

The Pennsylvania State University
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CHARACTERIZATION AND MAPPING OF QTLS CONFERRING
RESISTANCE TO LATE BLIGHT IN POTATO

A Thesis in
Plant Pathology
by
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Abstract

Field resistance to *Phytophthora infestans* (Mont.) de Bary, the causal agent of late blight in potatoes, has been genetically characterized by analyzing trait-marker association in a potato diploid segregating family of 230 full-sib progenies derived from a cross between two hybrid *Solanum phureja* × *S. stenotomum* clones. Trait data were developed at two locations in Pennsylvania in three replicated field trials between 1999 and 2002. Area under the disease progress curve (AUDPC) was calculated for individual clones in each environment. The distribution of AUDPC values was consistent with the inheritance of a quantitative trait. Relatively high levels of resistance and transgressive segregations were observed within this family. Broad-sense heritability was estimated to be 0.67 with a 95% confidence interval of 0.65-0.78. Since *P. infestans* can rapidly overcome major race-specific resistance genes, identifying the basis for quantitative resistance is a crucial element for implementing advanced breeding strategies. For this purpose, a genetic linkage map of this population was constructed using previously mapped restriction fragment length polymorphism (RFLP) markers on 132 clones from the same family. A total of 114 RFLP markers have been used and 14 linkage groups, covering approximately 855 cM, have been identified. The total number of loci mapped was 126, and the genome coverage by the map is estimated to be at least 70% with an average distance of 6.8 cM between two markers. Two methods were employed to determine trait-marker association: the non-parametric Kruskal-Wallis test and interval mapping analysis. Analysis of the trait scores combined with the marker segregation data allowed the identification of regions of the genome that were significantly correlated with components of disease resistance. Three major QTLs (quantitative trait loci) were detected on linkage group III, V and XI as a contribution from both parents, explaining 23, 17 and 10%, respectively, of the total phenotypic variation. One additional QTL was detected on linkage group VII with less statistical support. The present study revealed the presence of potentially new genetic loci in the potato genome contributing to general resistance against late blight. These QTLs could represent a specific contribution of the two diploid potato species used in this study.

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Dedication

I would like to dedicate this work to my parents, mamma Piera e papà Silvio, and my brother Francesco and sister Alessandra, for their love, support and encouragement throughout my graduate school tenure at The Pennsylvania State University.

Chapter 1

Introduction

Late blight, caused by the oomycete *Phytophthora infestans* (Mont.) de Bary, has been a worldwide problem for the past 150 years in the cultivation of potato (*Solanum tuberosum* L.). Epidemics of *P. infestans* cause heavy losses in yield due to both foliar destruction and rotting of blighted tubers in storage.

The pathogen is currently controlled by frequent applications of fungicides. However, this practice creates environmental concern and contributes to the emergence of fungicide insensitive isolates (Cohen and Reuveni, 1983). Furthermore, this disease has recently become more severe in major U.S. potato growing regions and other areas throughout the world, due to the establishment of new genotypes of *P. infestans* belonging to the A2 mating type (Fry et al., 1993; Goodwin et al., 1995; Spielman et al., 1991). Concurrently, pathogenic strains of *P. infestans* insensitive to metalaxyl, a systemic fungicide, were first reported in the Pacific Northwest of the United States and Canada in 1991 (Deahl et al., 1993).

Since the beginning of this century, much effort has been devoted to breeding for resistance to *P. infestans* (Wastie, 1991). Two types of resistance exist in potato: hypersensitivity (vertical or specific resistance) and field resistance (horizontal or general resistance). A number of dominant alleles conferring race-specific resistance controlled by single loci (*R* genes) have been introduced into cultivars from the wild species *Solanum demissum* Lindley (Müller and Black, 1952) and later from *S. stoloniferum* Schlecht. et Bché. (Schick et al., 1958). This type of resistance was overcome quickly by new races of the pathogen having virulence alleles compatible with the resistance alleles in these cultivars.

Current breeding strategies concentrate, therefore, on improving horizontal, race-nonspecific resistance, which is polygenically inherited, and for which selection is difficult. The identification of the map positions of molecular markers linked to qualitative and quantitative resistance genes is, therefore, an essential step toward implementing better breeding strategies for *P. infestans* resistance based on marker-assisted selection (MAS) (Leonards-Schippers et al., 1992).

The potato, as a crop of worldwide importance with a vast underutilized germplasm pool, is an excellent candidate to benefit from the application of MAS strategies. Moreover, the more recent application of various types of DNA-based molecular markers (restriction fragment length polymorphisms - RFLPs, random amplified polymorphic DNA - RAPDs, simple sequence repeats - SSRs and amplified fragment length polymorphisms - AFLPs) for plant genome studies, is a breakthrough that can be utilized to introgress wild species germplasm into the cultivated germplasm base of many crops. During the last decade, several linkage maps of the potato based on RFLP, AFLP and SSR markers have become available (Bonierbale et al., 1988; Gebhardt et al., 1989; Milbourne et al., 1998; Van Eck et al., 1995). Despite the availability of these new tools, genetic studies and breeding efforts toward potato improvement are still hampered by the high level of heterozygosity and polyploidy in *Solanum tuberosum*, and techniques that promise to lead more directly to the identification, selection and production of desired genotypes are particularly attractive for such a crop.

Here we report an analysis of partial resistance to late blight, in a diploid, segregating, potato population considered devoid of *R* genes. Representative genotype data for 132 members of the population were collected using co-dominant RFLP markers. Phenotypic data was collected from field plots in Pennsylvania over multiple seasons. The full-sib segregating family has been developed from a cross between clone BD142-7, partially resistant to late blight, and a susceptible clone, BD142-1. The research will extend previous studies to tag major QTLs (Quantitative Trait Loci) of late blight resistance with molecular markers and to convert them into PCR-based markers, so that they could be applied in marker-assisted selection.

The hypotheses underling this research are:

1. The full-sib diploid potato family utilized in this study possesses high levels of resistance against *Phytophthora infestans*.
2. The late blight resistance present in this segregating population is controlled by several genes, and can be described as polygenic or horizontal resistance.
3. This general resistance can be associated to various QTLs of the potato genome, each of them conferring only a portion of the overall resistance to this fungus.

The purpose of this research was to determine, through replicated field assessment, the quantitative late blight resistance possessed by a hybrid diploid potato *Solanum phureja* × *S. stenotomum* family. Moreover, a molecular linkage map of this family based on RFLP markers was constructed, with the ultimate goal of identifying and characterizing QTLs conferring resistance to late blight.

Chapter 2

Literature Review

Late Blight of *Solanum tuberosum* L. (Potato)

Of all the pathogens of economically important plant species, *P. infestans* can rightly claim its place as one of the most notorious. Late blight, first reported in the early 1840's causing problems in the northeastern United States, totally destroyed Irelands staple potato crop during 1845 and 1846. The most immediate effects were poverty and mass starvation, which led to profound sociological and economic changes in that country (Bourke, 1991; Gregory, 1983; Large, 1940) and to the massive emigration of Irish to the United States and elsewhere. *Phytophthora* species cause a wide variety of diseases on a tremendous number of hosts, including both herbaceous and woody species. Although late blight has been traditionally associated with potatoes, in certain cool and moist climates, the same pathogen can be a significant factor limiting the yields of tomato crops (Griffith et al., 1995) and several other species in the family Solanaceae.

The disease symptoms, which may appear on the foliage any time during the development of the plant, consist of purple, black or brownish-black lesions that usually appear first at the tip or margin of the leaf and around the lesions margins on the adaxial side. Later, lesions may occur anywhere on the leaf, petiole, or even the stem. If cool, moist conditions prevail, whitish masses of sporangia appear on the abaxial side of the leaf. The tubers become affected later in the season. In the early stages, slightly brown or purple blotches appear on the skin. In damp soil the disease progresses rapidly, and the tuber decays either before or after harvest.

When soil is dry, the brown discoloration extends only to a depth of about 1 cm into the tuber; however, in storage, infection progresses throughout the tuber (Erwin and Ribeiro, 1996). When weather conditions are favorable and no control measures are applied, late blight may cause total destruction of the entire field within a week or two.

Disease Development

Initial infection of potato plants originates from diseased potato tubers in which the mycelium survives. The pathogen grows into the new healthy tissues sprouting from the potatoes and sporulates on the aerial parts of plants. Secondary infection of potato plants takes place by means of sporangia that are transported by water or are blown by wind.

Sporangia are normally produced on infected leaves at a temperature of 21°C when relative humidity is near 100%. Disease development is favored by cool (16 to 21°C), cloudy, moist weather, during which new sporangia are continuously being formed. Slightly warmer weather favors colonization of plant tissues. If the temperature is elevated and the relative humidity stays low, the progress of the disease is checked, and the characteristic white mycelium and sporangia are not produced. With the return of cool, moist weather, the fungus again becomes active and symptoms reappear. Sporangia lose their viability in 3-6 hours at relative humidity below 80%.

When the sporangia land on wet potato leaves or stems, they germinate either directly or by means of zoospores and cause new infections. The germ tube penetrates through the leaf cuticle or enters through a stoma and grows profusely between the cells and sends long, curled haustoria into the cells. The cells on which the mycelium feeds are killed, and as they begin to decay, new sporangiophores emerge from the stomata of the leaves and produce numerous sporangia, which are spread by the wind and infect new plants. The established lesions increase in size and new ones develop resulting in premature killing of the foliage and proportional reduction in potato tuber yields.

The second phase of the disease, the infection of tubers, begins in the field when, during wet weather, sporangia are washed down from the leaves and are

carried into the soil. The tubers near the surface of the soil are attacked by the emerging zoospores, which germinate and penetrate the tubers through lenticels or through wounds. Tubers are rarely infected by mycelium growing down the stem of a diseased mother plant. In most regions of the world the primary source of *P. infestans* inoculum is mycelium in infected tubers. In areas where both A1 and A2 mating types exist, oospores, the product of sexual reproduction, are considered to be a source of both inoculum and pathogen variability (Andrivon, 1995).

The pathogen: *Phytophthora infestans*

P. infestans, a heterothallic oomycete, produces mycelium with branched sporangiophores of unrestricted growth. Lemon-shaped, papillate sporangia are produced at the tips of the sporangiophore branches. This pathogen requires two mating types, designated A1 and A2 (Smoot et al., 1958), which are essential for sexual reproduction and production of oospores. Until recently, only the A1 mating type was found outside Mexico. In Central Mexico where both mating types are present, genetic diversity is high and oospores are found (Gallegley and Galindo, 1958).

