Integration of Major QTLs of Important Agronomic Traits in Soybean

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1. Introduction

Soybean [Glycine max (L.) Merr.] is one of the most important crops in the world, accounting for 48% of the world market in oil crops, and is used mostly for animal feed and for oil production. In soybean, most agronomic traits, such as abiotic stress, biological stress, protein concentration, oil content and yield, are quantitative traits controlled by multiple genes. Moreover, genotypic expression of the phenotype is environmentally dependent, which affected QTLs detection greatly. QTLs detection was also affected by marker sets, experimental design, mapping populations, and statistical methods, which result in the location of QTLs mapped by the same marker differently.

From the first publication of quantitative trait locus (QTL) of soybean using molecular markers (Paterson et al. 1988), numerous QTLs underlying different traits of soybean have been identified in different genetic backgrounds and environments. However, few identical QTLs were identified in same experimental population or same environment by different researchers or in different years (Orf 1999; Mansur 1993, 1996). All of these interfered in QTLs to improve oil content of soybean by marker-assisted selection (MAS). Integrated QTL analysis can facilitate the identification of “real” QTL and has attracted a great deal of attention.

Recently, the International Maize and Wheat Improvement Center put forward a proposal to find universal QTLs by building a consensus map. This proposal offers a basis for QTL analysis and marker-assisted selection (MAS). Meta-analysis method led to about twofold increase in precision in the estimates of QTL position compared to the most precise initial QTL position within the corresponding region.

In this chapter, QTL meta-analysis for major agronomic traits in soybean was performed for the first time. Published QTLs were collected, a consensus map of published maps with a reference map was created, consensus QTLs were acquired by the meta-analysis approach, genes were mined using bioinformatic tools, and markers of consensus QTLs with high effects and small CIs were provided for MAS.
2. Collection of important agronomic traits QTLs

2.1 Collection of seed quality QTLs

2.1.1 Oil content QTLs

Oil and protein concentration account for about 60% of dry soybeans by weight, protein at 40% and oil at 20%. The 130 QTLs for soybean oil content published in the last 20 years were

| No. of QTL | Parent 1          | Parent 2          | Population Size | Analysis Method | Population type | Reference                  |
|------------|-------------------|-------------------|-----------------|-----------------|-----------------|----------------------------|
| 11         | Charleston        | Dong nong594      | 154             | CIM             | RIL             | Shan,2008                  |
| 10         | Zhong Dou 29      | Zhong Dou 32      | 255             | CIM             | RIL             | Wang,2008                  |
| 4          | Charleston        | Dong nong594      | 154             | CIM             | RIL             | Chen,2007                  |
| 2          | 01-042 (G.max)    | KT-156(G.soja)    | 120             | CIM             | F_2             | Zhang,2008                 |
| 1          | Wan 82-178        | Tong Shan Bo Pi   | 133             | CIM             | RIL             | Xu,2007                    |
| 3          | He Feng 25        | Xin Min 6         | 122             | CIM             | RIL             | Lv,2006                    |
| 2          | Ke Xin 3          | Zhong Huang 20    | 192             | CIM             | F_4             | Zhu,2006                   |
| 2          | Sui Nong 14       | Sui Nong 20       | 94              | CIM             | F_2             | Zhu,2006                   |
| 4          | Jin 23            | Hui Bu-Zhi        | 474             | CIM             | RIL             | Liang,2005                 |
| 3          | N87-984-16        | TN93-99           | 101             | ANOVA           | RIL             | Panthee,2005               |
| 3          | BSR 101           | LG82-8379         | 167             | ANOVA           | RIL             | Kabelka,2004               |
| 6          | Essex             | Williams          | 131             | CIM             | RIL             | Hyten,2004                 |
| 4          | Wan 82-178        | Tong Shan Bo Pi   | 133             | CIM             | RIL             | Li,2004                    |
| 4          | Charleston        | Dong nong594      | 154             | CIM             | RIL             | Zhang ZC,2004              |
| 3          | Zheng 92116       | Shang 951099      | 105             | IM              | F_{2.3}         | Yang,2004                  |
| 1          | Ke Feng 1         | Nan Nong1138-2    | 184             | CIM             | RIL             | Zhang WK,2004              |
| 1          | A3733             | PI437088A         | 76              | ANOVA           | RIL             | Chung,2003                 |
| 3          | Ke Feng 1         | Nan Nong1138-2    | 201             | CIM             | RIL             | Wang,2001                  |
| 2          | Ke Feng 1         | Nan Nong1138-2    | 201             | IM              | RIL             | Wu,2001                    |
| 3          | Ma.Belle          | Proto             | 82              | ANOVA           | F_2             | Csanadi,2001               |
| 5          | Minsoy            | Noir 1            | 236             | ANOVA           | RIL             | Specht,2001                |
| 1          | A81-356022        | PI468916          | 98              | IM              | BC_3F_4         | Sebolt,2000                |
| 1          | Parker            | PI468916          | 100             | IM              | BC_3F_4         | Sebolt,2000                |
| 2          | Archer            | Minsoy            | 233             | IM              | RIL             | Orf,1999                   |
| 3          | Archer            | Noir 1            | 240             | IM              | RIL             | Orf,1999                   |
| 1          | Essex             | Peking            | 200             | ANOVA           | F_{2.3}         | Orf,1999                   |
| 1          | Minsoy            | Noir 1            | 240             | IM              | RIL             | Orf,1999                   |
Table 1. Information of oil content QTLs collected from Soybase and 28 published articles (Table 1). Mansur (1996) mapped five oil QTLs of soybean by the population Minsoy and Noir 1 with the ANOVA method. Sebolt (2000) mapped a oil QTLs of soybean by the population A81-356022 and PI 468916 with the Interval Mapping (IM) method. Hyten (2004) mapped six oil QTLs of soybean by the population Essex and Williams with the Composite Interval Mapping (CIM) method. Shan (2008) first reported the interaction between QTLs and environments with RIL population, crossed by Charleston and Dongnong594, with CIM and Multiple Interval Mapping (MIM) method.

The population used for above research involved RIL, F$_2$, F$_{4}$, F$_2$:3, F$_2$:5, and BC$_3$F$_4$. Information on interval mapping (IM), composite interval mapping (CIM), multiple interval mapping (MIM), and the ANOVA analysis method was obtained. 1 to 11 QTLs were mapped from different papers.

### 2.1.2 Protein concentration QTLs

In the former researches, QTLs come from the 18 papers and soybase website listed in Table 2. Diers (1992) mapped eight protein QTLs of soybean by the population A81-356022 and PI 468916 with the ANOVA method. Furthermore, Diers (2000) reanalyzed and mapped a protein QTLs of soybean by the population A81-356022 and PI 468916 with the IM method, so the new QTLs were used in this study. In several cases, the same populations had been used by different research in independent experiments. For the Minsoy × Noir 1 population, Mansur (1996) mapped three protein QTLs of soybean with the ANOVA method, Orf (1999) mapped two protein QTLs of soybean with the IM method, Specht (2001) mapped five protein QTLs of soybean with the ANOVA method. For the Charleston × Dongnong 594 population, QTL × Environment effects were developed (Shan Dapeng et al., 2009), and used to reanalyze the new phenotypic data (Chen Qingshan et al., 2007; Zhang Zhongchen et al., 2004).

The set of 107 seed protein concentration QTL (Table 2) was obtained from 21 populations, varying in size from 60 to 284. The analytical methods used to predict the QTL included ANOVA and both simple and composite interval mapping. The population type included RILs, F$_2$, F$_{2,3}$, F$_4$, F$_{2,5}$, and BC$_3$F$_4$. A few QTLs with a LOD score below 2.0 were discarded from the analysis to reduce the risk of including false positives.
| QTL Number | Parent1    | Parent2    | Population Size | Analysis Method | Population Type | Reference         |
|------------|------------|------------|-----------------|-----------------|-----------------|-------------------|
| 10         | Charleston | Dongnong 594 | 154             | CIM             | RIL             | Shan, 2009        |
| 5          | Charleston | Dongnong 594 | 154             | CIM             | RIL             | Chen, 2007        |
| 2          | Charleston | Dongnong 594 | 154             | CIM             | RIL             | Zhang, 2004       |
| 3          | Zheng 92116 | Shang 951099 | 105             | IM              | F2.3            | Yang, 2004        |
| 3          | Kefeng 1   | Nannong 1138-2 | 201             | IM              | RIL             | Wu, 2001          |
| 1          | A3733      | PI437088A  | 76              | ANOVA           | RIL             | Chung, 2003       |
| 1          | A81-356022 | PI468916   | 98              | IM              | BC3F4           | Sebolt, 2000      |
| 1          | Parker     | PI468916   | 100             | IM              | BC3F4           | Sebolt, 2000      |
| 1          | M82-806    | HHP        | 71              | ANOVA           | F2.5            | Brummer, 1997     |
| 1          | M84-49     | Sturdy     | 92              | ANOVA           | F2.5            | Brummer, 1997     |
| 2          | McCall     | PI 445.815 | 92              | ANOVA           | F2.5            | Brummer, 1997     |
| 2          | A87-29601  | CX1039-99  | 100             | ANOVA           | F2.5            | Brummer, 1997     |
| 3          | C1763      | CXII59-49  | 89              | ANOVA           | F2.5            | Brummer, 1997     |
| 2          | C1763      | CX1039-99  | 83              | ANOVA           | F2.5            | Brummer, 1997     |
| 1          | LN83-2356  | PI 360.843 | 69              | ANOVA           | F2.5            | Brummer, 1997     |
| 2          | Archer     | Minsoy     | 233             | IM              | RIL             | Orf, 1999         |
| 1          | Archer     | Noir 1     | 240             | IM              | RIL             | Orf, 1999         |
| 2          | Minsoy     | Noir 1     | 240             | IM              | RIL             | Orf, 1999         |
| 10         | BSR 101    | LG82-8379  | 167             | ANOVA           | RIL             | Kabelka, 2004     |
| 6          | PI97100    | Coker237   | 111             | ANOVA           | F2              | Lee, 1996         |
| 13         | Young      | PI416937   | 120             | ANOVA           | F4              | Lee, 1996         |
| 6          | Essex      | Williams   | 131             | CIM             | RIL             | Hyten, 2004       |
| 2          | Essex      | Peking     | 200             | ANOVA           | F2.3            | Qiu, 1999         |
| 4          | Ma.Belle   | Proto      | 82              | ANOVA           | F2              | Csanadi, 2001     |
| 6          | Misuzudaiz | Moshidou   | -               | ANOVA, IM       | -               | Tajuddin, 2003    |
| 1          | N87-984-16 | TN93-99    | 101             | ANOVA           | RIL             | Panthee, 2005     |
| 5          | Minsoy     | Noir 1     | 236             | ANOVA           | RIL             | Specht, 2001      |
| 3          | Minsoy     | Noir 1     | 284             | ANOVA           | RIL             | Mansur, 1996      |
| 8          | A81-356022 | PI 468916  | 60              | ANOVA           | F2.3            | Diers, 1992       |
| Total :    |            |            |                 |                 |                 | 107               |

Table 2. The origin of the set of seed protein concentration QTL included in the meta-analysis (The table details the number of QTL mapped in each population, along with the identity of the parents, the size and the type of each population)

