adding other markers, nucleotide-binding site (NBS) profiling, and Diversity Arrays Technology. Two QTLs for Fusarium resistance were located on linkage groups 4 and 7 of the new map (Shahin *et al.*, 2009). Previous studies on *Cucumber mosaic virus*, *Lily symptomless virus* and *Lily mottle virus* (LMoV) determined the three viruses through reverse transcription-polymerase chain reaction (YOSHIJI *et al.*, 2002; Sharma *et al.*, 2005). Resistance gene for tulip breaking virus in *Lilium* was placed on linkage group 9 of the 'Connecticut' map by using AFLP markers (VAN HEUSDEN *et al.*, 2002). LMoV resistance was positioned on linkage group 9 of the AFLP map, away from the nearest marker 9 cM. However, it was found on the 20$^{th}$ linkage group of the AFLP, NBS, and DArT maps, away from the closest NBS marker 7.5 cM (SHAHIN *et al.*, 2009).

**QTLs on flower**

ABE *et al.* (2002) constructed a molecular linkage map by using a double pseudo-testcross strategy in Asiatic hybrid lily 'Montreux' × 'Connecticut King'. They also located the floral anthocyanin pigmentation traits on linkage group 1 of the 'Montreux' map and QTLs for tepal spot number in linkage groups 1 and 19 of the 'Connecticut King' map. Three years later, the research

team mapped the QTL *qCARmon6* (on the six linkage groups of the 'Montreux' map) for carotenoid pigmentation in flower petals on the molecular genetic linkage map, which explained 58.2% of the total phenotypic variation (NAKANO *et al.*, 2005). QTLs for flowers on other plants, such as inflorescence-related traits in chrysanthemum, have been mapped to the SRAP map constructed by the same strategy. Four flower diameter QTLs were located on linkage group 1 of the 'Yuhualuoying' map and on linkage groups 1, 18, and 19 of the 'Aoyunhanxiao' map. Four ray floret layer number QTLs were mapped to linkage groups 10 and 17 of the 'Yuhualuoying' map and to linkage groups 20 and 30 of the 'Aoyunhanxiao' map (ZHANG *et al.*, 2011).

**High-density molecular linkage Maps**

The more valuable maps are, the more molecular markers are distributed on molecular linkage maps. For a high-density linkage map or a saturated linkage map, large amounts of molecular markers can reveal interesting information on chromosomes at the molecular level. This information can be used for chromosome walking, quantitative trait mapping, marker-assisted breeding, and evolutionary studies. In general, the linkage group number of a high-density linkage map is consistent with the chromosome number. The information of several high-density linkage maps in plants is listed in Table 2.

*Table 2. High-density molecular linkage maps of several plants*

| Chromosome | Linkage groups | No. of total markers | Average interval cM | Markers | Plant names | Year |
|---|---|---|---|---|---|---|
| 2n=24 | 12 | 1000 | 1.2 | RFLP | Potato/tomato | 1992 |
| 2n=24 | 12 | 2275 | 1.1 | EST | Rice | 1998 |
| 2n=14 | 7 | 385 | 3.7 | AFLP, RFLP, TAS | Italian ryegrass | 2004 |
| 2n=18 | 9 | 2744 | 0.7 | RFLP, SSR, RAPD | Lettuce | 2007 |
| 2n=14 | 7 | 1818 | 2.68 | DArT | Rye | 2009 |
| 2n-24 | 12 | 1,111 | 1.6 | AFLP, SAMPL, EST, P | Black spruce | 2010 |
| 2n=40 | 20 | 5,500 | 0.6 | SNP, SSR, RFLP | Soybean | 2010 |
| 2n=22 | 11 | 2053 | 1.2 | SFP | Eucalyptus | 2011 |

TANKSLEY *et al.* (1992) constructed a high-density molecular linkage map consisting of more than 1000 markers, with an average spacing between markers of approximately 1.2 cM, in the tomato genome (1276 cM) and the potato genome (684 cM). The genetic content of both maps was nearly identical, except for five inversions of marker order within chromosomes. In this study, all of the morphological markers tested could be located in the molecular linkage map.