Based on DNA and isozyme fingerprint analyses, it was suggested that before the 1980s a single clonal lineage of the A1 mating type, termed US-1, dominated most populations of *P. infestans* worldwide (Goodwin et al., 1994). US-1 isolates are thought to have propagated by asexual reproduction from *P. infestans* strains introduced in the 1840s from Mexico to North America and later to Europe and the rest of the world (Goodwin, 1997).

This situation changed drastically during the late 1970s. New strains of the fungus were detected in Europe that were metalaxyl-insensitive. It has been suggested that this new, diverse population of *P. infestans* had been introduced into Europe through a large shipment of commercial potatoes originated from Mexico during 1976 and 1977 (Goodwin, 1997). This last migration brought new A1 mating type strains as well as introducing for the first time the A2 mating type into Europe, causing the establishment of sexual reproduction. (Drenth et al., 1994; Fry and Goodwin, 1995, 1997a; Fry et al., 1993). In Europe these new genotypes had greater fitness rapidly causing the displacement of the older populations

(Alexopoulos et al., 1996).

There are also indications that a third migration of *P. infestans* occurred again out of Mexico into the U.S. in the late 1970s. In 1979, the US-6 genotype was thought to be responsible for a late blight epidemic on potato and tomato in southern California. Additionally, there is strong evidence for a fourth migration from northwestern Mexico into the U.S. and Canada (Goodwin, 1999). For the first time in 1992, two new genotypes, US-7 and US-8, of the A2 mating and highly insensitive to metalaxyl, were detected in the U.S. Probable sources of this last introduction were infected tomatoes imported into the U.S. from Mexico. Once in the U.S., the new genotypes spread rapidly and particularly the US-8 form proved to be a very efficient colonizer of potato tubers, contributing to its rapid increase during the last decade. Moreover, there is circumstantial evidence indicating that a new lineage, US-11, recently causing problems on potatoes and tomatoes in the western U.S. and now moving into the eastern states, could have been generated by a sexual recombination event occurring within the same area (Fry and Smart, 1999; Gavino et al., 2000).

Breeding for late blight resistance

The complete loss of the potato crop in Ireland and elsewhere after the late blight epidemic in 1845 led to intensified breeding efforts throughout Europe and North America. Although no highly resistant or immune cultivars had been produced by the beginning of the 20th century, sufficient resistance was apparently built up to prevent further disaster. *S. demissum* Lindl. was identified as the most important source of late blight resistance, particularly that associated with hypersensitive reaction, also described as vertical or race-specific resistance (Black and Gallegley, 1957; Vanderplank, 1984).

The simply inherited resistance found in this source made many researchers believe that the development of new disease resistant cultivars would be easy (Müller, 1928). By 1968, the number of dominant genes for race-specific resistance (*R* genes) identified had already risen to the 11 currently recognized (Malcolmson, 1969; Malcolmson and Black, 1966). Consequently, most breeding programs promptly discontinued breeding for horizontal or nonspecific resistance. Many cultivars with

vertical resistance to late blight were produced in breeding programs concerned with late blight, until the late 1960s (Umaerus et al., 1983).

In the 1970s, however, it became clear that using *R* genes was unreliable since *P. infestans* proved to be a highly variable pathogen capable of easily overcoming this race-specific resistance. As a consequence, soon most programs abandoned breeding for vertical resistance. Efforts were then redirected towards horizontal resistance, although at a much lower rate due to the availability of less expensive chemical control and preventive application techniques that provided reliable crop protection. The introduction in 1977 of a systemic compound belonging to the class of phenylamides, metalaxyl, provided outstanding protection under high disease pressure and became widely used. Unfortunately, the intensive employment of this product caused the appearance of insensitive strains of *P. infestans* in the 1980s, almost simultaneously in Switzerland, the Netherlands (Davidse et al., 1983) and Ireland (Cooke, 1981; Dowley and O'Sullivan, 1981), and later in all the potato growing regions.

Presently, even with the generalized adoption of new strategies that slow down the formation of insensitive strains, the most widely grown varieties are generally susceptible to late blight, although vast amounts of protectant fungicides are used. Other less popular varieties may carry some degree of horizontal resistance, which does not provide adequate protection (Vos, 1992).

In the early 1990s, the International Potato Center (CIP) started new significant efforts to breed for quantitatively inherited resistance in the absence of dominant race-specific resistance genes. Probabilities for increasing horizontal resistance through this strategy are far greater than those for sources containing unknown *R* genes (Landeo et al., 1995). Moreover, the addition of newer sources of resistance from wild species to current gene pools will undoubtedly enrich their genetic diversity. The major sources of known horizontal resistance to late blight are diverse and include: *S. tuberosum* germplasm with *S. demissum*-derived resistance; native cultivars from *S. andigena* and *S. phureja* germplasm; *S. andigena* germplasm adapted to long days (Neotuberosum); and hybrid materials between wild species *S. acaule* and *S. bulbocastanum*, and cultivated *S. phureja* and *S. tuberosum* germplasm (Landeo, 1989).

The introgression of several of these wild potato species possessing general

resistance to late blight into tetraploid *S. tuberosum* is often a difficult task due to various genetic incompatibilities. The plant material utilized in the proposed research derived from two diploid potato species, *S. phureja* and *S. stenotomum*, which are short-day species. These *Solanum* species have been intermated and successfully adapted to long-day growing conditions of the United States by Haynes (1972). The diploid hybrid population derived from these crosses has been reported to have good levels of resistance to early blight (Herriot et al., 1986), which was subsequently transferred to tetraploid *S. tuberosum* via $4\times-2\times$ crosses (Herriot et al., 1990).

In view of reports in the literature that identified some general resistance toward late blight in *S. phureja*, it was determined that this long-day hybrid population would be a valuable source of nonspecific resistance against this disease. Conventional potato breeding by sexual hybridization, however, is a complicated and lengthy process due to the genetic nature (heterozygous, tetraploid) of the potato (Bradshaw and Mackay, 1994; Howard, 1978). Nonconventional methods of crop improvements, such as somaclonal variation and marker assisted selection (MAS), are being developed as alternative sources of variability and for the efficient selection of elite genotypes (Cassells et al., 1991; Oberhagemann et al., 1999; Wenzel, 1985).

Genetic mapping in potato breeding

Prior to the utilization of molecular markers, there was no genetic map for potato, with only isolated cases of linkage among a few morphological markers having been reported. In 1987, Douches and Quiros (1987) monitored the segregation of isozyme markers in an interspecific diploid potato progeny, opening the door to more comprehensive molecular genetic mapping. The first genetic map of potato, based on single copy DNA probes from tomato, was constructed in a segregating cross between *Solanum phureja* and a *Solanum tuberosum* \times *Solanum chacoense* hybrid (Bonierbale et al., 1988). A total of 134 DNA and isozyme markers were mapped in 12 linkage groups corresponding to the 12 potato chromosomes and covering 606 cM. The employment of tomato genetic markers was possible because potato and tomato are closely related species in the family *Solanaceae*, and

have nearly identical karyotypes with the same basic chromosome number of 12 (Yeh and Peloquin, 1965) and significant nucleotide sequence homology (Zamir and Tanksley, 1988).

This high degree of DNA homology and the use of tomato clones allowed the development of comparative maps between potato and the genetically well-characterized tomato, as was similarly performed for tomato and pepper (Tanksley et al., 1988). Localization of economically important genes has already been demonstrated with some simply inherited loci that confer disease and pest resistances. For example, the *R1* locus on chromosome 5, which controls a race-specific resistance to late blight, was mapped by using two F₁ populations (Leonards-Schippers et al., 1991) and, more recently, cloned using a combination of positional cloning and a candidate gene approach (Ballvora et al., 2002). Two loci that confer high levels of resistance to potato virus X were mapped to two independent chromosomal positions (Ritter et al., 1991). A simply inherited locus *Gro1* for resistance to cyst nematode (*Globodera rostochiensis*) pathotype *Ro1* was mapped to chromosome VII at a locus close to marker TG20 (Barone et al., 1990). Furthermore, the simply inherited *H1* gene from CPC 1673, *S. tuberosum* subsp. *andigena*, which shows resistance to the same *Ro1*, was located on chromosome V (Pineda et al., 1992).

Recently, the study of number and effect of major QTLs has been greatly facilitated by the advent of molecular markers and the development of saturated linkage maps (Tanksley, 1993). Once DNA markers linked with target traits are available, screening for the trait should be quickly but accurately achieved, compared with conventional screening procedures. Since availability of pathogens/pests of interest is not essential for resistance screening by molecular markers, testing for resistance to quarantined pathogens and pests can be greatly facilitated. More than 1400 molecular markers are available for potato, which makes this species one of the most fully covered plant genomes. Attempts to precisely identify and map genes affecting quantitatively inherited traits of various nature are currently in progress.

Field resistance, like most other important agronomic traits, is believed to be a quantitative character resulting from the joint action of polygenes and the environmental component (Black, 1970). Tagging of genes conferring resistance to late blight proposed in this study will be facilitated by the availability of several de-

tailed molecular maps of potato constructed with diploid populations. Molecular marker systems that employ RFLPs have been successfully applied in several studies (Bonierbale et al., 1988; Gebhardt et al., 1989; Tanksley et al., 1992). Moreover, several race-specific resistance (*R*) genes for pathogenic bacteria, viruses, fungi and nematodes have been isolated from a variety of plant species (Baker et al., 1997; Hammond-Kosack and Jones, 1997; Staskawicz et al., 1995). These genes not only share similar sequence structures, but also form clusters in the genomes. Conserved domains and motifs have been extensively used to obtain resistance gene analogs (RGAs) from diverse plant species using a PCR technique (Leister et al., 1996; Speulman et al., 1998). Thus, use of cloned RGAs as probes will have a high likelihood of detecting linked markers to disease resistance genes. The RFLP technique still remains among the most widely used DNA marker assays in plants. Furthermore, the technique is relatively robust, and readily transferable between different labs. Other advantages offered by this technique include the accurate identification of introgressed foreign genes and their use for screening quantitatively inherited characters. RFLP markers segregate in a manner that is Mendelian and codominant, phenotype-neutral and free of epistatic interactions. Although it remains widely used, a major limitation of the RFLP technique is the large quantity of DNA required to generate a DNA fingerprint of the entire genome.