2.1.3 Fatty acid QTLs
83 QTLs come from the 8 papers and soybase website were listed in Table 3. Among them, 16 QTLs were related with palmitic acid content; 11 QTLs related with stearic acid content; 32 QTLs related with oleic acid content; 10 QTLs related with linoleic acid content; and 14
QTLs related with linolenic acid content. In 2007, Lee summerized 60 QTLs related with fatty acid from 2002 to 2008. Some RFLP markers, not appear in the soybean public genetic map, were discarded. The analytical methods used to predict the QTL included ANOVA, IM, CIM, and MIM. The population type included RILs, $F_2$, $F_2:3$, $F_4$, RIL, and BC$_1$F$_1$.

| Trait           | Marker      | LG    | Population Type | Data analysis | Reference     |
|-----------------|-------------|-------|-----------------|---------------|---------------|
| Palmitic acid   | Satt537     | D1b   | RIL             | CIM           | Panthee, 2006 |
| Palmitic acid   | Satt330-Sat_155 | I | BC$_1$F$_1$ | CIM MIM | Zheng, 2005 |
| Palmitic acid   | Satt175     | M     | F$_2$           | ANOVA         | Li, 2002      |
| Palmitic acid   | Sat_132     | O     | RIL             | CIM ANVOA     | Yarmilla, 2006|
| Palmitic acid   | Satt684     | A1    | $F_1$           | SAS           | Andrea, 2007  |
| Stearic acid    | Sat_245-Satt373 | L | BC$_1$F$_1$ | CIM MIM | Zheng, 2005 |
| Stearic acid    | Satt249     | J     | RIL             | CIM           | Panthee, 2006 |
| Stearic acid    | Satt474     | B2    | $F_2$           | BSA           | Spencer, 2004 |
| Stearic acid    | Sat_090     | F     | RIL             | CIM & ANVOA   | Yarmilla, 2006|
| Oleic acid      | Satt143     | L     | $F_{2:3}$       | CIM           | Maria, 2008   |
| Oleic acid      | Sat_356-Satt615 | D2 | BC$_1$F$_1$ | CIM & MIM | Zheng, 2005 |
| Oleic acid      | Satt263     | E     | RIL             | CIM           | Panthee, 2006a|
| Oleic acid      | Satt163     | G     | RIL             | CIM ANVOA     | Yarmilla, 2006|
| Linoleic acid   | Satt349     | K     | RIL             | CIM & ANVOA   | Yarmilla, 2006|
| Linoleic acid   | Satt166-Satt156 | L | BC$_1$F$_1$ | CIM & MIM | Zheng, 2005 |
| Linoleic acid   | Satt235     | G     | RIL             | CIM           | Panthee, 2006 |
| Linoleic acid   | Sat_274     | O     | RIL             | IM            | Masayuki, 2008|
| Linolenic acid  | Satt579-Satt600 | D1b | BC$_1$F$_1$ | CIM & MIM | Zheng, 2005 |
| Linolenic acid  | Satt185     | E     | RIL             | CIM           | Panthee, 2006 |
| Linolenic acid  | Satt349     | K     | RIL             | CIM & ANVOA   | Yarmilla, 2007|

Table 3. Reported information of fatty acid QTLs in soybean

2.1.4 Amino acid content QTLs
For the QTL information of amino acid content, only 3 researches involved (Panthee, 2006b, 2006c; Bingchang Zhuang, 2000). In total, 111 QTLs were mapped with RIL population.

2.1.5 Isoflavone content QTLs
The research of isoflavone content was very few. 70 QTLs were mapped in 3 papers (Kassem, 2004; Meksem, 2001a; Guoliang Zeng, 2007) by RIL population.

2.2 Collection of biotic stress resistance QTLs
2.2.1 Fungal disease resistance QTLs
Diseases caused by fungal pathogens account for approximately 50% of all soybean disease losses around the world. Conflicting results of fungal disease resistance QTLs from different populations often occurred. 107 QTLs in recent years of fungal disease resistance content were collected from 23 papers (Table 4). Only 1 to 5 QTLs were obtained in most researches. These QTLs had been mapped on the soybean linkage groups (LGs). not all fungal disease resistance content QTLs were collected because of some QTLs could not be projected to the reference map.
| QTL number | Population-type | Name of fungal disease | Reference       |
|------------|-----------------|------------------------|-----------------|
| 5          | F₂              | Soybean rust           | Alexandre, 2008 |
| 2          | RIL             | Brown stem rot         | Bachman, 2001   |
| 8          | RIL             | Phytophthora root rot  | Burnham, 2003   |
| 3          | RIL             | Phytophthora root rot  | Weng, 2007      |
| 2          | RIL             | Asian soybean rust     | Danielle, 2008  |
| 5          | RIL             | Sclerotinia stem rot, White mold | Guo, 2008 |
| 1          | NIL             | Soybean rust           | Hyten, 2007     |
| 5          | RIL             | Sudden death syndrome  | Kazi, 2008      |
| 2          | RIL             | Asian soybean rust     | Monteros, 2007  |
| 1          | F₂              | Frogeye leaf spot      | Mian, 1999      |
| 34         | RIL             | Sclerotinia stem rot, White mold | Arahana, 2001 |
| 1          | RIL             | Frogeye leaf spot      | Zhang, 2004     |
| 3          | RIL             | Sudden death syndrome  | Njiti, 2002     |
| 10         | RIL             | Brown stem rot         | Patzoldt, 2005a |
| 6          | RIL             | Rhizoctonia root and Hypocotyl rot | Zhao, 2005 |
| 5          | F₂              | Sudden death syndrome  | Austeclinio, 2007 |
| 2          | RIL             | Phytophthora root rot  | Han, 2008       |
| 2          | RIL             | Brown stem rot         | Lewers, 1999    |
| 1          | NIL             | Brown stem rot         | Patzoldt, 2005b |
| 4          | RIL             | Sudden death syndrome  | Iqbal, 2001     |
| 2          | NIL             | Sudden death syndrome  | Meksem, 1999    |
| 1          | RIL             | Sudden death syndrome  | Bell-Johnson, 1999 |
| 2          | F₂              | Phomopsis seed decay   | Berger, 1999    |

Table 4. QTLs information of fungal disease resistance in soybean

### 2.2.2 Insect resistance QTLs

81 QTLs from the 15 papers and soybase website were listed in Table 5. Among them, 12 QTLs were related with soybean aphid resistance, 42 QTLs related with corn ear worm(CEW) resistance, 11 QTLs related with common cut worm(CCW) resistance, and 16 QTL related with Mexican bean beetle and soybean pod borer resistance. The average interval of all above QTLs were 15 cM. The analytical methods used to predict the major site included BSA, ANOVA, IM, CIM, and MIM. The population type included RILs, F₂, F₂:3, F₂:4, RIL, and BC₆ population.
### Table 5. QTLs information of insect-resistance in soybean

| Name of insect-resistance | QTL number | Population-type | Analysis Method | Reference          |
|---------------------------|------------|-----------------|-----------------|--------------------|
| Soybean aphid             | 2          | F_{2:3}         | BSA             | Li, 2007           |
| Soybean aphid             | 2          | F_{2}, F_{2:3}  | BSA             | Mian, 2008         |
| Soybean aphid             | 8          | F_{3:4}         | CIM, MIM, ANOVA | Zhang, 2009        |
| CCW                       | 2          | F_{2}           | CIM             | Kunihiko, 2005     |
| CCW                       | 2          | RIL             | CIM             | Liu, 2005          |
| CCW                       | 3          | RIL             | CIM             | Fu, 2007           |
| CCW                       | 4          | F_{2}           | CIM             | Kunihiko, 2007     |
| CEW                       | 2          | F_{2}           | ANOVA, IM       | Rector, 1998       |
| CEW                       | 10         | RIL             | SAS, IM         | Terry, 1999        |
| CEW                       | 20         | RIL             | IM              | Terry, 2000        |
| CEW                       | 5          | F_{2:3}         | IM              | Narvel, 2001       |
| CEW, SBL                  | 3          | BC_{6} F_{2:3}  | ANOVA           | Zhu, 2006          |
| Mexican bean beetle       | 1          | F_{2:3}         | ANOVA           | Boerma, 2005       |
| Soybean pod borer         | 15         | RIL             | CIM             | Zhao, 2008         |
| **Total**                 | **81**     |                 |                 |                    |

Note: CIM, composite interval mapping; BSA, bulk segregant analysis; IM, Interval mapping; ANOVA, Analysis of variance; CCW, common cut worm; CEW, corn ear worm; SBL, Soybean looper

2.2.3 Soybean cyst nematode resistance QTLs
Soybean cyst nematode is a very serous disease, reducing yields by as much as 75 percent. Many research was focus on the major QTL mapping. 135 QTLs underlying SCN No.1, 2, 3, 4, 5, 6, and 14 resistance from 23 papers and soybase website were listed in Table 6. For different research, 1 to 19 QTLs were analyzed. The analytical methods included GLM, BSA, ANOVA, IM, and CIM. The population type included RILs, F_{2}, F_{2:3}, F_{4}, RIL, NIL, and BC.

2.3 Collection of yield trait QTLs
2.3.1 100-Seed weight QTLs
Soybean seed size is determined by the genetics of the variety and the environment where the seed was produced. In America, seed size was described as seeds per pound, but in China, seed size was often defined as 100-seed weight. So the research of QTL mapping for 100-seed weight was mainly in China. Among them, the population crossed by Kefeng 1 and Nannong 1138-2 were used for 3 times. The analytical methods included IM and CIM. The population type included RILs and F_{2}. In total, 78 QTLs were collected(Table 5).
Table 6. QTLs reported on resistance to soybean cyst nematode

| QTL number | Population-type | Analysis method | References |
|------------|----------------|----------------|------------|
| 10         | F2:3           | CIM            | Guo, 2006a |
| 17         | F2             | GLM            | Kabelka, 2005 |
| 4          | F4             | CIM            | Glover, 2004 |
| 1          | RIL            | GLM            | Prabhu, 1999 |
| 9          | F2:3           | CIM            | Guo, 2006b |
| 7          | F2:3           | GLM            | Yue, 2001a |
| 4          | BC3F2:3, F2:3  | IM             | Schuster, 2001 |
| 19         | F2:3           | GLM            | Yue, 2001b |
| 11         | BC1F2, BC1F4   | CIM,MIM        | Lu weiguo, 2005 |
| 1          | F2             | BSA            | Wang hui, 2007 |
| 1          | RIL            | BSA            | Li Yongchun, 2007 |
| 1          | RIL, NIL       | ANOVA          | Meksem, 2001b |
| 4          | F2             | BSA & CIM      | Meng Xi, 2008 |
| 12         | F2, BC1F2      | CIM            | Wang, 2001 |
| 1          | F2:3           | Stepwise regression | Vierling, 1996 |
| 3          | RIL            | CIM            | Ferdous , 2006 |
| 6          | F2:3           | ANOVA          | Qiu, 1999 |
| 1          | NIL            | ANOVA          | Meksem, 1999 |
| 9          | F2:3           | GLM            | Brucker, 2005 |
| 3          | F2:3           | GLM            | Concibido, 1994 |
| 1          | Population     | GLM            | Mahalingam, 1995 |
| 5          | F2:3           | GLM            | Heer, 1998 |
| 3          | F2:3, RIL      | ANOVA          | Concibido, 1996 |
| Total      | 135            |                |            |