Rice, as an important crop, has been widely used as a model to clone functional genes and construct genetic linkage maps. HARUSHIMA, *et al.* (1998) constructed a 2275-marker (most were derived from EST clone libraries) genetic map of rice with 186 $F_2$ progenies. Covering 1521.6 cM in the Kosambi function, the average distance between adjacent markers was 1.1 cM. SHIMIZU *et al.* (2009) constructed a high-density rice linkage map by using a high-efficiency genome scanning system. The total length was 1777 cM, and the average interval of markers was 2.3 cM. With the increasing number of related molecular markers, especially with the performance of genome sequencing in rice, saturated maps of rice are expected to become easily obtained. Such maps could provide precise locus information on rice chromosomes (physical maps).

INOUE *et al.* (2004) completed a high-density linkage map of Italian ryegrass with 82 $F_1$ individuals using a two-way pseudo-testcross strategy, which spanned 1244.4 cM, covering 385 molecular markers (containing 229 RFLP markers, 116 AFLP markers, and TAS markers). The average interval between markers was 3.7 cM.

DArT is a microarray-based method used to detect DNA polymorphism at several thousand loci in a single assay without relying on DNA sequence information. TRUCO *et al.* (2007) constructed an integrated map for lettuce with 2744 markers, spanning 1505 cM and ranging from 136 to 238 cM, with a mean interval of 0.7 cM. Hanna *et al.* (2009) constructed a saturated rye linkage map with 1818 DArT markers (solely on transferable markers), which spanned 3144.6 cM and had an average interval of 2.68 cM, on the basis of 16 rye varieties, 15 inbred lines, and 82 recombinant inbred lines. KANG *et al.* (2010) developed a near-saturated genetic linkage map of black spruce with 1111 markers (809 AFLPs, 255 SAMPL, 42 microsatellites, and 5 ESTPs), which spanned 1770 cM and had an average of one marker every 1.6 cM.

Single nucleotide polymorphisms (SNPs), which are well-known advanced molecular markers for high-throughput, widespread, and large-scale statistical analysis, have been applied to construct linkage maps universally. Basing from a consensus genetic linkage map, HYTEN *et al.* (2010) finished a high-density linkage map for soybean involving 3792 SNPs, 1006 SSRs, 664 RFLPs, and 38 other markers, which spanned 2296.4 cM and had an average density of 0.6 cM.

Single feature polymorphisms (SFPs) or indel polymorphisms are particularly amenable to microarray-based genotyping, which can be discovered through sequence alignments or by hybridization of genomic DNA with whole genome microarrays. STICKNEY *et al.,* (2002) reported that spotted oligonucleotide microarrays can provide low-cost genotyping platforms. LEANDRO *et al.* (2011) successfully finished a high-density transcript linkage map with 1845 SFPs and 208 microsatellites in *Eucalyptus*, wherein the total genetic length was estimated at 1275 cM, with an average density of 1.2 cM.

**Prospect of linkage maps in *Lilium***

**Effect of huge genome in *Lilium* on linkage Maps**

In the electronic Plant DNA C-values' database (www.kew.org/genomesize/homepage.html), the genome size in *Lilium* ranged from 33.45 pg (*Lilium jankae*) to 47.90 pg (*Lilium canadense*) with 1C DNA values. No significant differences among studied species and populations from the same section were found in Muratovi´c's research on European lilies (Muratovi´c *et al.,* 2010). The maximum DNA amount of *Lilium martagon* with 1C was calculated to be approximately $4.5\times10^{10}$ bp (more than 300-fold of Arabidopsis, nearly 100-fold of rice) (SILJAK-YAKOVLEV *et al.,* 2003; DOLEŽEL *et al.,* 2007; MURATOVIC *et al.,* 2010).