Preceding studies

The full-sib segregating family that has been utilized in this project was originally derived from a cross between two diploid potato species, *S. phureja* × *S. stenotomum*. A previous report (Haynes et al., 1995) has shown that this population possesses valuable agronomic characteristics such as high specific gravity and early blight resistance. More recently, the same population was also evaluated for resistance to late blight in repeated experiments conducted in Pennsylvania (Haynes and Christ, 1999). Seventy-five percent of the diploid clones were found to have a significantly lower mean area under the disease progress curve (AUDPC) than the control cultivar Atlantic. Broad-sense heritability on a mean basis was estimated as 0.79. Narrow-sense heritability on a family mean basis was estimated as 0.78.

Based on these preliminary data, several full-sib families were developed to

further examine heritability of resistance and combining ability among the parental clones. A detached leaf assay was implemented to examine various components of resistance in twelve clones, three late blight resistant and nine susceptible: rate of lesion development, percent lesion area covering the leaf, total lesion size, and sporulation capacity (Liu et al., 1998a). From the results of these tests on the twelve clones and on the basis of reproducibility and correlation to field data, two clones BD172-1 and BD142-1 were chosen as parents to generate the full-sib family constituting the basic plant material in this research.

The RFLP probes for screening our full-sib segregating family were initially obtained from Dr. Christiane Gebhardt at Max-Planck-Institut für Züchtungsforschung, Köln, Germany. These probes, which have been used in several other mapping projects, were specifically chosen to be representative of all 12 chromosomes, ensuring a good coverage of the genome, and also to allow us to compare our map with others. Survey filters were prepared from parental DNA digested with five different restriction endonucleases, *DraI*, *EcoRI*, *HindIII*, *XbaI* and *TaqI*. Restriction digestion was carried out with 0.5 - 1 U restriction enzyme per microgram of DNA. Approximately 10 μ g of restricted potato DNA was loaded per lane and separated on 0.8% agarose gels in 1 \times TBE buffer for 12 h at 40 V. Of all 49 DNA probes initially surveyed, 93% (45) detected polymorphism between the parental clones with at least one of the five restriction enzymes (Liu et al., 1998b).

Chapter 3

Late blight resistance in a full-sib diploid potato family

3.1 Introduction

Potato late blight, caused by *Phytophthora infestans* (Mont.) de Bary, is one of the most common and destructive diseases of cultivated potatoes (*Solanum tuberosum* L.) in the U.S. and worldwide. The oomycete *P. infestans* can infect foliage, stems and tubers, and cause severe damage during all stages of plant development, which may result in complete loss of the crop. In recent years, late blight has become a reemerging disease worldwide due to the development of resistance to phenylamide fungicides in pathogen populations and the widespread occurrence of new and more aggressive genotypes (Deahl et al., 1991; Drenth et al., 1993; Fry and Goodwin, 1997b). Moreover, the presence of both the A1 and A2 mating types among this new population of *P. infestans* provides a ground for a potential increase in the overall genetic variability of this fungus through sexual recombination.

Breeding for resistance to this disease became a major priority after its destructive character was revealed during the epidemic of 1845 that led to the Irish potato famine and the mass emigration and death of millions of people in Ireland. Due to the tetraploid nature of cultivated potatoes, breeding is much more complex than in diploid crop species. Furthermore, the breeding effort has been hampered by the use of closely related germplasm in breeding programs that resulted in high genetic similarity among the various potato commercial varieties (Mendoza and

Haynes, 1974).

In potato, two types of resistance against *P. infestans* exist: race-specific resistance (vertical resistance or hypersensitivity) and field resistance (horizontal or general resistance) (Vanderplank, 1968). Hypersensitive genotypes are generally characterized by a rapid necrotic response in the attacked cells. This type of resistance is under direct control of a series of major genes (*R* genes), each of which is brought into action by a distinct race of the pathogen. So far, eleven of these major *R* genes have been identified, all derived from the hexaploid species *Solanum demissum* (Black et al., 1953; Malcolmson and Black, 1966). A few of these eleven *R* genes have been already introduced into modern potato varieties (Ross, 1986), but compatible races of *P. infestans* have also very rapidly arisen for all of them. Field resistance, on the other hand, consists of several components resulting in the overall hindrance of the parasitic attack on the host, and is controlled by many interacting genes. Both types of resistance can occur jointly in wild species like *S. demissum*, *S. bulbocastanum*, *S. polyadenium*, *S. stoloniferum*, *S. vernei*, *S. verrucosum* and others (Black, 1970; Graham, 1963; Toxopeus, 1964).

Disease control methods based solely on the introgression of a single or a combination of several race-specific resistant genes into tetraploid *S. tuberosum* have not been successful (Thurston, 1971). Therefore, potato breeders presently focus their effort on improving general resistance, which is expected to be a more successful and durable strategy. Moreover, breeding for effective forms of durable resistance should also significantly alleviate the detrimental impact on the environment of frequent and costly fungicide applications currently required to control late blight in commercial production.

Besides the difficulties of dealing with more variable and aggressive isolates of the pathogen, breeding for field resistance against *P. infestans* is complicated by the quantitative nature of this type of resistance. Traditional breeding methods based on crossing and phenotypic selection appear to be inefficient when trying to incorporate the numerous components of field resistance, each likely inherited by minor genes, into cultivated varieties. Fortunately, in the last decade, molecular marker technology has provided new valuable tools for the localization and effective manipulation of quantitative trait loci (QTL) in breeding programs.

To expand the present germplasm breeding base of potato, Haynes and Christ

(1999), investigated the late blight resistance in 281 clones derived from 72 families of a diploid random-mated population, considered devoid of *R* genes, of *S. phureja* × *S. stenotomum* (*phu-stn* population) which are short-day species of South American origin. After two years of replicated experiments in Pennsylvania, it was determined that this *phu-stn* population had relatively high levels of field resistance to late blight and that both broad-sense and narrow-sense heritability in it were high. To facilitate breeding efforts, a new project was initiated to discern the genetic basis of late blight resistance in this population, including mapping the responsible QTLs with the ultimate goal of transferring them to the tetraploid level via marker assisted selection (MAS).

For this purpose, in the present study, a full-sib diploid potato family has been characterized for segregation of late blight resistance and the stability of this trait among different environments. This family, constituted in 1997, resulted from a cross between two highly heterozygous diploid clones: BD142-1 (susceptible to late blight) and BD172-1 (partially resistant). The origin of these two individuals can be traced back to the random mated population constituted from 36 plant introductions each of *S. phureja* and *S. stenotomum* (Haynes, 1972).

The specific purposes of this study were to: (i) evaluate a full-sib family of *phu-stn* which was developed for mapping molecular markers associated with resistance to *P. infestans*; (ii) estimate broad-sense heritability for resistance to late blight in this full-sib family; and, (iii) determine the stability of resistance to *P. infestans* in individual clones from this full-sib family.

3.2 Materials and Methods

3.2.1 Plant materials

The full-sib offspring of the cross between the heterozygous diploid hybrid clones BD142-1 and BD172-1 were chosen for mapping. The cross of the seed parent BD142-1 (highly susceptible to late blight) with the pollen parent BD172-1 (partially resistant) was made in the spring of 1997. Four plants of each clone were planted in the crossing block, controlled crosses were made, and true seeds were collected and planted. True seeds were planted in individual test tubes contain-

ing Murashige & Skoög media (Murashige and Skoog, 1962) after treatment with 1500 mg/kg gibberelic acid (GA_3) for 24 hr. and subsequent drying for 24 hr. A number of plantlets per clone were rapidly micropropagated. The plantlets were transplanted into 9 cm clay pots from January 28 to February 17 and harvested from April 30 to May 2, 1998. Since then, tubers from each clone have been propagated and maintained at the Chapman Farm in Presque Isle, Maine, and then shipped to Pennsylvania for disease testing. Both parents were initially selected from the 281 *phu-stn* clones evaluated for resistance to *P. infestans* by Haynes and Christ (1999). Each parent belonged in the top 5% of those 281 clones for either susceptibility or resistance, respectively. The progeny obtained consisted of approximately 230 individuals and is referred to as the mapping population (BD42/72).

3.2.2 Field experiments

Three separate field experiments were conducted in Pennsylvania between 1999 and 2002. In 1999 the entire diploid potato population was grown in field trials at the Russell E. Larson Agricultural Research Center at Rock Springs, PA. In 2002 the same family was tested in two locations, at the Southeastern Research and Extension Center at Landisville, PA., and again at Rock Springs, but plot location within the research farm was, for this year, different than the one used in the 1999 experiment. For brevity, the three field experiments will be hereafter referred to as: 1999 Rock Springs, 2002 Rock Springs and 2002 Landisville.

The entire BD42/72 population, two parental clones and three standard commercial cultivars ‘Atlantic’, ‘Kennebec’ and ‘Kathadin’ were included in all three experiments and evaluated for reaction to late blight under field conditions. The experimental plots were all planted during the month of June. Planting dates were: 4 June 1999 and 11 June 2002 at Rock Springs, and 27 June 2002 at Landisville. For all experiments, plants were grown in a randomized complete block design (RCBD) with two blocks. Plots consisted of four/ five tubers of a clone and were hand planted, spaced 22 cm within and 91 cm between rows with a 1.2 m break within rows between plots.

To ensure uniform disease pressure, each treatment plot had an adjacent row

of the susceptible cultivar ‘Russet Burbank’ acting as a disease spreader row. Standard commercial management practices were followed throughout the season, with no traditional fungicides applied except for 1-3 early season applications of Folicur 3.6[®] (Tebuconazole) specifically targeting *Alternaria solani* causing early blight. Fertilization was applied in furrow at an approximate rate of 171 kg ha⁻¹ of 10-10-10 (N-P-K). If the environmental conditions were less than ideal for disease development, a sprinkler irrigation system was used to create a more conducive environment by extending dew periods, increasing relative humidity and decreasing temperature within the plant canopy.