Table 7. Information of 100-Seed Weight QTLs

| No. of QTLs | Parents | Population Size | Analysis methods | Population type | Reference |
|-------------|---------|-----------------|------------------|-----------------|-----------|
| 3           | Kefeng 1×Nannong 1138-2 | 201 | CIM | RIL | Gai,2007 |
| 1           | Kefeng 1×Nannong 1138-2 | 184 | CIM | RIL | Zhang,2004 |
| 6           | Kefeng 1×Nannong 1138-2 | 201 | IM | RIL | Wu,2001 |
| 3           | Zheng 951099×Shang 92116 | 105 | IM | F2 | Guan,2004 |
| 11          | G.max7499×G.soja PI 245331 | 148 | CIM | BIL | Li,2008 |
| 8           | Charleston×Dongnong 594 | 154 | CIM | RIL | Chen,2007 |
| 2           | Jindou 23×Huibusiheidou | - | CIM | RIL | Wang,2004 |
| 28          | Zhongdou 29×Zhongdou 32 | 255 | CIM | RIL | Wang,2008 |
| 3           | Suinong 14×Suinong20 | 94 | CIM | F2 | Zhu, 2006 |
| Total       | 65      |                 |                 |                 |          |
2.3.2 Lodging QTLs
Soybean (*Glycine max* [L.] Merr.) grain yields may be reduced when the plants lodge, so soybean lodging characteristics are an important consideration when conditions favor high yields. Lodging also creates harvesting problems. Where higher yields are obtained under irrigation, lodging is a major factor to consider in variety selection, water management, and planting density. 59 QTLs from 16 papers and soybase website were listed in Table 8. For different research, 1 to 8 QTLs were obtained. Most research only got only 1 to 2 QTLs. The analytical methods included IM, CIM, ANOVA, SSMD, and MNTECRLO. The population type included RILs and F$_2$, F$_5$, and BC$_2$F$_4$.

| No. of QTLs | Parents | Population size | Analysis Methods | Population type | Reference |
|-------------|---------|-----------------|------------------|-----------------|-----------|
| 4           | Kefeng 1×Nannong 1138-2 | 184 | CIM | RIL | Huang, 2008 |
| 6           | Zhongdou 29×Zhongdou32 | 165 | CIM | RIL | Zhou, 2009 |
| 6           | Jindou 23×Huibuzhiheidou | 257 | SSMD | RIL | Wang, 2004 |
| 7           | Pis×Beeson/ kenwood/ Lawrence | 236 | CIM | RIL | Guzman, 2007 |
| 1           | G. max × G. soja | 120 | CIM | RIL | Li, 2008 |
| 4           | Essex × Forrest | 100 | CIM | RIL | Li, 2008 |
| 1           | Kefeng 1×Nannong 1138-2 | 206 | CIM | RIL | Zhang, 2004 |
| 1           | Essex × Forrest | 100 | CIM | RIL | Kassem, 2006 |
| 1           | G. max IA2008×G. soja PI468916 | 468 | CIM | BC$_2$F$_4$ | Wang, 2003 |
| 8           | PI416937×Young | 120 | ANOVA | F$_4$ | Lee, 1996 |
| 5           | Minsoy × Noir 1 | 240 | IM | RIL | Orf, 1999 |
| 2           | Archer × Minsoy | 233 | IM | RIL | Orf, 1999 |
| 5           | Minsoy × Noir 1 | 236 | ANOVA | RIL | Chase, 2001 |
| 1           | --- | 177 | ANOVA | F$_{16}$ | Chase, 2001 |
| 2           | Noir 1 × Minsoy | 284 | ANOVA | RIL | Mansur, 1996 |
| 1           | BSR 101 × LG82-8379 | 167 | ANOVA | F$_5$ | Kabelka, 2004 |
| 1           | IA2008 × PI 468916 | 468 | MNTECRLO | BC$_2$F$_4$ | Wang, 2003 |
| 2           | Coker237 × PI97100 | 111 | ANOVA | F$_2$ | Lee, 1996 |
| 1           | --- | 248 | BSA | RIL | Mansur, 1993 |
| Total       | 59                     |      |    |    |           |

Table 8. Information of lodging QTLs in soybean

2.3.3 Plant height QTLs
Plant height become one of important agronomic traits with the increase of planting density. Many factors affect the height of a soybean plant, but the genetic loci is the most important, and the rapid developments of molecular markers have provided powerful tools to map the height-related QTL at the genomic level. 93 QTLs from 13 papers and soybase website were
listed in Table 9. For different research, 1 to 19 QTLs were obtained. The analytical methods were mainly IM and CIM. The population type included RILs and F₂.

| No. Of QTLs | Parents | Population size | Analysis methods | Population type | Reference |
|-------------|---------|----------------|------------------|-----------------|-----------|
| 5           | Zheng92116×Shang951099 | 105 | IM | F₂ | Guan,2004 |
| 4           | Kefeng1×Nannong1138-2 | 201 | IM | RIL | Wu,2001 |
| 19          | Zhongdou29×Zhongdou32 | 255 | CIM | RIL | Wang,2008 |
| 5           | Suinong14×Suinong20 | 94 | CIM | F₂ | Zhu,2006 |
| 8           | Kefeng1×Nannong1138-2 | 184 | CIM | F₂ | Zhang,2004 |
| 1           | G. max ‘7499’ × G. soja PI 245331 | 295 | CIM | RIL | Li,2008 |
| 6           | G. max IA2008×PI 468916 | 468 | CIM | RIL | Wang,2004 |
| 1           | Minsoy × Noir 1 | - | IM | RIL | Mansur,1993 |
| 11          | BSR 101× LG82-8379 | 167 | - | RIL | Kabelka,2004 |
| 2           | Essex ×Williams | - | - | RIL | Chapman,2003 |
| 8           | Jindou23 × Huibuzheheidou | - | CIM | RIL | Wang Z.,2004 |
| 8           | Charleston×Dongnong594 | 154 | CIM | RIL | Chen,2007 |
| 15          | Charleston×Dongnong594 | 147 | CIM & MIM | RIL | Sun,2010 |
| Total       | 93 | | | | |

Table 9. Information of soybean height QTLs

2.4 Soybean growth stages QTLs
Soybean growth stages divides plant development into vegetative (V) and reproductive (R) stages. The vegetative stages are numbered according to how many fully-developed trifoliate leaves are present. The reproductive (R) stages begin at flowering and include pod development, seed development, and plant maturation. 98 QTLs from 10 papers and soybase website were listed in Table 10. For different research, 1 to 44 QTLs were obtained. The analytical methods were Multiple-QTL model, CIM, IECM, ANOVA, SIM, and Chi-square. The population type included F₂, RIL and BC₂.

| QTL-number | Population type | Analysis method | References |
|------------|----------------|----------------|------------|
| 1          | F₂         | Multiple-QTL model | Naoki,2001 |
| 13         | F₂         | CIM            | Wang Zhen,2004 |
| 3          | NIL        | IECM           | Wang Ying,2008 |
| 14         | RIL        | ANOVA          | Green,2001 |
| 10         | RIL        | SIM            | Adler,1999 |
| 3          | RIL        | ANOVA          | Funastuki,2005 |
| 5          | RIL        | Chi-square     | Chase,2001 |
| 3          | BC₂        | CIM            | Diers,2004 |
| 2          | F₂         | ANOVA          | Mansur,1996 |
| 44         | RIL        | CIM            | Dawei Xin,2007 |
| Total      | 98         |                |            |

Table 10. QTLs published of soybean growth stages
3. QTL projection and integration: a consensus map of soybean important agronomic traits

3.1 QTL projection of seed quality traits
3.1.1 Oil content QTLs projection on a consensus map

In total, 110 QTLs for oil content were projected onto the reference map soymap2, and a consensus map was generated. The projected QTLs covered all LGs of the reference map (Fig. 1). Some QTLs could not be projected onto the reference map because they had no common markers with the reference map. As Fig. 1 shows, each LG contained many QTL clusters, and at least two original QTLs were found in each QTL cluster. On LG A1, 7 independent QTLs from different research were projected on the same interval.

Fig. 1. Consensus map of soybean oil content
3.1.2 Protein concentration QTLs projection on a consensus map

In total, 70 QTLs of 23 clusters identified, Fig. 2 illustrates the QTL clusters identified: there appear to be one very common site on chromosomes I, at this site, nine QTL was predicted from the various populations to be present. Four metaQTL sites, one each on chromosomes A1, B2, E, and M, at each of these sites, at least four QTL were predicted from the various populations to be present. Eighteen metaQTL site, one each on chromosomes A2, B1, B2, C1, C2, E, G, H, N and O. At each of these sites, at least two QTL were predicted from the various populations; the CIs of these clustered QTL shared a 3cM overlap with one another.

Fig. 2. Consensus map of soybean protein concentration
3.1.3 Fatty acid content QTLs projection on a consensus map
Different genetic maps with their QTLs were projected onto the soybean public map Soymap2 to construct a consensus map of major QTLs for fatty acid content in soybean. The consensus QTLs distributed in clusters on A1, B2, D1b, D2, E, G, and L linkage groups (Fig. 3).

Fig. 3. Consensus map of fatty acid QTLs in soybean

3.1.4 Amino acid content QTLs projection on a consensus map
For amino acid content in soybean, 26 consensus QTLs for different amino acid on 16 linkage groups, that is A1, A2, B2, C1, D1a, D1b, D2, E, F, G, I, J, K, L, M, and O, were constructed (Fig.4). However, each consensus QTL included not only one kind but a few different kinds of amino acids, which would be a key to explain that the same locus could influence the content of many kinds of amino acids.
3.1.5 Isoflavone content QTLs projection on a consensus map

For isoﬂavone content in soybean, 10 consensus QTLs for different amino acid on 6 linkage groups, A1, B1, B2, H, K, and N, were constructed.
3.2 QTL projection of biotic stress resistance traits

3.2.1 Fungal disease resistance QTLs projection on a consensus map

QTLs of original map were projected on the reference map by map-projection function of BioMercator2.1. In total, 107 QTLs of fungal disease resistance were projected on the reference map, soymap2, and a consensus map was obtained (Fig. 6).

As the Fig. 6 shown, projected QTLs were covered 11 linkage groups of the reference map. Although these original QTLs were mapped in different genetic backgrounds and with different methods, they were projected on the same regions by the common marker. If a QTL cluster contained more than two QTLs from different researches, this region could contain a potential allele in a high probability.

3.2.2 Insect-resistance QTLs projection on a consensus map

81 QTLs of original map were projected on the reference map. For single insect-resistance trait, the consensus QTLs mainly focused on 4 linkage groups, E, F, H, and M (Fig. 7). The cluster on linkage group E was obviously in a narrow interval. In detail, 3 consensus QTLs were distributed on linkage group F and M for soybean aphid-resistance. 9 consensus QTLs were discovered on 6 linkage group D1a, D2, E, G, H, and M for Corn Earworm. No consensus QTLs were found for Common Cutworm. For multiple insect-resistance trait, 14 consensus QTLs were combined on 8 linkage group D1a, D2, E, F, G, H, M, and N (Fig. not shown).
Fig. 6. QTLs of original map projection. BSR (Brown stem rot) ; Phytoph (Phytophthora root rot) ; ASR (Asian soybean rust) ; Sclero (Sclerotinia stem rot, White mold) ; SBR (Soybean rust) ; SDS (Sudden death syndrome) ; FLS (Frogeye leaf spot) ; RR-HR (Rhizoctonia root and Hypocotyl rot) ; PSD (Phomopsis seed decay)
3.2.3 Soybean cyst nematode resistance QTLs projection on a consensus map
151 QTLs of original map were projected on the reference map (Fig. 8). 16 consensus QTLs on 8 linkage groups A2, B1, B2, D2, E, G, H, and J were integrated. In detail, 3 consensus QTLs were distributed on linkage group B1, B2, and G for SCN Race 1-resistance. 1 consensus QTLs were distributed on linkage group B1 for SCN Race 2-resistance. 7 consensus QTLs were distributed on linkage group A2, E, G, and J for SCN Race 3-resistance. 3 consensus QTLs were distributed on linkage group A2, G, and H for SCN Race 4-resistance. 1 consensus QTLs were distributed on linkage group B1 for SCN Race 5-resistance. 1 consensus QTLs were distributed on linkage group D2 for SCN Race 14-resistance.