The genus *Lilium* contains one of the largest genomes. Sequencing of the *Arabidopsis thaliana* genome and the rice genome has been accomplished in the early 2000s and 2002s, respectively. The cost of funds and labor force is rather high, wherein the completion is a collective effort among several countries and organizations. Although the cost of genome sequencing has significantly decreased, genome sequencing in *Lilium* has still a long way to go. Consequently, other approaches such as molecular linkage maps must be considered to reveal the genome information in *Lilium*. However, few studies focused on the molecular markers and molecular linkage maps of *Lilium*. Previous works attempted to construct molecular linkage maps for *Lilium*, but the density of molecular markers distributed on linkage groups is still low. Thus, the relationship between the linkage map and genome size remains uncertain.

Differences in genome size among plant species are caused not only by ploidy but also by high amounts of mobile repetitive DNAs. Large genome plants appear to accumulate the small subsets of these repeat sequences at high copy numbers (BENNETZEN, 1996).

**Types and Sizes of Mapping Population affect Linkage Maps**

General mapping population $F_2$, backcross (BC), RILs, double haploids (DHs), near isogenic lines (NILs), and sizes of mapping populations influence the construction of detailed genetic linkage maps. However, the main mapping populations used in constructing molecular genetics linkage maps in *Lilium* are $F_1$ and RILs. $F_2$ and BC are simple mapping populations that can be produced easily with less time. RILs, NILs, and DHs are permanent populations that are easy to conserve and exchange among different researchers. Another factor affecting linkage map quality is the size of mapping population. Although the optimal number of individuals for different types of mapping population has not been found, a large population size is necessary for high-density mapping.

**Effect of Marker Systems on Maps in *Lilium***

Molecular markers on *Lilium* linkage maps include RAPD, ISSRs, AFLPs, SRAPs, and DArT. RAPD facilitates non-specific amplification, allows simple operation, and consumes less time. ISSRs are highly polymorphic and simple. AFLPs and SRAPs are highly polymorphic and reproducible. DArT is quick, high-throughput, highly polymorphic, and reproducible. However, the applications of RAPD and ISSRs are limited by their non-reproducibility and comigration (MORENO *et al.*, 1998). Similar to RAPD and ISSRs, AFLPs are dominant markers that display no differences between dominant homozygous and heterozygous individuals. Although DArT has the limitation of dominant markers, the application of this marker on linkage maps is extensive and effective, and its other advantages have great effects (KHAN *et al.*, 2009). In addition, RFLPs, SSRs, ESTs, and SNPs are commonly used to construct a genetic linkage map. The high-density linkage maps in table 2 show that numerous markers to single efficient marker systems (such as SNPs and ESTs) or multiple marker systems provide close markers to assemble the linkage groups (as the haploid number of chromosomes).

ESTs, coding region of the genome, have been developed in many molecular markers based on EST sequences, such as EST–RFLP, EST–SSR and EST–SNP (HARUSHIMA *et al.*, 1998; CHO *et al.*, 2000; EUJAYL *et al.*, 2004). HARUSHIMA *et al.* (1998) successfully constructed a high-density linkage map using ESTs. With the increasing data of ESTs in *Lilium*, developing marker-derived EST-based sequences are expected to have a great potential.

SNPs, which feature a high density and genetic stability, facilitated automation. SNPs are the newest molecular markers commonly applied in molecular linkage maps. This work may serve as a reference for the development of molecular linkage maps in the future.

The development of a high-density molecular linkage map in *Lilium* needs an appropriate mapping population and efficient marker system that features reproducibility, co-dominant inheritance, high information content, locus specificity, high transferability, and easy automation for high-throughput screening.

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## PREGLED MOLEKULARNO GENETIČKIH MAPA *Lilium* SPP.

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Izvod

Molekularna genetička mapa je snažno sredstvo za identifikaciju lokusa za kvantitativna svojstva i olakšava oplemenjivanje pomoću markera. Pregled primene molekularnih markera i genetičkih mapa konstruisanih za *Lilium* je prikazan. Molekularne genetičke mape konstruisane za druge biljne vrste su takođe analizirane. Ukazano je na probleme vezane za konstrukciju genetičkih mapa za *Lilium*. Molekularno genetičke mape za *Lilium* mogle bi se razviti na osnovu strategije nekoliko detaljnih mapa.

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