3.2.3 *P. infestans* isolates and inoculum preparation

Three different isolates of *P. infestans* were used to produce the artificial fungal inoculum. All isolates utilized were US-8 and A2 mating type. They were all originally isolated from naturally infected leaves of potatoes at various locations in Pennsylvania, and maintained on pea agar media. These isolates have been previously tested on a set of potato late blight differentials possessing a single or a combination of the following resistance genes: *R1*, *R2*, *R3*, *R4*, *R5*, *R6*, *R8*, *R9*, *R10*, and *R11*. All of the tested *R* genes were clearly overcome by the *P. infestans* isolates used in the present study (Christ and Valluru, unpublished). To ensure pathogenicity and virulence of the isolates, these were periodically re-isolated following the protocol described in the International Potato Center (CIP) training manual (Forbes, 1997). In order to obtain a high concentration of virulent sporangia from each isolate, surface disinfected leaflets (2% sodium hypochlorite for 5 min) of ‘Katahdin’ were placed on the surface of seven-day-old V8/Lima bean agar plate cultures and incubated for seven days at 15-18°C in the dark. After this period, sporangia were removed from the leaflet and agar surface with distilled water. Equal amounts of the three isolates were pooled together to constitute the inoculum and subsequently the sporangial concentration was adjusted, using a haemocytometer, to 1×10^4 sporangia ml⁻¹. Inoculum was then chilled for 2-3 h at 4°C prior to inoculation to promote the release of zoospores. Since no natural late blight infestation occurred in the experimental fields by early to mid-August in all three experiments, a sporangial suspension of *P. infestans* was prepared and

spreader rows were inoculated with hand held sprayers. The infection spread naturally from those rows into the treatment plots. The ‘Russet Burbank’ spreader rows, were inoculated in the evenings of 20 August 1999 and 11 August 2002 at Rock Springs and 23 September 2002 at Landisville.

3.2.4 Data analysis

Disease assessment was initiated approximately 10 days after inoculation for all 230 full-sib clones, two parental clones plus three standard cultivars, by visually estimating the percentage of necrotic tissue and/ or defoliation present in each plot. Three or four assessments were made at two to four day intervals. In 1999, at Rock Springs, the experimental plots were assessed four times near the end of the growing season: 9, 13, 17 and 19 September. At the same location, in 2002, four assessments were made 26 and 29 August and 2 and 5 September. The experiment conducted at Landisville in 2002 had only three assessments dates 7, 14 and 17 October. In all three experiments (hereupon referred to as environments), the area under the disease progress curve (AUDPC) was calculated for each individual plot (Shaner and Finney, 1977).

Values for AUDPC, of the three separate and combined experiments, were analyzed using the general linear models procedure in SAS (SAS Institute, 1987). Residuals were plotted against predicted values and visually examined (Neter and Wasserman, 1974). For this study we applied a square-root transformation to the original trait values to obtain normality. All effects were considered random. Estimates of the clonal variance (σ_C^2), environment \times clone variance (σ_{EC}^2), and the error variance (σ_e^2) were calculated by the mixed procedure in SAS (SAS Institute, 1996) using the restricted maximum likelihood covariance estimation method (Table 3.2). Broad-sense heritability (H) was calculated from these estimates of variance as:

$$H = \sigma_C^2 / (\sigma_C^2 + \sigma_{EC}^2 / r + \sigma_e^2 / rE)$$

where r = number of replications and E = number of environments (Nyquist, 1991), and a 95% confidence interval on H was calculated from mean squares (Knapp et al., 1985).

The environment \times clone interaction was partitioned into stability-variance

(σ_i^2) components assignable to each clone (Shukla, 1972), using PROC IML in SAS (Kang, 1989). An environmental index was calculated as the average AUDPC score of all clones in each environment minus the average AUDPC score of all clones over three environments. Heterogeneity, or nonadditivity, due to this environmental index was removed from the environment \times clone interaction, and the remainder of the environment \times clone interaction was partitioned into s_i^2 components assignable to each clone (Kang, 1989).

3.3 Results

The distribution of the mean AUDPC for the three separate experiments is shown in Fig.3.1, while the distribution of the averaged AUDPC across the three environments for the BD42/72 population is presented in Fig.3.2. The frequency distribution of phenotypic classes for foliage resistance to late blight observed in the full-sib family was continuous and normal in all three experiments (Fig.3.1). Significant skewness of the frequency distributions was present in the 1999 Rock Spring (toward resistance) and 2002 Landisville (toward susceptibility) data. No significant skewness was present in the 2002 Rock Springs data and on the three location averaged data. In all three experiments the presence of a significant number of clones exhibiting transgressive segregation were observed. Approximately 4% of the BD42/72 clones had mean AUDPC values lower than the moderately resistant parent (BD172-1), but no clones had mean AUDPC values higher than the susceptible parent (BD142-1).

Area under the disease progress curve for the 235 clones tested was initially analyzed separately for each location. Mean AUDPC values were 609 in Rock Springs-1999, 409 in Rock Springs-2002, and 317 in Landisville-2002. The error variance in the 1999 data set was considerably higher than in either of the two 2002 data sets. Therefore, all AUDPC scores were square root transformed to allow for a combined data set analysis. There were significant differences among environments, and among clones and the clone \times environment interaction was also significant (Table 3.1). However, the rep(env) effect was not significant, indicating that disease pressure was uniform across the entire field. Mean AUDPC values ranged from a minimum of 143 (BD410-123) to a maximum of 823 (BD142-1). The

standard commercial varieties ‘Atlantic’, ‘Kathadin’ and ‘Kennebec’ had average AUDPC values of 800, 679 and 596, respectively. The mean AUDPC value across two years for the female parent (BD142-1) was 823, and 259 for the male parent (BD172-1).

Estimates of the covariance parameters based on the mixed procedure in SAS (SAS Institute, 1996) were not significant for either environment or rep(env) effects. A significant effect was instead found for the two covariance parameters, clones and the env \times clone interaction (Table 3.2). From the result of the stability variance test, thirty-seven clones were identified which made a significant contribution to the overall variance. Twenty-three clones were significant at a 5% level and only fourteen at a 1% level. Broad-sense heritability for late blight resistance was estimated at 0.67 with a 95% confidence interval of 0.65-0.78.

Table 3.1. Analysis of variance on area under the disease progress curve for 235 clones, including parental and standard cultivars, from a diploid mapping population evaluated for percentage foliar late blight in Pennsylvania, in 1999 and 2002

Source	df	Mean Squares	F Value	Pr > F	Expected Mean Squares
env	2	5513.40	312.91	< 0.0001	$\sigma_e^2 + 235\sigma_{R(E)}^2 + 2\sigma_{EC}^2 + 470\sigma_E^2$
rep (env)	3	10.91	1.91	0.1261	$\sigma_e^2 + 235\sigma_{R(E)}^2$
clone	234	44.24	3.56	< 0.0001	$\sigma_e^2 + 2\sigma_{EC}^2 + 6\sigma_C^2$
env \times clone	468	12.41	2.18	< 0.0001	$\sigma_e^2 + 2\sigma_{EC}^2$
Error	702	5.70			σ_e^2
Total	1409				

3.4 Discussion

In agreement with a previous report (Haynes and Christ, 1999), the present study confirms the presence of several clones with relatively high levels of late blight resistance in this full-sib segregating family. Although the value of the mean AUDPC of the susceptible parent (BD142-1) was only two times greater than that for the moderately resistant parent, it should be noted that 66 clones (29%) had a significant lower mean AUDPC than the best performing commercial cultivar ‘Kennebec’. The estimated broad-sense heritability in the population was 0.67

Table 3.2. Estimates of the covariance parameters on area under the disease progress curve for 235 clones, including parental and standard cultivars, from a diploid mapping population evaluated for percentage foliar late blight in Pennsylvania, in 1999 and 2002

Cov Parm ^a	Estimate	Standard Error	Z Value	Pr Z
env	11.6931	11.7306	1.00	0.1594
rep (env)	0.02216	0.03794	0.58	0.2795
clone	5.3041	0.6949	7.63	< 0.0001
env × clone	3.3539	0.4333	7.74	< 0.0001
Residual	5.7042	0.3045	18.73	< 0.0001

^aCovariance parameter

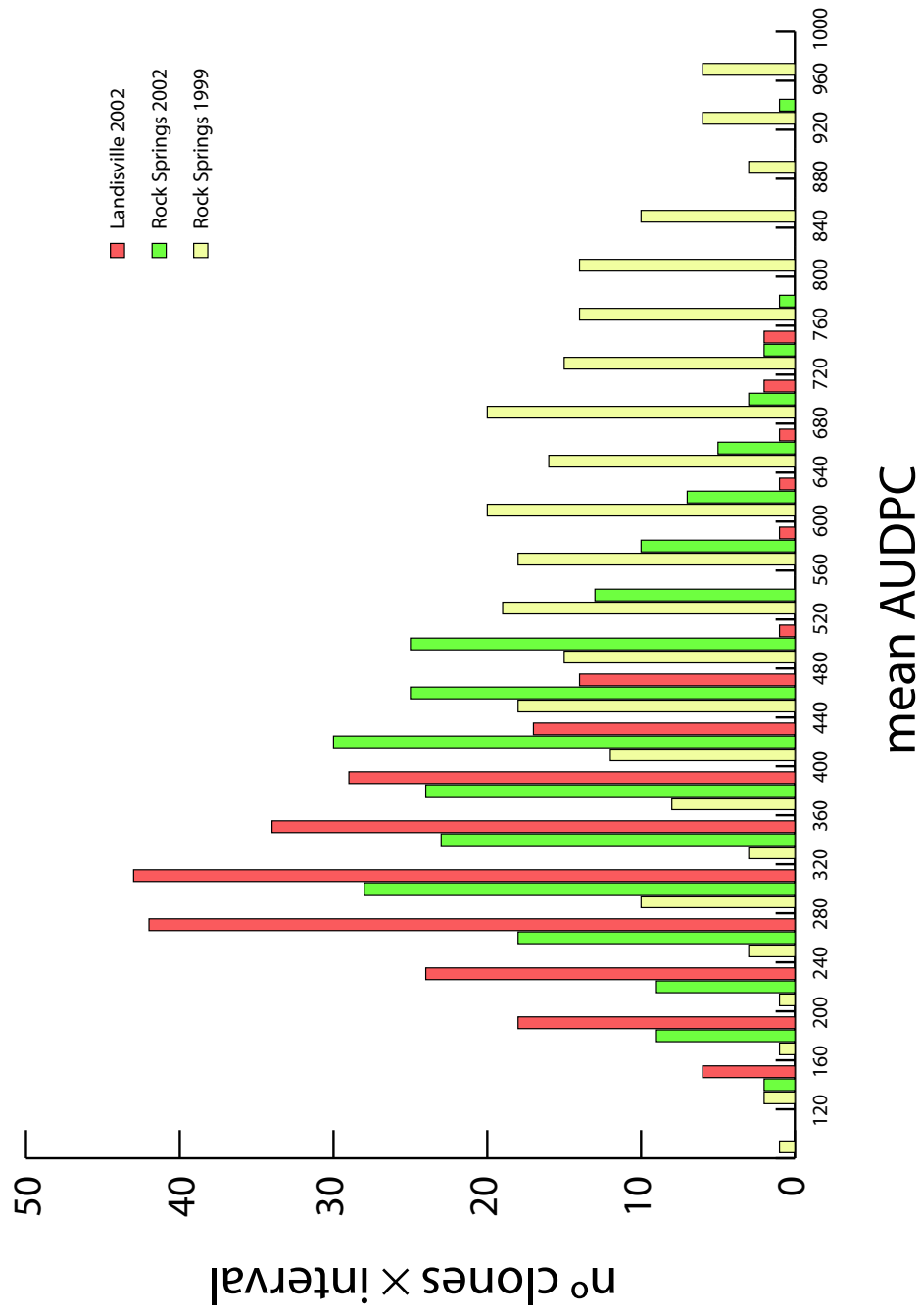


Figure 3.1. Distribution by AUDPC in three individual locations of the 235 clones, including parental and standard cultivars, evaluated for percentage foliar late blight in Pennsylvania, in 1999 and 2002.