3.3 QTL projection of yield traits
3.3.1 100 seed weight QTLs projection on a consensus map
65 QTLs of original map were projected on the reference map (Fig. 9). 10 consensus QTLs on 9 linkage groups B1, C2, D2, K, M, and O were integrated for additive effect. 4 consensus QTLs on 3 linkage groups B2, H, and I were clustered for reductive effect.

3.3.2 Lodging QTLs projection on a consensus map
59 QTLs of original map were projected on the reference map (Fig. 10). 11 consensus QTLs were distributed on 5 linkage group, B1, C2, F, G, and L. Only one consensus cluster were found on linkage group B1 and G, but 2 on linkage group C2 and F, and 5 on linkage group L.
Fig. 8. Consensus map of QTLs resistant to SCN
3.3.3 Plant height QTLs projection on a consensus map
78 QTLs of original map were projected on the reference map (Fig. 11). 12 consensus QTLs were distributed on 7 linkage group, B1, C2, D1a, F, G, K, and M.
3.4 Soybean growth stage QTLs projection on a consensus map

98 QTLs of original map were projected on the reference map (Fig. 12). 7 consensus QTLs were distributed on 3 linkage group C2, L, and M for R1 period. 2 consensus QTLs were distributed on 2 linkage group C2 and L for R8 period. 10 consensus QTLs were distributed on 5 linkage group C1, D1a, D1b, F, and J for mixed periods (Fig. not all shown).
4. Meta-analysis for important agronomic traits

4.1 Meta-analysis results of seed quality QTLs

4.1.1 Meta-analysis of Oil content QTLs

A meta-analysis was carried out on the consensus QTL sites on 25 QTL clusters (Table 11). The site on linkage group A1 merged five QTL, with flanking markers at 92.56cM and 94.20cM, a C.I. of 1.49cM and an R² value of 10.83%. The site on linkage group I merged five QTL into a single consensus QTL. The flanking markers for this site lay at 36.03cM and 49.30cM, the CI of the QTL was 12.35cM, and its R² value was 18.22%. The site on linkage group G merged four QTL into a single consensus QTL. The flanking markers for this site lay at 94.40cM and 96.60cM, the CI of the QTL was 1.71cM, and its R² value was 13.27%. The confidence interval at all sites ranged from 1.49-12.35cM. The mean R² values ranged from 5.5% to 39.15%.

| LG | AIC value | Meta-QTL position (cM) | 95% C.I. (cM) | Map distance | Original QTL number | Mean R² | L-marker | L-marker Position (cM) | R-marker | R-marker Position (cM) |
|----|-----------|-------------------------|--------------|--------------|---------------------|--------|----------|------------------------|----------|------------------------|
| A1 | 48.99     | 93.5                    | 92.75-94.24  | 1.49         | 5                   | 10.83  | A170_1   | 92.56                  | Satt511  | 94.20                  |
| A1 | 48.99     | 29.19                   | 28.18-30.21  | 2.03         | 2                   | 29.18  | Satt454  | 28.08                  | A329_2   | 30.28                  |
| A1 | 48.99     | 88.24                   | 86.91-89.57  | 2.66         | 2                   | 38.41  | Satt599  | 85.58                  | Bng077_1 | 91.24                  |
| A2 | 18.01     | 70.96                   | 66.97-74.95  | 7.98         | 2                   | 39.15  | A111_1   | 67.32                  | Satt341  | 77.695                 |
| B2 | 53.37     | 72.83                   | 69.15-76.51  | 7.36         | 3                   | 9.56   | Sat_083  | 68.98                  | Sat_009  | 78.66                  |
| C1 | 54.37     | 10.43                   | 7.68-13.19   | 5.51         | 3                   | 8.67   | Satt690  | 5.36                   | A351_2   | 15.70                  |
| C1 | 54.37     | 123.94                  | 122.95-124.93| 1.98         | 2                   | 13.6   | AI794821 | 122.63                 | Satt338  | 123.79                 |
| C2 | 36.90     | 98.42                   | 96.2-100.63  | 4.43         | 2                   | 5.50   | R092_3   | 96.13                  | Sat_076  | 99.18                  |
| D1a| 28.99     | 57.45                   | 56.53-58.36  | 1.83         | 3                   | 8.56   | Satt254  | 56.40                  | Satt203  | 59.00                  |
| D1a| 28.99     | 70.74                   | 68.87-72.62  | 3.75         | 2                   | 9.10   | Satt198  | 68.62                  | Satt439  | 72.30                  |
| D2 | 22.25     | 77.41                   | 75.24-79.58  | 4.34         | 3                   | 10.17  | Sat_292  | 75.29                  | Satt461  | 80.20                  |
| E  | 22.24     | 26.14                   | 23.51-28.77  | 5.26         | 2                   | 14.35  | OP_M12b  | 22.84                  | K229_1   | 28.30                  |
| E  | 22.24     | 32.71                   | 29.92-35.5   | 5.58         | 2                   | 20.50  | K229_1   | 28.27                  | Satt573  | 35.80                  |
| F  | 27.42     | 2.16                    | 1.29-3.02    | 1.73         | 2                   | 12.17  | M8E6mr1  | 1.09                   | Satt343  | 3.04                   |
| F  | 27.42     | 18.45                   | 16.11-20.80  | 4.69         | 2                   | 13.59  | Satt252  | 16.08                  | Satt423  | 20.56                  |
| C  | 33.03     | 67.32                   | 66.09-71.10  | 5.01         | 3                   | 12.53  | A073_1   | 68.56                  | Sat_143  | 73.40                  |
| G  | 33.03     | 95.12                   | 94.26-95.97  | 1.71         | 4                   | 13.27  | Sct_199  | 94.40                  | Satt191  | 96.60                  |
| H  | 16.58     | 89.27                   | 88.33-90.22  | 1.89         | 3                   | 9.63   | Satt142  | 86.49                  | A748_2   | 90.30                  |
| I  | 27.16     | 32.5                    | 30.93-34.07  | 3.14         | 2                   | 27.00  | B214_2   | 30.56                  | A352_2   | 34.70                  |
| I  | 27.16     | 37.4                    | 36.23-48.58  | 12.35        | 5                   | 18.22  | Sat_219  | 36.03                  | Sat_105  | 49.30                  |
| K  | 29.90     | 102                     | 98.26-105.74 | 7.48         | 2                   | 11.20  | R        | 97.13                  | M7E8mr3  | 107.00                 |
| L  | 49.37     | 34.78                   | 33.84-35.71  | 1.87         | 2                   | 19.50  | Satt497  | 33.71                  | Satt613  | 36.10                  |
| L  | 49.37     | 93.10                   | 91.60-94.60  | 3.00         | 3                   | 11.83  | DUBC015  | 90.34                  | A489_1   | 95.40                  |
| N  | 17.54     | 73.14                   | 69.19-77.09  | 7.90         | 2                   | 6.57   | A808_1   | 68.76                  | Sat_304  | 77.10                  |
| N  | 15.19     | 95.56                   | 92.22-98.90  | 6.68         | 3                   | 37.31  | Satt257  | 92.56                  | Satt022  | 102.06                 |

Table 11. Meta-analysis results of oil content QTLs
4.1.2 Meta-analysis of protein concentration QTLs

A meta-analysis was carried out on the consensus QTL sites on 23 QTL clusters (Table 12). The site on chromosome I merged nine QTL from seven populations, with flanking markers at 33.3cM and 37.0cM, a CI of 3.7cM and an \( R^2 \) value of 20.8%. The site on chromosome A1 merged four QTL, predicted from four populations, into a single consensus QTL. The flanking markers for this site lay at 88.83cM and 97.49cM, the CI of the QTL was 8.66cM, and its \( R^2 \) value was 9.4%. The site on chromosome B2 merged four QTL, predicted from two populations, into a single consensus QTL. The flanking markers for this site lay at 71.7cM and 73.22cM, the CI of the QTL was 1.52cM, and its \( R^2 \) value was 3.5%. The site on chromosome E merged five QTL, predicted from three populations, into a single consensus QTL. The flanking markers for this site lay at 23.5cM and 30.3cM, the CI of the QTL was 6.7cM, and its \( R^2 \) value was 7.4%. The site on chromosome M merged five QTL (five populations), with flanking markers at 34.2cM and 41.5cM, a CI of 7.2cM and an \( R^2 \) value of 12.4%. In total, twenty-three consensus QTL were detected. The confidence interval at all sites ranged from 1.52-14.31cM, and the proportion of the phenotypic variance associated with each of them from 1.5%-20.8%.

| LG | AIC value | Meta-QTL Position (cM) | 95% C.I. (cM) | Map distance | Original 1 QTL number | Mean \( R^2 \) | L-marker | L-marker Position (cM) | R-marker | R-marker Position (cM) |
|----|-----------|-------------------------|--------------|-------------|------------------------|-------------|----------|------------------------|----------|------------------------|
| A1 | 15.64     | 93.16                   | 88.83-97.49  | 8.66        | 4                      | 9.40        | Satt174  | 88.58                  | Sat_271  | 97.76                  |
| A2 | 39.23     | 147.79                  | 142.48-153.09| 10.61       | 2                      | 3.10        | T036_1   | 141.08                  | Satt228  | 154.11                 |
| B1 | 16.19     | 32.56                   | 29.33-35.79  | 6.46        | 3                      | 7.00        | A109_1   | 29.17                  | Satt251  | 36.48                  |
| B2 | 7.98      | 31.16                   | 25.86-36.46  | 10.60       | 2                      | 14.50       | Sat_342  | 20.31                  | A343_1   | 37.99                  |
| B2 | 7.98      | 49.65                   | 44.35-54.95  | 10.60       | 2                      | 6.80        | B142_1   | 43.58                  | Satt168  | 55.20                  |
| B2 | 7.98      | 72.46                   | 71.70-73.22  | 1.52        | 4                      | 3.50        | Satt272  | 71.68                  | DOP_F04  | 73.54                  |
| C1 | 73.46     | 15.69                   | 10.39-20.99  | 10.60       | 2                      | 9.40        | SOYGPATR | 10.34                  | A463_1   | 21.04                  |
| C1 | 73.46     | 63.08                   | 57.78-68.38  | 10.60       | 2                      | 13.70       | V38a     | 54.19                  | A519_3   | 69.30                  |
| C1 | 73.46     | 93.85                   | 88.55-99.15  | 10.60       | 2                      | 11.00       | Sat_207  | 87.31                  | Bng044_2 | 107.61                 |
| C1 | 73.46     | 123.76                  | 119.43-128.09| 8.66        | 3                      | 13.20       | Bng012_1 | 108.08                  | Satt164  | 132.46                 |
| C2 | 29.4      | 119.19                  | 115.55-122.82| 7.27        | 3                      | 15.40       | Satt708  | 115.49                  | A538_1   | 123.37                 |
| E  | 54.51     | 26.90                   | 23.55-30.25  | 6.70        | 5                      | 7.40        | OP_M12b  | 22.84                  | B174_1   | 30.88                  |
| E  | 54.51     | 45.21                   | 43.88-45.98  | 2.10        | 3                      | 12.00       | Satt268  | 44.27                  | R028_2   | 46.10                  |
| E  | 18.24     | 61.40                   | 56.08-66.72  | 10.64       | 3                      | 5.40        | A226H_2  | 54.85                  | Satt553  | 67.92                  |
| G  | 43.52     | 67.62                   | 62.31-72.92  | 10.61       | 2                      | 13.80       | Satt199  | 62.16                  | Sat_143  | 73.42                  |
| G  | 43.52     | 93.60                   | 88.30-98.91  | 10.61       | 2                      | 10.20       | AF162283 | 87.94                  | L154_1   | 99.33                  |
| H  | 26.99     | 87.97                   | 81.09-93.70  | 12.61       | 3                      | 9.20        | Satt302  | 81.04                  | A810_1   | 97.53                  |
| I  | 77.57     | 35.78                   | 33.31-36.97  | 3.66        | 9                      | 20.80       | A144_1   | 32.42                  | Satt239  | 36.94                  |
| M  | 42.72     | 37.89                   | 34.27-41.50  | 7.23        | 5                      | 12.38       | Satt567  | 33.47                  | DOP_H1/4 | 41.84                  |
| N  | 18.33     | 32.38                   | 27.07-37.68  | 10.61       | 2                      | 9.50        | Satt631  | 26.14                  | Satt584  | 37.98                  |
| N  | 9.78      | 79.50                   | 74.50-84.50  | 10.00       | 3                      | 11.00       | BLT015_1 | 74.49                  | Satt234  | 84.60                  |
| N  | 9.78      | 98.03                   | 94.02-102.06 | 8.04        | 2                      | 1.50        | Sat_306  | 93.11                  | Satt022  | 102.06                 |
| O  | 14.12     | 72.10                   | 64.95-79.26  | 14.31       | 2                      | 7.50        | Sat_282  | 63.81                  | Satt477  | 82.09                  |

Table 12. Meta-analysis results of protein concentration QTL
4.1.3 Meta-analysis of Fatty acid QTLs
A meta-analysis was carried out on the consensus QTL sites on 19 QTL clusters (Table 13). Some sites were related with only one trait. The site on linkage group A1, with flanking markers Sat_137 and A487_1, a C.I. of 7.44cM was related with Palmitic Acid Content. The site on linkage group B2, with flanking markers Sat_189 and Satt556, a C.I. of 0.4cM was related with Stearic Acid Content. The site on linkage group D2, with flanking markers Satt461 and Sat_114, a C.I. of 8.66 cM was related with Oleic Acid Content. The site on linkage group N, with flanking markers Satt530 and Satt683, a C.I. of 3.34cM was related with Linoleic Acid Content. The site on linkage group E, with flanking markers OP_M12b and A636_1, a C.I. of 3.09cM was related with Linolenic Acid Content. However, several sites were related with at least two traits. The site on linkage group C2, with flanking markers Sat_312 and Satt319, a C.I. of 10.6cM was related with Oleic Acid Content and Palmitic Acid Content. The site on linkage group D2, with flanking markers L026_1 and Satt615, a C.I. of 0.38cM was related with Linoleic Acid Content and Oleic Acid Content. The site on linkage group G, with flanking markers K493_1 and T005_2, a C.I. of 6.12cM was related with Oleic Acid Content, Palmitic Acid Content, and Stearic Acid Content.

| Trait   | LG  | AIC value | Meta-QTL position(cM) | 95% C.I. (cM) | Map distance | L-marker | R-marker |
|---------|-----|-----------|------------------------|---------------|--------------|----------|----------|
| Pal     | A1  | 64.01     | 3.54                   | 0-7.44        | 7.44         | Sat_137  | A487_1   |
| Pal     | A1  | 64.01     | 15.76                  | 10.46-21.07   | 10.61        | Satt572  | Satt276  |
| Ole     | A1  | 64.01     | 92.41                  | 89.06-95.77   | 6.71         | A104_1   | A170_1   |
| St      | B2  | 60.00     | 73                     | 72.8-73.2     | 0.4          | Sat_189  | Satt556  |
| Lio     | B2  | 60.00     | 90.49                  | 86.19-94.78   | 8.59         | AW620774 | A741_1   |
| Ole,Pal | C2  | 11.04     | 113.39                 | 108.09-118.69 | 10.6         | Sat_312  | Satt319  |
| Pal     | D1b | 28.81     | 73.12                  | 70.57-75.67   | 5.10         | Satt141  | Satt290  |
| Ole     | D2  | 34.21     | 83.00                  | 78.67-87.33   | 8.66         | Satt461  | Sat_114  |
| Lin,Ole | D2  | 34.21     | 91.00                  | 90.81-91.19   | 0.38         | L026_1   | Satt615  |
| Lio     | E   | 35.08     | 25.38                  | 23.84-26.93   | 3.09         | OP_M12b  | A636_1   |
| Lio,Ole | E   | 35.08     | 45.09                  | 41.34-48.84   | 7.50         | Satt483  | Satt452  |
| Ole,Lin | G   | 127.82    | 0.72                   | 0-3.65        | 3.65         | Satt163  | Satt038  |
| Ole,lin | G   | 127.82    | 21.90                  | 16.59-27.2    | 10.61        | Satt235  | Satt130  |
| Ole     | G   | 127.82    | 49.25                  | 45.5-53       | 7.50         | Satt131  | Satt566  |
| Ole,Pal,St | G | 127.82 | 80.67 | 77.61-83.73 | 6.12 | K493_1 | T005_2 |
| Lin,Lio | K   | 11.08     | 42.89                  | 37.58-48.19   | 10.61        | Satt555  | Sct_196  |
| Ole     | L   | 69.71     | 31.89                  | 27.56-36.22   | 8.66         | Sat_397  | Sat_191  |
| Ole     | L   | 69.71     | 66.11                  | 62.36-69.86   | 7.50         | gy3E_1   | Satt166  |
| Lin     | N   | 6.69      | 34.09                  | 32.42-35.76   | 3.34         | Satt530  | Satt683  |

Note: Pal, St, Ole, Lin, Lio were the abbreviation of Palmitic acid, Stearic acid, Oleic acid, Linoleic acid, and Linolenic acid, individually.

Table 13. Meta-analysis results of fatty acid QTLs
4.1.4 Meta-analysis of amino acid content QTLs

A meta-analysis was carried out on the consensus QTL sites on 26 QTL clusters (Table 14). Most sites were related with more than two kind of amino acid content. The site on linkage group A1, with flanking markers Sat_344 and Sat_410 at 19.38cM and 29.63cM, a C.I. of 8.66cM was an admixture related with Glycine, Threonine, and Alanine content. The site with the minimal confidence interval on linkage group L, with flanking markers Satt495 and Sat_408 at 0.00 cM and 1.31cM, a C.I. of 1.86cM was related with Alanine, Glycine, Serine, Threonine, and Phenylalanine content. However, the site on linkage group M, with flanking markers GMSC514 and Satt201 at 3.05cM and 13.56cM, a C.I. of 8.66cM was mainly related with Methionine content.

| LG | AIC value | Meta-QTL position(cM) | 95% C.I. (cM) | Map distance | L-marker | L-marker Position (cM) | R-marker | R-marker Position (cM) |
|----|-----------|-----------------------|---------------|-------------|----------|------------------------|----------|------------------------|
| A1 | 23.69     | 25.56                 | 21.23-29.89   | 8.66        | Sat_344  | 19.38                  | Sat_410  | 29.63                  |
| A2 | 47.19     | 36.77                 | 32.44-41.10   | 8.66        | Satt589  | 33.96                  | Satt315  | 45.29                  |
| A2 | 47.19     | 107.05                | 102.72-111.38 | 8.66        | Satt233  | 100.09                 | Sct_194  | 113.57                 |
| B2 | 24.61     | 55.2                  | 51.45-58.95   | 7.50        | Sct_034  | 51.45                  | Satt416  | 56.96                  |
| C1 | 11.04     | 74.46                 | 69.16-79.76   | 10.60       | Satt607  | 67.03                  | Satt476  | 80.62                  |
| D1a| 47.19     | 59                    | 55.65-62.35   | 6.70        | Satt515  | 55.68                  | Satt580  | 62.37                  |
| D1b| 53.30     | 75.67                 | 70.37-80.97   | 10.60       | Satt135  | 70.65                  | Satt644  | 79.42                  |
| D1b| 53.30     | 116.35                | 113.52-119.18 | 5.66        | Sat_183  | 112.63                 | Sat_198  | 118.95                 |
| D2 | 47.37     | 47.73                 | 42.43-53.03   | 10.6        | Satt372  | 39.35                  | Satt582  | 53.85                  |
| D2 | 47.37     | 92.12                 | 89.06-95.18   | 6.12        | Satt488  | 89.20                  | Satt301  | 93.71                  |
| E  | 11.04     | 44.76                 | 39.46-50.06   | 10.60       | Satt136  | 39.16                  | Satt273  | 47.50                  |
| F  | 38.17     | 16.08                 | 13.43-18.73   | 5.30        | Satt269  | 11.37                  | Satt149  | 18.13                  |
| G  | 62.32     | 16.4                  | 13.05-19.75   | 6.7         | Satt570  | 12.74                  | Satt235  | 21.89                  |
| G  | 62.32     | 54.51                 | 50.76-58.26   | 7.50        | Satt303  | 53.42                  | Satt088  | 58.00                  |
| I  | 11.04     | 82.78                 | 77.48-88.08   | 10.60       | Satt330  | 77.84                  | Satt623  | 92.52                  |
| J  | 23.69     | 11.74                 | 6.44-17.04    | 10.60       | AW310961 | 5.19                    | Satt674  | 15.95                  |
| J  | 23.69     | 43.01                 | 37.71-48.31   | 10.60       | Sat_370  | 37.40                   | Sat_366  | 52.84                  |
| K  | 40.45     | 30.28                 | 25.95-34.61   | 8.66        | Satt102  | 30.28                   | Satt137  | 36.99                  |
| K  | 40.45     | 46.63                 | 41.33-51.93   | 10.60       | Satt178  | 40.86                   | Satt116  | 52.28                  |
| L  | 103.86    | 0.00                  | 0.00-1.86     | 1.86        | Satt495  | 0.00                   | Sat_408  | 1.31                   |
| L  | 103.86    | 31.72                 | 29.22-34.22   | 5.00        | Sat_405  | 29.62                   | Satt313  | 34.54                  |
| L  | 103.86    | 61.35                 | 56.05-66.65   | 10.6        | Satt156  | 56.14                   | Satt166  | 66.51                  |
| M  | 101.13    | 7.84                  | 3.51-12.17    | 8.66        | GMSC514  | 3.05                    | Satt201  | 13.56                  |
| M  | 101.13    | 33.47                 | 29.14-37.80   | 8.66        | Satt567  | 33.47                   | Satt435  | 38.94                  |
| M  | 101.13    | 73.37                 | 70.87-75.87   | 5.00        | Satt494  | 71.71                   | Sat_288  | 76.41                  |
| O  | 35.53     | 13.60                 | 10.25-16.95   | 6.70        | Satt487  | 9.53                    | Satt492  | 17.25                  |