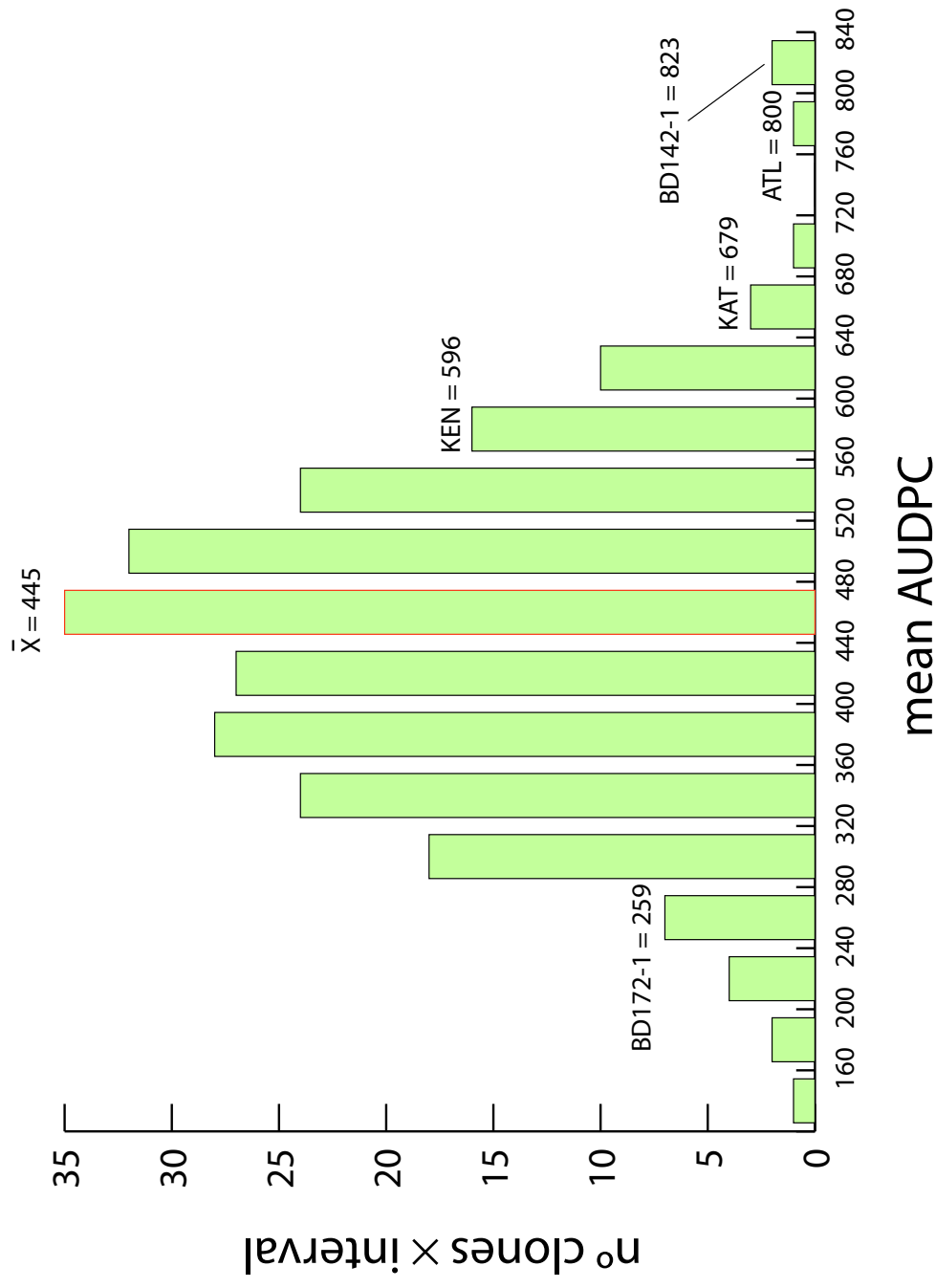


Figure 3.2. Distribution by AUDPC averaged over three locations of the 235 clones, including parental (BD142-1; BD172-1) and standard cultivars (ATL = ‘Atlantic’; KAT = ‘Katahdin’; KEN = ‘Kennebec’), evaluated for percentage foliar late blight in Pennsylvania.

which fell within the 5% CI from that previously reported (0.79). These estimates provide confidence that the observed phenotypic variation for late blight resistance has a large genetic component and thus is readily selectable.

None of the clones, as expected, were immune to infection by *P. infestans*. The frequency distribution of the mean AUDPC values for the BD42/72 population exhibited a continuous distribution consistent with an additive genetic model for the inheritance of a quantitative trait. Furthermore, the presence of several clones with transgressive segregation suggests that even the susceptible female parent may have contributed some genes to late blight resistance in the progeny or that the gene governing late blight resistance in the male parent may have existed in a homozygous condition and upon crossing exhibited over-dominance.

Thirty-seven clones (16% of the entire family) made a significant contribution to the overall environment \times clone interaction. Removing these clones from the mapping population will improve the statistical power of the QTL analysis. It is a specific interest of this QTL mapping project to identify QTLs associated with resistance to late blight that are independent of the environment in which the plant is grown and evaluated. Moreover, previous studies demonstrated the stability of genotypes (cultivars) ranked for resistance across multiple locations and different environments effecting the severity of late blight epidemics (Haynes et al., 1998). Also Inglis et al. (1996) reported identical ranking of cultivars when evaluated using different *P. infestans* isolates. Therefore these issues are not of greatest importance or limitation in this research.

The environmental conditions in which the three experiments were conducted were clearly different between the two years and locations. Average temperatures throughout the growing season were generally two to four degrees lower in 1999 than in 2002. Moreover, in 2002 the average temperatures in Landisville were always 1 – 2° warmer than in Rock Springs and Landisville had a higher relative humidity. The mean AUDPC value for the Rock Springs 1999 experiment was significantly higher (609) than the other two locations in 2002 (409 in Rock Springs and 317 in Landisville). The higher incidence of late blight in 1999 was most likely attributable to the relatively lower temperatures, greater number of rainy days and larger total rainfall (393 mm) during the growing season at Rock Springs. Moreover, in 1999, the interval between time of inoculation and first assessment

was 20 days (compared to 14 days in the other two experiments) due to adverse weather conditions. This initial delay in the epidemic assessment may have been one additional factor contributing towards the overall increase of the AUDPC scores measured that year.

As expected, in the 2002 Landisville experiment the incidence of late blight was relatively low. Southeastern, south-central Pennsylvania has a different climate than the rest of the state (a longer growing season, higher average temperatures and higher relative humidity). These environmental conditions are not particularly conducive for the establishment of a late blight epidemic. In addition, the prolonged warmer temperatures also delayed the inoculation date, by approximately one month in comparison to the two experiments at the Rock Springs location. Consequently, plant age was also an additional factor negatively effecting the observed disease incidence.

Chapter 4

DNA marker analysis and linkage map construction

4.1 Introduction

As a vegetatively propagated crop, potato (*Solanum tuberosum* L.) is particularly vulnerable to pathogen attack because infections can be transferred to the next growing season simply through asymptomatic infected tubers. Selecting cultivars with resistance to major pests is, therefore, an important goal of potato breeding. Late blight, caused by the oomycete *Phytophthora infestans* (Mont.) de Bary, is the most economically important disease in cultivated potato world wide. When not controlled, late blight can lead to complete loss of the crop. Resistance toward this pathogen is controlled by both single genes (*R* genes) expressing hypersensitive resistance to only particular races of *P. infestans* and by multiple genes all contributing to general or quantitative resistance, which is effective against all strains of the pathogen.

Single or major genes for resistance to late blight (*R* genes) were introduced into the cultivated potato, *S. tuberosum*, from the wild species *S. demissum*, which is indigenous to Mexico, during the early 20th century. The utilization of *R* genes constituted the basis for breeding for resistance to the disease between the early 1930s and 1950s (Bradshaw et al., 1995). Eleven *R* genes are currently recognized, although others have been reported from this and other wild species (Malcolmson and Black, 1966). However, introgression of *R* genes conferring race-specific resis-

tance into potato cultivars provided only transient resistance to late blight, as new races rapidly overcame the *R* gene-mediated resistance (Fry and Goodwin, 1997b). Genetic variation in wild *Solanum* germplasm for quantitative or field resistance has been also identified (Ross, 1986). This resistance is more durable than the one mediated by *R* genes, but remains largely underutilized due to the inadequacy of conventional breeding methods to fully exploit it. With the advent of DNA-based genetic markers this limitation, however, can apparently be overcome, since these markers provide us new tools for genome-wide studies on quantitative disease resistance.

The ability to detect, map, and follow loci affecting both qualitative and quantitative traits by their linkage to molecular markers increases the efficiency of their introgression into desirable genetic backgrounds. The mapping of genes of interest based on their linkage with RFLP markers enhances selection in segregating populations by permitting a more precise assessment of the genotype of individuals than is possible based on phenotype or progeny testing alone. Marker-enhanced selection can also be used to identify recombinant individuals which bear the genes to be introgressed with the potential for a drastic reduction of linkage drag (Tanksley, 1993).