Table 14. Meta-analysis results of amino acid content QTLs
4.1.5 Meta-analysis of isoflavone content QTLs
A meta-analysis was carried out on the consensus QTL sites on 10 QTL clusters (Table 15). Although there were five sub-component of isoflavone content. Most sites were related with more than only one kind among them. The site on linkage group A1, with flanking markers Sat_368 and Satt165 at 10.60cM and 14.37cM, a C.I. of 10.60cM was related with daidyzin content. The three sites on linkage group B1, with flanking left markers Sat_261, Satt 197, and Sct_026 at 32.95 cM, 46.39, and 78.13cM, corresponding right markers Satt638, Sat_247, and Satt444 at 37.80cM, 49.73cM, and 85.92cM, the C.I. of 6.12cM, 6.12cM, and 7.55cM were all related with Gly content.

| LG  | AIC value | Meta-QTL position(cM) | 95% C.I. (cM) | Map distance | L-marker | L-marker Position (cM) | R-marker | R-marker Position (cM) |
|-----|-----------|------------------------|--------------|--------------|----------|------------------------|----------|------------------------|
| A1  | 11.04     | 17.16                  | 11.86-22.46  | 10.60        | Sat_368  | 14.37                  | Satt165  | 23.00                  |
| B1  | 109.03    | 36.48                  | 33.42-39.54  | 6.12         | Sat_261  | 32.95                  | Satt638  | 37.80                  |
| B1  | 109.03    | 46.39                  | 43.33-49.45  | 6.12         | Satt197  | 46.39                  | Sat_247  | 49.73                  |
| B1  | 109.03    | 81.7                   | 77.90-85.45  | 7.55         | Sct_026  | 78.13                  | Satt444  | 85.92                  |
| B2  | 11.04     | 93.49                  | 88.19-98.79  | 10.60        | Satt534  | 87.59                  | Satt560  | 97.92                  |
| H   | 15.57     | 81.04                  | 76.71-85.37  | 8.66         | Sat_158  | 73.46                  | Satt637  | 85.79                  |
| K   | 40.51     | 41.52                  | 36.21-46.82  | 10.61        | Satt055  | 32.96                  | Satt727  | 46.80                  |
| K   | 40.51     | 52.28                  | 47.95-56.61  | 8.66         | Satt337  | 47.38                  | Satt273  | 56.62                  |
| N   | 29.61     | 45.14                  | 39.84-50.44  | 10.60        | Sat_208  | 39.35                  | Satt387  | 53.25                  |
| N   | 29.61     | 74.99                  | 70.66-79.32  | 8.66         | Satt549  | 53.25                  | Sat_091  | 79.51                  |

Table 15. Meta-analysis results of isoflavone content QTLs

4.2 Meta-analysis results of biotic stress resistance QTLs
4.2.1 Meta-analysis of fungal disease resistance QTLs
A meta-analysis was carried out on the consensus QTL sites on 23 QTL clusters (Table 16). In total, 9 kind of soybean fungal disease-resistance QTLs were integrated. For brown stem rot, in short BSR, one site was the most notable cluster of integrating 14 former researches with flanking markers Sctt011 and Satt547 at 62.88cM and 67.79cM on linkage group J, a C.I. of 3.78cM. For phytophthora root rot, in short phytoph, one site was on linkage group F with flanking markers Satt252 and Satt149 at 16.08cM and 18.12cM, a C.I. of 0.84cM. Another was on linkage group J with flanking markers Satt414 and Satt596 at 37.04cM and 39.64cM, a C.I. of 1.82cM. For sclerotinia stem rot, in short Sclero, the former research results were more dispersed. one main site was on linkage group E with flanking markers Satt720 and A517_1 at 20.80cM and 26.02cM, a C.I. of 4.52cM. Another was on linkage group O with flanking markers Satt243 and Sat_190 at 119.50cM and 129.80cM, a C.I. of 8.66cM. For sudden death syndrome, in short SDS, one main site was on linkage group D2 with flanking markers Satt662 and Sat_001 at 87.88cM and 92.12cM, a C.I. of 4.11cM. Another was on linkage group G with flanking markers Satt163 and B053_1 at 0.00cM and 5.77cM, a C.I. of 4.21cM. Other results for remain diseases were listed in table and above Fig. 6.
| LG  | AIC value | Meta-QTL position (cM) | 95% C.I. (cM) | Map distance | L-marker Position (cM) | R-marker Position (cM) |
|-----|-----------|------------------------|--------------|-------------|----------------------|-----------------------|
| A2  | 24.04     | 36.77                  | 31.47-42.07  | 10.60       | Satt480              | 28.44                 |
| A2  | 24.04     | 106.72                 | 102.46-110.98| 8.52        | Satt233              | 100.09                |
| C2  | 26.31     | 40.30                  | 35.00-45.60  | 10.60       | Sat_062              | 30.80                 |
| C2  | 26.31     | 115.47                 | 111.23-119.70| 8.47        | Satt365              | 111.68                |
| D2  | 53.21     | 81.29                  | 77.54-85.04  | 7.50        | Sat_222              | 76.69                 |
| D2  | 53.21     | 106.72                 | 102.46-110.98| 8.52        | Satt662              | 87.88                 |
| E   | 13.94     | 23.85                  | 21.59-26.11  | 4.52        | Satt720              | 20.80                 |
| F   | 32.21     | 16.91                  | 16.49-17.33  | 0.84        | Satt252              | 16.08                 |
| F   | 32.21     | 19.21                  | 17.99-20.43  | 2.44        | Satt252              | 16.08                 |
| F   | 32.21     | 84.17                  | 78.87-89.47  | 10.6        | Satt334              | 78.06                 |
| G   | 117.8     | 3.87                   | 1.77-5.98    | 4.21        | Satt163              | 0.00                  |
| G   | 117.8     | 46.80                  | 43.31-50.29  | 6.98        | Sat_308              | 43.09                 |
| G   | 117.8     | 83.00                  | 78.20-87.79  | 9.59        | A12_1_2              | 78.05                 |
| G   | 117.8     | 95.70                  | 90.40-101.01 | 10.61       | A245_2               | 89.97                 |
| J   | 139.2     | 38.36                  | 37.45-39.27  | 1.82        | Satt414              | 37.04                 |
| J   | 139.2     | 49.98                  | 46.98-52.98  | 6.00        | Sat_093              | 46.09                 |
| J   | 139.2     | 65.66                  | 63.77-67.55  | 3.78        | Sctt011              | 62.88                 |
| K   | 13.94     | 80.43                  | 73.15-87.71  | 14.56       | Satt499              | 71.00                 |
| L   | 19.65     | 30.93                  | 26.02-35.85  | 9.83        | Satt388              | 23.55                 |
| M   | 25.49     | 54.83                  | 51.08-58.58  | 7.50        | Satt463              | 50.10                 |
| N   | 15.83     | 42.15                  | 41.40-42.91  | 1.51        | Sat_275              | 40.81                 |
| O   | 43.87     | 84.99                  | 79.77-90.21  | 10.44       | A878_1               | 78.33                 |
| O   | 43.87     | 125.43                 | 121.10-129.76| 8.66        | Satt243              | 119.50                |

Table 16. Meta-analysis results of fungal disease resistance QTLs

4.2.2 Meta-analysis of insect-resistance QTLs

A meta-analysis was carried out on the consensus QTL sites on 14 QTL clusters (Table 17). The QTL intervals were reduced from 15 cM to 3.67 cM in average. For single insect-resistance, only the sites of soybean aphid-resistance and corn earworm-resistance got the meta-analysis results. 3 true QTLs were related with soybean aphid resistance. Two sites were on linkage group F, with flanking left markers j11_1 and R045_1 at 7.31 cM and 70.12 cM, corresponding right markers BLT030_1 and Satt510 at 8.67 cM and 71.41 cM, the C.I. of 4.68 cM and 2.37 cM. The other was on linkage group M with flanking markers DOP_H14 and A131_1 at 41.84 cM and 47.12 cM, a C.I. of 4.07 cM. 9 true QTLs were related with corn earworm resistance. One site was on linkage group D1a with flanking markers Sat_353 and R013_2 at 36.23 cM and 38.09 cM, a C.I. of 6.02 cM. Another was on linkage group G with flanking markers Satt472 and Satt191 at 94.84 cM and 96.57 cM, a C.I. of 1.22 cM. Others were shown in the Table 17.
Most QTLs were related with multiple insect-resistance (Table 18). For example, the site on linkage group E, with flanking markers A135_3 and Satt575 at 0.06cM and 3.30cM, a C.I. of 3.11cM was related with corn earworm resistance and common cutworm.

| Trait         | LG  | AIC value | Meta-QTL position (cM) | 95% C.I. (cM) | Map distance | L-marker | L-marker Position (cM) | R-marker | R-marker Position (cM) |
|---------------|-----|-----------|------------------------|---------------|--------------|----------|----------------------------|----------|------------------------|
| Soybean aphid | F   | 30.07     | 7.56                   | 5.22-9.90     | 4.68         | j11_1    | 7.31                       | BLT030_1 | 8.67                   |
| Soybean aphid | F   | 30.07     | 71.09                  | 69.90-72.27   | 2.37         | R045_1   | 70.12                      | Satt510  | 71.41                  |
| Soybean aphid | M   | 34.20     | 43.85                  | 41.82-45.89   | 4.07         | DOP_H14  | 41.84                      | A131_1   | 47.12                  |
| CEW D1a       |     | 15.8      | 38.08                  | 35.07-41.09   | 6.02         | Sat_353  | 36.23                      | R013_2   | 38.09                  |
| CEW D2        |     | 10.64     | 100.12                 | 95.33-104.92  | 9.59         | GMHSP179 | 99.04                      | Satt186  | 105.45                 |
| CEW E         |     | 48.13     | 2.14                   | 0.59-3.70     | 3.11         | A135_3   | 0.06                       | Satt575  | 3.30                   |
| CEW G         |     | 8.77      | 95.71                  | 95.10-96.32   | 1.22         | Satt472  | 94.84                      | Satt191  | 96.57                  |
| CEW H         |     | 145.95    | 38.53                  | 35.69-41.37   | 5.68         | A036_1   | 34.29                      | Sctt009  | 38.89                  |
| CEW M         |     | 31.68     | 56.69                  | 55.28-58.11   | 2.83         | Satt220  | 56.29                      | A584_3   | 58.50                  |