In the past several years, molecular linkage maps have been made available for many plant species and successfully used in many applications in plant genetics and breeding. The genetic analysis and construction of a genetic linkage map for the cultivated potato (*S. tuberosum*) has been difficult for a long time. This is due to its highly heterozygous autotetraploid genetic constitution ($2n=4x=48$) in which the segregation of traits is complex and often masked by heterozygosity (Howard, 1970). Moreover, genetic analysis is also complicated by the severe inbreeding depression that occurs in this crop. For these reasons, among others, the use of diploid cultivated and/or wild species and the development of dihaploid clones of *S. tuberosum* has become more frequent in order to simplify the study of potato genetics.

The first molecular linkage map of potato was developed in 1988 based on tomato RFLP markers analyzing segregation data derived from the interspecific cross *Solanum phureja* \times (*S. tuberosum* \times *S. chacoense*). The results of that study, based on a diploid potato population, demonstrated an extensive genome

colinearity between the closely related plant species tomato and potato (Bonierbale et al., 1988). It is believed that a relatively small number of genes and differences in gene copy number or highly repeated DNA sequences, might be responsible for the distinct morphological differences between the two species. A second map using potato RFLP markers was developed from a diploid population based on an intraspecific cross of *S. tuberosum* (Gebhardt et al., 1989, 1994; Leonards-Schippers et al., 1994). Over the past fourteen years, several other linkage maps have been obtained for potato based on different types of molecular markers: RFLP, AFLP (amplified fragment length polymorphism) (Vos et al., 1995), SSR (simple sequence repeat) (Milbourne et al., 1998), and other PCR-based markers (Jacobs et al., 1995). These maps have been useful for many genetics and breeding purposes and provided us with a rich series of molecular markers for constructing linkage maps of other inter- and intraspecific crosses of potato.

Recently, Haynes and Christ (1999) evaluated a diploid random-mated hybrid population of *Solanum phureja* \times *S. stenotomum* for resistance to late blight. This population exhibited relatively high levels of resistance to this disease in replicated field trials conducted in Pennsylvania in both 1996 and 1997. To facilitate the characterization and utilization of the genetic potentials of this breeding material, a selected resistant clone and a susceptible one from this population were intermated to generate a mapping family. The resulting full-sib family, was initially constituted of 276 individuals. Based on the breeding scheme which generated this population, as well as the tremendous phenotypic variability observed for numerous traits in the field, there was a high likelihood that it would exhibit polymorphism at the DNA level. Based on this diploid population, a medium-density RFLP linkage map was developed to provide the basis for the identification and characterization of QTLs involved in resistance to the oomycete *Phytophthora infestans*.

4.2 Materials and Methods

4.2.1 Plant materials

Parental clones for the mapping population (BD42/72) were identified and selected (Liu et al., 1998a) from among 281 clones derived from 72 families of a

diploid random-mated hybrid population of *Solanum phureja* × *S. stenotomum* (Haynes and Christ, 1999). In both replicated field and lab trials, clone BD142-1 had consistently shown high levels of susceptibility towards late blight, while clone BD172-1 had moderate but significant levels of resistance to it. Moreover, preliminary work indicated that DNA polymorphisms present between these two clones was adequate for mapping purposes (Liu et al., 1998b). The seed parent BD142-1 (P1) was crossed with the pollen parent BD172-1 (P2) and a progeny of 230 individuals were constituted. One-hundred and thirty-two randomly selected clones from the BD42/72 population were also grown under greenhouse conditions and used for DNA extraction, RFLP marker analysis and linkage map construction.

4.2.2 Sources of DNA probes and phenotypic markers

The DNA probes used in this study were obtained from three different sources including: (i) 118 random cDNA and genomic clones (CP and GP markers, respectively) of potato provided by Dr. Christiane Gebhardt, Max-Planck-Institute for Plant Breeding Research, Köln, Germany, (ii) 31 random cDNA and genomic clones (CT and TG markers, respectively) of tomato from Dr. Steven D. Tanksley, Cornell University, Ithaca, NY, (iii) 13 resistance gene analog (RGA) clones developed by Dr. Ivan Simko, USDA-ARS, Beltsville, MD. Two morphological traits segregating in the BD42/72 population were recorded and used as phenotypic markers: *PFC* potato flower color (pink versus colorless) and *PSC* tuber skin color (purple versus colorless). The genetic characterization of the two genes *PFC* and *PSC* in potato has already been described in previous studies (Gebhardt et al., 1991; Van Eck et al., 1994, 1993). The random genomic or cDNA clones utilized in the present work were selected to uniformly cover all twelve chromosomes of the potato genome based on their estimated chromosomal map location from previously published potato and tomato molecular genetic linkage maps (Bonierbale et al., 1988; Gebhardt et al., 1991; Tanksley et al., 1992). Moreover, to facilitate comparison of different maps, primarily single copy markers were chosen.

4.2.3 RFLP analysis

DNA extraction

All plant tissue was collected from young leaves of greenhouse-grown plants. Total DNA was extracted from approximately 5 g of frozen leaf tissue of parental and 132 clones. The procedure was a modification of those described by Porebski (Porebski et al., 1997) and Doyle (Doyle and Doyle, 1987). The tissue was ground in a mortar in the presence of liquid nitrogen. Ground tissue was transferred into centrifuge tubes containing 20 ml of CTAB extraction buffer (100 mM Tris-Cl pH 8.0; 20 mM EDTA; 2% (w/v) CTAB; 1.4 M NaCl, plus 1% (v/v) β -mercaptoethanol). 0.5 g polyvinylpyrrolidone (40,000) was added to the suspension and incubated at 65°C for 25–30 min. The lysate was extracted with an equal volume of chloroform/isoamylalcohol (24:1), and centrifuged at 4,200 rpm for 15–20 min. Nucleic acids were precipitated with one-half volume of 5 M NaCl and one volume of cold (–20°C) isopropanol, and collected by centrifugation at 4,200 rpm for 10 min. The pellet was washed once with 1 ml of cold solution of 76% alcohol and 0.2 M sodium acetate, and once with 1 ml of cold 70% ethanol, and dissolved in 1 ml Tris-EDTA buffer. The solution was extracted once again with chloroform/isoamylalcohol (24:1), and treated with 2 μ l RNase (10 mg/ml) at 37°C for 30 min. The chloroform/isoamylalcohol step was then repeated and DNA was precipitated after the addition of 1/10 volume 3M sodium acetate with 2 volumes of cold (–20°C) absolute ethanol. The DNA was collected by centrifugation at 14,000 rpm for 10 min, the pellet was washed one time with 1 ml of cold solution of 76% alcohol and 10 mM ammonium acetate. After centrifugation, the pellet was re-dissolved in 1.0 ml Tris-EDTA buffer. DNA concentration was determined spectrophotometrically and its integrity was determined by electrophoresis on a 0.8% agarose gel.

Identification of polymorphic DNA markers

Approximately 10 μ g total genomic DNA from each parental clone was digested with five restriction enzymes including *Hind*III, *Eco*RI, *Dra*I, *Xba*I and *Taq*I following the manufacturer's instructions, and polymorphism survey blots were prepared. Parental DNA polymorphisms were examined using the 162 genomic or cDNA clones. Size separation of restriction fragments was performed by elec-

trophoresis on 0.8% agarose horizontal gels in $0.5\times$ TBE buffer (45 mM Tris-borate, 1 mM EDTA) for 12 h at 40 V. Following electrophoresis, gels were processed for Southern blotting (Southern, 1975) following the specific recommendations provided by the nylon membrane suppliers. Gels were blotted for approximately 8–12 h onto nylon membrane (Hybond-XLTM, Amersham Pharmacia Biotech Inc.) by alkaline transfer with 0.4 M NaOH (Reed and Mann, 1985). Nucleic acid samples were fixed to the membrane by UV crosslinking with a UV exposure suitable for the specific membrane. The blots were prehybridized at 65°C in 7% sodium-dodecyl-sulfate (SDS), 0.25 M Na₂HPO₄ (pH 7.4), 1 mM EDTA (pH 8.0), 1% Fraction-V-grade bovine serum albumine (BSA) for at least 2 h. Probes were labeled with [α -³²P] dCTP using the random hexamer procedure (Oligolabelling Kit; Amersham Pharmacia Biotech Inc.), and unincorporated nucleotides were removed using ProbeQuantTM G-50 Micro Columns (Amersham Pharmacia Biotech Inc.). Labeled probes were denatured by heat at 95°C for 5 min then added to filters in 10–15 ml hybridization buffer (7% SDS, 0.25 M Na₂HPO₄ (pH 7.4), 1 mM EDTA (pH 8.0), 1% BSA), at a concentration of 2 ng/ml and a specific activity of 1×10^9 dpm/ μ g (Sambrook et al., 1989). Hybridization was carried out in glass tubes at 65°C for 24 h. After hybridization, filters were washed twice at 65°C for 10 min each in 5% SDS - 50 mM Na₂HPO₄ (pH 7.4) - 1 mM EDTA (pH 8.0) - 0.5% BSA and once (2–5 min) in 1% SDS - 50 mM Na₂HPO₄ (pH 7.4) - 1 mM EDTA (pH 8.0). The final wash was conducted in $2\times$ saline-sodium citrate (SSC) solution at room temperature and subsequently membranes were wrapped in plastic film, exposed to Kodak BioMax MS X-ray film in X-ray cassettes, and placed at -80°C for 1–3 days, depending on the strength of the signal. Standard film development procedures were followed (Kodak, Rochester, N.Y.). After films were developed, probes were stripped off from the blots by washing twice in 0.2 M NaOH for 10 min at 45°C and subsequently once in $2\times$ SSC for 15 min at 45°C, and the blots were reused.

Genotyping of the full-sib family

Genomic DNAs of the 132 full-sib individuals were digested with the five restriction enzymes and Southern blots were produced. Blots were hybridized with clones which detected polymorphism between the two parents and a total of 130 markers,

consisting of 120 RFLPs and 10 RGA markers, were scored in the segregating full-sib family.