Table 17. Meta-analysis results of single insect-resistance QTLs

| LG  | AIC value | Meta-QTL position (cM) | 95% C.I. (cM) | Map distance | L-marker | L-marker Position (cM) | R-marker | R-marker Position (cM) |
|-----|-----------|------------------------|---------------|--------------|----------|----------------------------|----------|------------------------|
| D1a | 25.01     | 38.08                  | 35.07-41.09   | 6.02         | Sat_353  | 36.23                      | R013_2   | 38.09                  |
| D2  | 10.64     | 100.12                 | 95.33-104.92  | 9.59         | GMHSP179 | 99.04                      | Satt186  | 105.45                 |
| E   | 48.13     | 2.14                   | 0.59-3.70     | 3.11         | A135_3   | 0.06                       | Satt575  | 3.30                   |
| F   | 50.58     | 7.56                   | 5.22-9.90     | 4.68         | j11_1    | 7.31                       | BLT030_1 | 8.67                   |
| F   | 50.58     | 71.03                  | 69.84-72.22   | 2.38         | R045_1   | 70.12                      | Satt510  | 71.41                  |
| G   | 22.76     | 95.71                  | 95.27-96.14   | 0.87         | Satt472  | 94.84                      | Satt191  | 96.57                  |
| H   | 235.12    | 35.04                  | 32.39-37.69   | 5.30         | A036_1   | 34.29                      | Sctt009  | 38.89                  |
| H   | 235.12    | 57.56                  | 55.65-59.48   | 3.83         | A130_1   | 56.18                      | Satt469  | 58.91                  |
| H   | 235.12    | 68.96                  | 68.07-69.84   | 1.77         | Satt676  | 68.86                      | Satt314  | 69.12                  |
| H   | 235.12    | 81.57                  | 79.75-83.40   | 3.65         | Satt302  | 81.04                      | Sat_175  | 83.19                  |
| M   | 124.22    | 42.75                  | 40.85-44.64   | 3.79         | DOP_H14  | 41.84                      | A131_1   | 47.12                  |
| M   | 124.22    | 56.70                  | 55.74-57.66   | 1.92         | Satt220  | 56.29                      | A584_3   | 58.50                  |
| M   | 124.22    | 60.74                  | 60.54-60.94   | 0.4          | Sat_258  | 60.47                      | Satt702  | 61.04                  |
| N   | 7.28      | 25.60                  | 23.53-27.66   | 4.13         | BLT004_1 | 25.49                      | Satt631  | 26.14                  |

Table 18. Meta-analysis results of multiple insect-resistance QTLs
4.2.3 Meta-analysis of soybean cyst nematode resistance QTLs

A meta-analysis was carried out on the consensus QTL sites on 16 QTL clusters (Table 19). 3 true QTLs were related with SCN race1 resistance. The main site was on linkage group G, with flanking markers H3_c6_2 and Satt309 at 2.77 cM and 4.53 cM, the C.I. of 1.48 cM. One true QTL was simultaneously related with SCN race2 resistance and SCN race5 resistance on linkage group B1 with flanking markers R244_1 and AQ851479 at 115.75 cM and 128.66 cM, a C.I. of 12.29 cM. 7 true QTLs were related with SCN race3 resistance. The main site was on linkage group G with flanking markers Satt309 and B053_1 at 4.53 cM and 5.77 cM, a C.I. of 1.01 cM. 3 true QTLs were related with SCN race4 resistance. The main site was on linkage group A2, with flanking markers Sat_162 and A486_1 at 51.86 cM and 53.16 cM, the C.I. of 0.86 cM. One true QTL was related with SCN race14 resistance on linkage group D2 with flanking markers Satt528 and i6_2 at 86.34 cM and 93.92 cM, a C.I. of 7.50 cM.

| Trait | LG | AIC value | Meta-QTL Position (cM) | 95% C.I. (cM) | Map distance | L-marker | L-marker Position (cM) | R-marker | R-marker Position (cM) |
|-------|----|-----------|------------------------|---------------|-------------|----------|------------------------|---------|------------------------|
| Race1 | B1 | 11.72     | 94.66                  | 89.08-100.24  | 11.16       | Satt444  | 85.92                  | Sat_123 | 100.88                 |
| Race1 | B2 | 27.24     | 57.89                  | 54.52-61.26   | 6.74        | A018_1   | 53.54                  | A329_1  | 62.74                  |
| Race1 | G  | 51.3      | 3.79                   | 3.05-4.53     | 1.48        | H3_c6_2  | 2.77                   | Satt309 | 4.53                   |
| Race2 | B1 | 19.81     | 121.68                 | 115.53-127.82 | 12.29       | R244_1   | 115.75                 | AQ851479| 128.66                 |
| Race3 | A2 | 53.68     | 58.43                  | 55.58-61.28   | 5.70        | Satt187  | 54.92                  | A975_2  | 61.29                  |
| Race3 | E  | 103.64    | 38.31                  | 36.47-40.15   | 3.68        | Satt573  | 35.79                  | A386_1  | 39.98                  |
| Race3 | G  | 334.49    | 5.11                   | 4.61-5.62     | 1.01        | Satt309  | 4.53                   | B053_1  | 5.77                   |
| Race3 | G  | 334.49    | 30.91                  | 27.88-33.94   | 6.06        | Sat_315  | 27.48                  | Sat_403 | 34.87                  |
| Race3 | G  | 334.49    | 72.98                  | 70.13-75.84   | 5.71        | Satt517  | 69.87                  | Satt288 | 76.77                  |
| Race3 | G  | 334.49    | 94.8                   | 91.45-98.15   | 6.70        | A245_2   | 89.97                  | H3_54HE_1| 98.52                  |
| Race3 | J  | 20.29     | 74.00                  | 69.67-78.33   | 8.66        | Sat_396  | 69.30                  | Satt431 | 78.57                  |
| Race4 | A2 | 9.90      | 52.30                  | 51.87-52.73   | 0.86        | Sat_162  | 51.86                  | A486_1  | 53.16                  |
| Race4 | G  | 12.36     | 3.87                   | 3.20-4.53     | 1.33        | H3_c6_2  | 2.77                   | Satt309 | 4.53                   |
| Race4 | H  | 18.30     | 59.33                  | 54.13-64.53   | 10.40       | Satt541  | 53.35                  | Satt052 | 64.10                  |
| Race5 | B1 | 27.13     | 121.68                 | 115.53-127.82 | 12.29       | R244_1   | 115.75                 | AQ851479| 128.66                 |
| Race14 D2 | 22.17 | 90.20 | 86.45-93.95 | 7.50 | Satt528 | 86.34 | i6_2 | 93.92 |

Table 19. Meta-analysis results of resistance QTLs to soybean cyst nematode

4.3 Meta-analysis results of yield QTLs

4.3.1 Meta-analysis of 100-seed weight QTLs

A meta-analysis was carried out on the consensus QTL sites on 10 QTL clusters (Table 20). All the sites were dispersed on 9 linkage groups, only 2 clusters were found on LG B2. The site with the minimal confidence interval was on linkage group D2, with flanking markers Satt458 and Satt135 at 24.52 cM and 26.05 cM, the C.I. of 1.52 cM.

4.3.2 Meta-analysis of lodging QTLs

A meta-analysis was carried out on the consensus QTL sites on 11 QTL clusters (Table 21). 5 clusters were found on LG L with the interval of 1.31-6.19 cM, 7.83-14.03 cM, 30.58-34.14 cM,
36.70-41.00cM, and 92.66-111.07cM, the C.I. were 3.55cM, 3.82cM, 3.12cM, 2.78cM, and 17.04cM, individually. The site with the minimal confidence interval was on LG G, with flanking markers Sat_372 and L120_1 at 107.75 cM and 110.45cM, the C.I. was 1.73cM.

| LG  | AIC value | Meta-QTL position(cM) | 95% C.I. (cM) | Map distance | L-marker | L-marker Position (cM) | R-marker | R-marker Position (cM) |
|-----|-----------|-----------------------|---------------|--------------|----------|------------------------|----------|----------------------|
| B1  | 27.34     | 40.85                 | 36.88-44.83   | 7.95         | Satt251  | 36.48                  | Satt197  | 46.39                |
| B2  | 31.71     | 50.36                 | 48.53-52.19   | 3.66         | B142_1   | 43.58                  | A108_1   | 53.54                |
| B2  | 31.71     | 65.56                 | 60.26-70.86   | 10.6         | BLT049_2 | 59.82                  | G214_4   | 70.88                |
| C2  | 16.89     | 110.19                | 108.64-111.75 | 3.11         | Satt277  | 107.59                 | Satt557  | 112.19               |
| D2  | 6.52      | 25.28                 | 24.52-26.04   | 1.52         | Satt458  | 24.52                  | Satt135  | 26.05                |
| H   | 16.28     | 50.72                 | 47.23-54.22   | 6.99         | Satt442  | 46.95                  | A404T_3  | 55.39                |
| I   | 33.65     | 55.1                  | 52.27-57.93   | 5.66         | A955_1   | 51.99                  | Satt049  | 58.82                |
| K   | 14.51     | 15.68                 | 14.33-17.04   | 2.71         | Satt242  | 14.35                  | Sat_119  | 17.11                |
| M   | 8.80      | 9.28                  | 6.25-12.31    | 6.06         | Satt636  | 5.00                   | Satt201  | 13.56                |
| O   | 14.37     | 40.19                 | 38.71-41.67   | 2.96         | Satt653  | 38.10                  | Satt347  | 42.30                |

Table 20. Meta-analysis results of 100-seed weight QTLs

| LG  | AIC value | Meta-QTL position(cM) | 95% C.I. (cM) | Map distance | L-marker | L-marker Position (cM) | R-marker | R-marker Position (cM) |
|-----|-----------|-----------------------|---------------|--------------|----------|------------------------|----------|----------------------|
| B1  | 28.82     | 73.73                 | 66.97-80.49   | 13.52        | BLT043-1 | 66.77                  | Satt332  | 80.89                |
| C2  | 29.46     | 112.02                | 110.63-113.4  | 2.77         | Bng164-1 | 110.14                 | Satt319  | 113.42               |
| C2  | 29.46     | 114.1                 | 112.71-115.49 | 2.78         | Satt289  | 112.35                 | A397_1   | 116.72               |
| F   | 24.04     | 17.5                  | 3.50-26.6     | 23.1         | Satt193  | 3.42                   | Satt659  | 26.71                |
| F   | 24.04     | 38.9                  | 34.90-43.70   | 8.80         | Satt160  | 33.19                  | Satt516  | 44.42                |
| G   | 9.99      | 109.86                | 108.47-110.20 | 1.73         | Sat_372  | 107.75                 | L120_1   | 110.45               |
| L   | 26.02     | 4.06                  | 2.29-5.84     | 3.55         | Sat_408  | 1.31                   | Slet3_4s | 6.19                 |
| L   | 26.02     | 10.23                 | 8.32-12.14    | 3.82         | BLT010_2 | 7.85                   | Satt182  | 14.03                |
| L   | 23.53     | 32.22                 | 30.66-33.78   | 3.12         | Satt398  | 30.58                  | G214_1   | 34.14                |
| L   | 23.53     | 38.16                 | 36.77-39.55   | 2.78         | A023_1   | 36.70                  | Satt462  | 41.00                |
| L   | 13.09     | 101.7                 | 93.18-110.22  | 17.04        | Satt664  | 92.66                  | A802_2   | 111.07               |

Table 21. Meta-analysis results of lodging QTLs

### 4.3.3 Meta-analysis of soybean height QTLs

A meta-analysis was carried out on the consensus QTL sites on 12 QTL clusters (Table 22). On LG B1 and LG K, 3 clusters were found, individually. The site with the minimal confidence interval was on LG K, with flanking markers Satt441 and Satt552 at 41.00 cM and 46.00cM, the C.I. was 0.24cM.
### 4.4 Meta-analysis of soybean growth stage QTLs

A meta-analysis was carried out on the consensus QTL sites on 7 QTL clusters for R1 period (Table 23), 2 QTL clusters for R8 period (Table 24), and 10 QTL clusters for multiple period (Table 25). Three main sites related with R1 period were on linkage group J, with flanking left markers Satt076, A461_1, and K385_1 at 61.40 cM, 87.90 cM and 101.30 cM, corresponding right markers L050_8, Bng095_1, and Sat_245 at 72.70 cM, 100.40 cM, and 115.10 cM, the C.I. were 10.61 cM, 8.66 cM, and 10.60 cM. The site with the minimal confidence interval was on LG C2, with flanking markers Satt365 and Satt658 at 111.70 cM and 113.60 cM, the C.I. was 1.63 cM.

One site related with R8 period was on LG C2, with flanking markers A397_1 and Sat_263 at 116.70 cM and 118.80 cM, the C.I. was 0.90 cM. The other site related with R8 period was on LG L, with flanking markers Satt156 and Satt678 at 56.10 cM and 70.20 cM, the C.I. was 9.64 cM.

### Table 22. Meta-analysis results of soybean height QTLs

| LG  | AIC value | Meta-QTL position(cM) | 95% C.I. (cM) | Map distance | L-marker Position (cM) | L-marker | R-marker Position (cM) | R-marker |
|-----|-----------|------------------------|--------------|--------------|------------------------|----------|------------------------|----------|
| B1  | 105.37    | 32.61                  | 30.75-34.47  | 3.72         | Satt426               | 28.00    | Sat_156                | 35.00    |
| B1  | 105.37    | 56.42                  | 54.25-58.58  | 4.33         | Sat_149               | 54.00    | Satt298                | 65.00    |
| B1  | 105.37    | 87.44                  | 81.87-93.01  | 11.14        | Sat_095               | 81.00    | Satt665                | 96.00    |
| C2  | 18.04     | 105.05                 | 102.33-107.78| 5.45         | Satt665               | 102.00   | Satt365                | 112.00   |
| D1a | 16.92     | 49.04                  | 48.20-49.88  | 1.68         | Satt342               | 48.00    | Sat_159                | 50.00    |
| F   | 27.28     | 111.34                 | 105.70-116.98| 11.28        | Sat_197               | 104.00   | Satt218                | 118.00   |
| G   | 21.53     | 10.08                  | 4.12-16.04   | 11.92        | Sat_168               | 3.90     | Satt217                | 18.00    |
| K   | 19.30     | 38.93                  | 36.99-40.86  | 3.87         | Satt137               | 37.00    | Satt178                | 41.00    |
| K   | 19.30     | 41.65                  | 40.89-42.41  | 1.52         | Satt178               | 41.00    | Satt555                | 43.00    |
| K   | 19.30     | 46.32                  | 46.20-46.44  | 0.24         | Satt441               | 41.00    | Satt552                | 46.00    |
| M   | 32.35     | 18.58                  | 11.08-26.08  | 15.00        | Satt590               | 7.80     | Satt567                | 33.00    |
| M   | 32.35     | 42.47                  | 37.06-47.88  | 10.82        | Satt540               | 34.00    | Sat_244                | 49.00    |

### Table 23. Meta-analysis results of R1 period QTLs

| LG  | AIC value | Meta-QTL position(cM) | 95% C.I. (cM) | Map distance | L-marker Position (cM) | L-marker | R-marker Position (cM) | R-marker |
|-----|-----------|------------------------|--------------|--------------|------------------------|----------|------------------------|----------|
| C2  | 24.64     | 106.39                 | 98.1-107.62  | 9.52         | Satt363               | 98.10    | Satt277                | 107.60   |
| C2  | 24.64     | 112.75                 | 111.98-113.61| 1.63         | Satt365               | 111.70   | Satt658                | 113.60   |
| M   | 20.03     | 33.48                  | 32.48-34.47  | 1.99         | Ts                    | 30.20    | Satt540                | 35.80    |
| M   | 20.23     | 18.58                  | 11.08-26.08  | 15.00        | Satt590               | 7.80     | Mng339_1               | 27.30    |
| L   | 47.46     | 67.38                  | 62.08-72.69  | 10.61        | Satt076               | 61.40    | L050_8                 | 72.70    |
| L   | 47.46     | 93.26                  | 88.93-97.59  | 8.66         | A461_1                | 87.90    | Bng095_1               | 100.40   |
| L   | 47.46     | 107.24                 | 101.94-112.54| 10.60        | K385_1                | 101.30   | Sat_245                | 115.10   |
For multiple periods, some sites were only related with reproductive periods, such as Mul1, Mul2, Mul3, Mul4, Mul9, and Mul10; some site were only related with vegetative periods, such as Mul5 and Mul6; some site were related with both reproductive periods and vegetative periods. Mul3 was very special for its long-term effect on the six of eight reproductive periods.

| LG | AIC value | Meta-QTL position(cM) | 95% C.I. (cM) | Map distance | L-marker | L-marker Position(cM) | R-marker | R-marker Position(cM) |
|----|----------|------------------------|---------------|--------------|----------|-----------------------|----------|-----------------------|
| C2 | 28.03    | 117.66                 | 117.21-118.11 | 0.90         | A397_1   | 116.70                | Sat_263  | 118.80                |
| L  | 16.87    | 64.19                  | 59.37-69.01   | 9.64         | Satt156  | 56.10                 | Satt678  | 70.20                 |

Table 24. Meta-analysis results of R8 period QTLs

| Locus name | LG | Position(cM) | Flanking Marker     | Period |
|------------|----|--------------|---------------------|--------|
| Mul1       | C1 | 105.06       | Sat_076-K011_3      | R1, R7 |
| Mul2       | C1 | 112.43       | Satt365-Satt658     | R1, R8 |
| Mul3       | D1a| 55.89        | Satt515-Sat_201     | R1, R2, R3, R4, R5, R7 |
| Mul4       | D1a| 63.76        | Satt343-Satt507     | R2, R4, R6, R8 |
| Mul5       | D1b| 67.09        | A605_1-Sat_423      | V8, V9 |
| Mul6       | D1b| 73.41        | Satt290             | V11, V12 |
| Mul7       | D1b| 78.02        | Bng047_1-Sat_169    | V13, V14, R3, R4, R5 |
| Mul8       | D1b| 80.84        | Satt644-Satt041     | V18, R1, R3 |
| Mul9       | F  | 26.98        | Satt659-Satt206     | R1, R3, R7 |
| Mul10      | J  | 43.01        | Satt380             | R1, R3, R7 |

Table 25. Meta-analysis results of multiple period QTLs

5. Discussion

Soymap2, the reference map

A new public map, soymap2, was constructed by Song (2004). Five soybean genetic maps, including molecular genetic maps of two F2 populations, A81-356022 × PI468916 and Clark × Harosoy, and three RIL populations, Minsoy × Noir1, Minsoy × Archer, and RILs of Noir 1 × Archer, were integrated. The public map contains 20 LGs and 1,849 markers, including 709 restriction fragment length polymorphism (RFLP) markers, 1,015 Simple Sequence Repeat (SSR) markers, 73 random amplified polymorphic DNA (RAPD) markers, six amplified fragment length polymorphism (AFLP) markers, and 46 markers of other types. This integrated map shows a very high density of SSR and RFLP markers, commonly used to map QTLs. Thus, QTLs from these maps could be easily projected onto the public map.

Using of meta-analysis in MAS

MAS is an important strategy for crop improvement. Recently, MAS has been successfully used to increase the quality and yield of wheat (Romagosa. 1999) and rice (Wang. 2004). However, due to its validity, cost, and the low number of markers, MAS has not been widely applied in crops. The accuracy of mapping QTLs decides the efficiency of gene discovery and cloning.

Meta-analysis is an important tool in linkage analysis, optimize QTL, shrink the confidence interval, and improve the accuracy and validity of QTL position (Löffler, 2009), and is of
particular relevance for the validation of known QTL. QTL location is affected by many factors, including genetic background, population size and analytical method, so a single study can only be taken as suggestive, unless it is based on a large enough set of experiments. Where the CI is large, it is difficult to distinguish between the presence of a single locus and the presence of two (or more) loci. The meta-analysis approach, as developed by Goffinet and Gerber (2000), however does provide a means to alleviate the extent of this uncertainty, since it improves the capacity to identify the true number of QTL present, and the precision of their location by reducing their associated CI. QTL associated with early maturity in bread wheat have recently been identified using a meta-analysis-based approach (Hanocq, 2007), and similarly, resistance to gray leaf spot in maize has been genetically defined by the integration of >50 QTL (Shi, 2007). The proportion of the phenotypic variance explained by a given QTL (its $R^2$ value) is the most important parameter in deciding whether marker assistance can be more efficient than conventional phenotypic selection alone (Bernardo 2001; Bernardo and Charcosset 2006).

The molecular markers in the consensus QTL could be used for individual selection in the original mapping population. In addition, some important intervals could be enhanced by backcrossing for QTL fine mapping. However, some key aspects of MAS still require improvement. The first is how to evaluate the contribution ratio of the allele for a special locus. For some populations, the allele is major, but for others it is minor. The second aspect is how to build a practical model for MAS or molecular design, which is important for the application of markers. We hope that the meta-analysis reported here will guide the choice of QTL targeted for marker assisted selection, and it was the foundation for the process of acquiring QTL-related genes in soybean.

Use of bioinformatics tools in mining candidate genes

With the advent of soybean genomic information and bioinformatics tools, finding consensus QTL intervals in the corresponding physical map is easier, particularly for mining candidate genes (Lv et al. 2008). Bioinformatics tools are important in the process leading from QTL to the quantitative trait gene, or QTG. Wang and Paigen (2002) found that 18 of the 22 human high-density lipoprotein-cholesterol (HDL-C) QTLs were within the murine HDL-C QTLs, suggesting that murine QTLs for HDL-C levels may have homologous locations in humans and that their underlying genes may be appropriate for testing in humans. GENSCAN is a general-purpose gene identification program that analyzes genomic DNA sequences from a variety of organisms, including humans, other vertebrates, invertebrates, and plants. The InterProScan server analyzes sequences (cDNA, protein) with respect to international GO terms. In this study, traditional QTLs were integrated, and some important genes related to the important agronomic traits could be mined in the future.

6. Conclusion

In this chapter, the QTLs of 12 important agronomic traits in soybean were integrated by meta-analysis. For seed quality traits, 25 consensus QTLs of oil content were extracted from 130 initial research QTLs, 23 consensus QTLs of protein concentration from 107 QTLs, 23 consensus QTLs of fatty acid from 83 QTLs, 111 consensus QTLs of amino acid content from 111 QTLs, 10 consensus QTLs of isoflavone content from 70 QTLs. For biotic stress resistance traits, 23 consensus QTLs of fungal disease resistance were extracted from 107 initial research QTLs, 14 consensus QTLs of insect resistance from 81 QTLs, 16 consensus
QTLs of soybean cyst nematode resistance from 135 QTLs. For yield trait, 6 consensus QTLs of 100-seed weight were extracted from 78 initial research QTLs, 11 consensus QTLs of lodging from 59 QTLs, 12 consensus QTLs of plant height from 93 QTLs. For soybean growth stages, 7 consensus QTLs were extracted from 98 initial research QTLs

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The book Soybean: Molecular Aspects of Breeding focuses on recent progress in our understanding of the genetics and molecular biology of soybean and provides a broad review of the subject, from genome diversity to transformation and integration of desired genes using current technologies. This book is divided into four parts (Molecular Biology and Biotechnology, Breeding for Abiotic Stress, Breeding for Biotic Stress, Recent Technology) and contains 22 chapters.

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Guohua Hu, Qingshan Chen, Chunyan Liu, Hongwei Jiang, Jialin Wang and Zhaoming Qi (2011). Integration of Major QTLs of Important Agronomic Traits in Soybean, Soybean - Molecular Aspects of Breeding, Dr. Aleksandra Sudaric (Ed.), ISBN: 978-953-307-240-1, InTech, Available from: http://www.intechopen.com/books/soybean-molecular-aspects-of-breeding/integration-of-major-qtls-of-important-agronomic-traits-in-soybean