4.2.4 Data analysis

Autoradiograms were scored in the BD42/72 mapping population for all segregating marker alleles, regardless of whether segregation was from one parent or both. As a result of using non-inbred parents, five types of single-locus segregation were found: 1:1 ♀, 1:1 ♂, 3:1, 1:2:1 and 1:1:1:1. Distorted segregation of markers was determined using the chi-square (χ^2) goodness-of-fit analysis using the JoinMap[®] (v. 3.0) computer program (Stam, 1993; Van Ooijen and Voorrips, 2001). Multipoint linkage analysis of the entire set of RFLP and phenotypic markers was performed using the software package JoinMap[®] (v. 3.0) and a genetic linkage map was constructed. The critical LOD value of 2.0 or more was used to assign marker loci to linkage groups. The Kosambi mapping function (Kosambi, 1944) was used to convert recombination frequencies to map distances in centi-Morgans (cM). Linkage groups were identified to represent specific chromosomes on the basis of the position of known RFLP “anchor” markers used in previously published potato and tomato maps (Gebhardt et al., 1991; Leister et al., 1996; Tanksley et al., 1992). The charts of genetic linkage and the overall chromosomal maps were produced using the computer package MapChart[©] (Voorrips, 2002).

4.3 Results

4.3.1 Linkage Map

Among the 162 markers originally selected and used for a survey of RFLPs between BD142-1 and BD172-1, 151 (93%) detected polymorphism between the two parental clones. There were no relevant differences for percentage of polymorphism among the different types of markers surveyed (cDNA *vs.* genomic *vs.* RGA). Of the polymorphic 151 probes, 23 (14%) did not produce a segregation banding pattern in the progeny blots that could be clearly scored and were subsequently eliminated. Of the 31 clones derived from tomato, 29 of them (94%) detected polymorphism in the parental survey blots. Among them, 7 produced

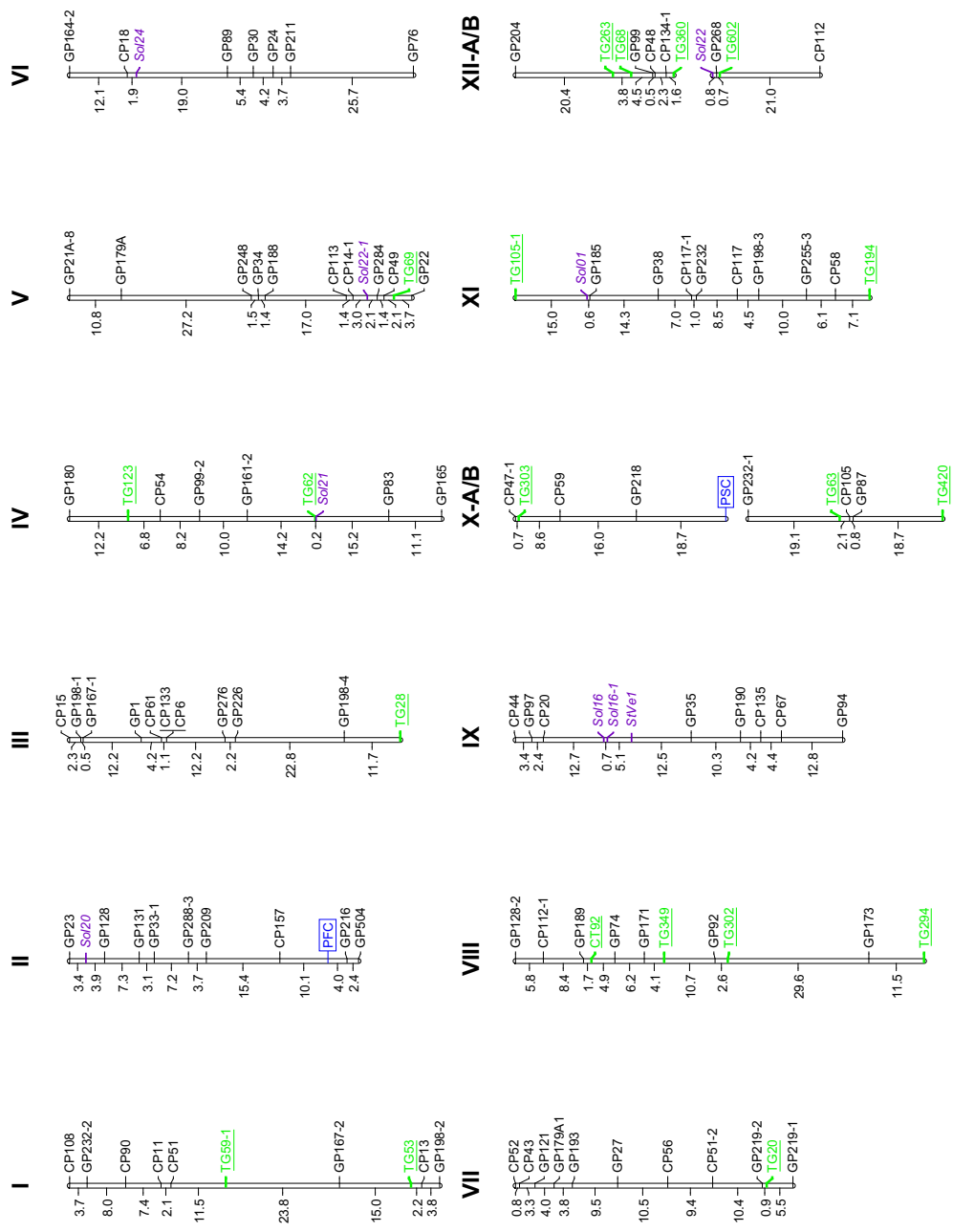


Figure 4.1. A restriction fragment length polymorphism (RFLP) linkage map of potato chromosomes based on a full-sib family of a cross between BD142-1 and BD172-1. The roman number identifying the chromosome is shown at the top of the chromosome. The names of the markers are listed at the right of chromosomes. Numbers on the left are centimorgan (cM) distances (Kosambi function) between adjacent markers. Multiple loci homologous to a single marker probe were suffixed with designations -1, -2, etc. beside the specific marker name. Tomato derived markers ('TG', 'CT', 'SIV') are indicated with a green color and underlined, RGA ('Sol') markers with a violet color and italicized, and morphological markers in blue within a rectangle.

unresolvable bands in the progeny blots and were therefore eliminated. Of the total 128 polymorphic markers identified, 114 (89%) met the minimum requirement for linkage at $\text{LOD} \geq 2.0$ and were used for map construction. Twenty-seven markers (21%) detected two or more loci.

Segregation ratios deviating from the expected 1:1, 1:2:1 and 1:1:1:1 ratios, were found for 27% of the segregating restriction fragments (Table 4.1). Specifically, linkage group I, II and part of XI showed the highest level of marker segregation distortion. From the analysis of the genotypic data a map was constructed composed of 14 linkage groups covering 855.4 cM in map units defined as by Kosambi (Kosambi, 1944) (Fig 4.1). Of the 12 recognized potato chromosomes, all but chromosome X and XII were represented in this map by a single linkage group. In the specific case of chromosome X and XII, each of them could be matched to two small linkage groups with markers known to be associated with them. These small linkage groups in this map remained unlinked despite the use of clones from the corresponding regions of the potato and tomato genome.

The total number of loci mapped was 126 with an average interval length between them of 6.8 cM. Genome coverage by the map is estimated to be at least 70% based on the results of a precedent potato chromosomes mapping study (Gebhardt et al., 1995). The number of markers mapped per chromosomes were on average 8.7, and ranged from 11 (Chr. II; VII; VIII; IX; XI) to 4 (Chr. XII-B). Chromosome VIII had the largest linkage group (85.5 cM) followed by chromosome IV and I (77.9 and 77.5 cM, respectively), whereas chromosome XII had the smallest one (33.1 cM), followed by chromosome X and VII (44 and 58.1 cM, respectively). The two morphological markers segregating in the mapping population, PFC and PSC, mapped on chromosome II and X respectively, and the ten RGA markers mapped to eight of the twelve potato chromosomes. In particular, chromosome IX had a cluster of three RGA markers (Sol16; Sol16-1; StVe1) within its linkage group.

The linear order of the common markers among the present map and already published ones was in good agreement but there were considerable differences in genetic distances in certain marker intervals. Furthermore, some differences were observed in the individual chromosome lengths between the compared maps (Table 4.2).

The position of twenty tomato clones is reported in the present map distributed

among eleven of the fourteen linkage groups identified (clone TG294 could not be linked to any of them). Their alignment was consistent with that of tomato genome except for TG63 and TG420 on chromosome X, TG194 on chromosome XI, and TG68 and TG360 on chromosome XII. These were in a reverse order in their original tomato map. Only one clone (TG28), was mapped on a linkage group representing a chromosome that differs from previous tomato and potato genome studies. (Tanksley et al., 1992).

4.4 Discussion

The presented map reflects the chromosome nomenclature and orientation as proposed by Dong et al. (2000), for the genetic map of potato. The adoption of this nomenclature makes this map consistent with others based on different potato genotypes and possibly different species within the genus *Solanum*. For this reason, the orientation of the linkage groups corresponding to chromosome VII, VIII and XI were reversed, in comparison to previously published potato maps, as suggested by Gebhardt C. (personal communication). Despite the phylogenetically close relation between the two diploid parental clones, BD142-1 and BD172-1, a relatively high level of polymorphism (93%) was observed and a medium density RFLP linkage map of a cross between the two was successfully constructed. Linkage analysis for each of the 14 linkage groups identified did not present particular problems except for those regions effected by an extreme distorted segregation or an insufficient number of markers, particularly in the case of chromosome X and XII where a single comprehensive linkage group could not be obtained.

Several markers displayed a skewed segregation confirmed by a significant χ^2 test (Table 4.1). The strongest distortion of segregating ratios was found for markers associated to linkage group I. This result was expected and can be attributed to the self-incompatibility locus (*S* locus) previously reported on chromosome I by Gebhardt et al. (1991) analyzing the occurrence of specific stylar glycoproteins. The segregation of markers flanking the *S* locus are assumed to be affected by the expression of gametophytic self-incompatibility in potato at the diploid level. Several other genomic regions of distorted segregation were observed, particularly on chromosome II and XI. This could partially be associated with the use of a full-sib

family obtained from non-inbred parents which could potentially determine the presence of (sub)lethal loci in both parental clones. This can presumably result in significant distortion of the segregation ratio in the mapping population as shown in earlier genetic mapping studies (Bonierbale et al., 1988; Gebhardt et al., 1989).

The morphological markers underlying traits such as flower color and tuber skin color in potato have already been described in previous studies (Gebhardt et al., 1991; Van Eck et al., 1994, 1993). The locus named *PFC* in the present work, should be related to locus *D* (on chromosome II) characterized by Van Eck et al. (1993) that is involved in the biosynthesis of red anthocyanins. The correspondence of the two loci could not be completely determined due to the absence of common markers in their close proximity. The position of the purple skin color (*PSC*) locus, determining the pigmentation of the tuber skin, on chromosome X, was in agreement with previous reports. The *PSC* locus was first described by Gebhardt et al. (1991) as the single locus determining this trait. Subsequently, Van Eck et al. (1994) proposed that tuber skin color is expressed due to the complementary action of both locus *D* and a second locus, referred as locus *I*, involved in tissue specific regulation of anthocyanin expression. The locus name '*PSC*' in the present map was maintained because of its confirmed linkage association with RFLP marker GP218 as reported in a recent review by Gebhardt et al. (2001).

On the presented map, 126 loci were mapped, covering a span of 855.4 cM with an average of 8.7 loci per linkage group. Although the linear order between common markers in other potato and tomato molecular maps was in agreement, the genetic distances between several markers differed significantly. Generally, these differences appear to be interval specific and not a characteristic of individual chromosomes. The reverse order observed for five of the twenty 'TG' markers mapped, with respect to the tomato genome, is however in complete agreement with a previous finding (Tanksley et al., 1992) that established the presence of five chromosomal inversions on chromosome V, IX, X, XI and XII, that differentiate the tomato and potato genome. The length of linkage groups corresponding to chromosome VIII and XII in the present map were in slight disagreement with a previous finding; however, the over-all map length for the remaining chromosomes was comparable to those of previously published RFLP maps that were constructed using inter-specific mapping populations (Table 4.2). The use of an intra-specific

mapping population can apparently result in an increase of the overall map length due to an augmented recombination frequency in the parents of such populations.

This map provides the initial framework on which other genetic markers, such as AFLPs and SSRs, can be incorporated to enable the identification and characterization of major genes and QTLs conferring increased general resistance against late blight disease of potato. PCR-based markers will ultimately offer an efficient means of screening large populations for the implementation of marker-assisted selection for the development of new resistant cultivars. Furthermore, this map will enable the introgression of several other economically important traits to selected germplasm at the tetraploid level.

Table 4.1. Segregation of RFLP and morphological markers exhibiting significant deviation from expected ratios in the potato mapping family

Locus	Chrom.	Expected ^a	Observed			χ^2 ^b
CP108	I	1:1 ♂	124	8		101.9***
GP232-2	I	1:1 ♂	10	122		95.0***
CP90	I	1:1 ♂	112	20		64.1***
CP11	I	1:1 ♂	23	109		56.0***
CP51	I	1:1 ♂	26	106		48.5***
TG59-1	I	1:1 ♂	37	95		25.5***
GP167-2	I	1:1 ♂	54	78		4.4*
GP23	II	1:1 ♀	82	50		7.8**
Sol20	II	1:1 ♀	85	47		10.9***
GP128	II	1:1 ♀	87	45		13.4***
GP131	II	1:1 ♀	39	93		22.1***
GP33-1	II	1:1 ♂	48	84		9.8**
GP288-3	II	1:2:1	5	71	56	40.2***
GP209	II	1:1 ♀	92	40		20.5***
CP157	II	1:1 ♂	79	53		5.1*
PFC	II	1:2:1	39	89	4	117.0***
GP216	II	1:1 ♀	88	44		14.7***
GP504	II	1:1 ♂	78	54		4.4*
CP15	III	1:1 ♂	78	54		4.4*
CP54	IV	1:2:1	47	59	26	8.2*
CP113	V	1:2:1	46	55	31	7.1*
Sol22-1	V	1:1 ♀	81	51		6.8**
GP284	V	1:1 ♀	79	53		5.1*
GP22	V	1:1 ♀	53	79		5.1*
CP56	VII	1:1 ♂	53	79		5.1*
GP190	IX	1:1 ♀	54	78		4.4*
CP47-1	X	1:2:1	37	95	0	111.0***
PSC	X	1:1 ♂	79	52		5.6*
GP232-1	X	1:1 ♀	49	83		8.8**
TG105-1	XI	1:2:1	34	42	56	24.8***
GP232	XI	1:2:1	38	94	0	114.0***
GP255-3	XI	1:1 ♂	47	85		10.9***
TG263	XII	1:2:1	31	101	0	93.0***

^a ♀: Locus heterozygous in the female parent; ♂: Locus heterozygous in the male parent

^b * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Table 4.2. Comparison of map length (in cM) with previously published potato RFLP maps

Chrom.	Mapping population ^a			
	<i>phu</i> × (<i>2</i> × <i>tbr</i> × <i>chc</i>) ^b	(<i>2</i> × <i>tbr</i> × <i>2</i> × <i>tbr</i>) ^c	(<i>2</i> × <i>tbr</i> × <i>ber</i>) × <i>ber</i> ^d	<i>stn-phu</i> × <i>stn-phu</i> ^e
I	63	127	76	78
II	46	76	50	61
III	47	62	64	69
IV	55	102	65	78
V	47	78	56	72
VI	59	83	54	72
VII	55	92	59	58
VIII	64	79	49	86
IX	50	97	50	69
X	53	49	51	44
XI	21	96	48	74
XII	46	93	63	33
Total span	606	1034	684	855
Total markers	135	492	261	132
Total loci	101	304	150	122

^a*phu*, *S. phureja*; *2* × *tbr*, haploid *S. tuberosum*; *chc*, *S. chaocoense*; *ber*, *S. berthaultii*; *stn-phu*, selected clone from *S. stenotomum*-*S. phureja* bulk population

^bBonierbale *et al.* (1988)

^cGebhardt *et al.* (1991)

^dTanksley *et al.* (1992)

^eThis study

Chapter 5

Quantitative Trait Loci (QTL) analysis

5.1 Introduction

Since its first devastating appearance in Ireland and other parts of Europe in 1845, late blight, caused by the oomycete *Phytophthora infestans* (Mont) de Bary, has remained the most important disease in potato cultivation. Without preventive control measures this disease can cause severe damage to both foliage and tubers, which can lead to a complete loss of the crop. The occurrence of new aggressive metalaxyl-resistant isolates of *P. infestans* (Fry and Goodwin, 1997a) has intensified breeding efforts worldwide to incorporate durable genetic resistance into new potato varieties. Moreover, because no modern commercial cultivar of potato (*Solanum tuberosum* L.) have adequate resistance to late blight, the development of resistant potato cultivars is currently a high priority in every potato breeding program.

Two types of genetic resistance to late blight have been identified in potato germplasm: (i) race-specific, controlled by individual *R* genes (Black et al., 1953; Malcolmson and Black, 1966) initially introgressed into potato cultivars from the Mexican hexaploid species *Solanum demissum*, and (ii) general, or field resistance which is partial and polygenic in nature (Umaerus et al., 1983), and regarded as effective against all strains of the pathogen. Despite initial success, the introduction of race-specific resistance has proven to confer only a transient and limited

protection against late blight due to the ability of *P. infestans* to rapidly overcome such resistance. Therefore, breeders have now directed their attention to enhancing potato general resistance against this pathogen since this type of resistance is thought to be more durable.

Although the understanding of the genetics of quantitative traits, such as this polygenically controlled resistance, has advanced over the past several decades, thus far, limited progress has been made in practical plant breeding due to the complex nature of these traits. Specifically, insufficient genetic knowledge of the many resistance components and their interaction, lack of efficient selection criteria, and difficulties in the identification and transfer of resistance-related genes from unadapted germplasm into the cultivated background, have been some of the most relevant limiting factors. More recently, the advent of molecular marker technology, particularly DNA-based markers, has provided new tools which are helping to determine the number, positions, and individual effects of resistance loci with quantitative inheritance. Therefore, many research programs are currently in progress whose primary objectives are the identification and characterization of the biological functions of genes underlying quantitative loci involved in disease resistance.

The genetic dissection of quantitative resistance against *P. infestans* in potato, *Solanum* spp., using various types of DNA-based markers, has been primarily conducted on diploid mapping populations (Collins et al., 1999; Ewing et al., 2000; Ghislain et al., 2001; Leonards-Schippers et al., 1994; Oberhagemann et al., 1999; Sandbrink et al., 2000) and only in two cases was a tetraploid population employed (Meyer et al., 1998; Naess et al., 2000). Results from these various studies have provided us with an initial genome-wide view on the complexity of the genetic control of the resistance mechanism. Genetic components controlling race-nonspecific resistance against *P. infestans* appear to be located on almost all potato chromosomes, thus confirming the quantitative nature of this character. The most frequently reported quantitative trait loci (QTLs) for late blight are those detected on linkage groups V, III and IV (Simko, 2002). No individual QTL was, however, detected consistently in all genetic backgrounds. This can be explained by the presence of different alleles at any given QTL in the genetic materials analyzed, which may have different effects on resistance and which also may interact differ-

ently with each other and with the environment. Furthermore, several *R* genes for late blight resistance have been mapped closely to factors controlling quantitative resistance (Bradshaw and Mackay, 1994), and some of these *R* genes are found organized in clusters along specific chromosomes. Recently, *R* genes as well as QTLs for late blight resistance have also been linked to resistance gene like sequences (RGLs), thus suggesting that RGLs could potentially harbor good candidate genes for controlling resistance to late blight (Gebhardt and Valkonen, 2001; Trognitz et al., 2002).

The aim of the present study was to identify QTLs for late blight resistance in a diploid family of a cross between a late blight susceptible clone, BD142-1, and a partially resistant clone, BD172-1. The parental clones were obtained from a diploid random-mated hybrid population of *Solanum phureja* \times *S. stenotomum*. Haynes and Christ (1999) previously reported that this hybrid diploid population exhibited relatively high levels of resistance to late blight under field conditions. From the analysis of the full-sib segregating family, a molecular linkage map was constructed using restriction fragment length polymorphism (RFLP) markers selected from previous studies (Bonierbale et al., 1988; Gebhardt et al., 1991; Tanksley et al., 1992).

5.2 Materials and Methods

5.2.1 Plant materials

A potato family comprised of 278 individuals resulted from a cross between two diploid clones: BD142-1, rather susceptible to late blight, was used as a female parent, and the moderately resistant BD172-1 was used as a male parent. The parental material had been identified and selected in 1997, by Liu et al. (Liu et al., 1998a), among 281 clones derived from 72 families of a diploid random-mated hybrid population of *Solanum phureja* \times *S. stenotomum* (Haynes and Christ, 1999). Clones from the entire full-sib family were tested for resistance to late blight over a three year period under field conditions with artificial infection pressure. The mapping family consisted of a subset of 132 randomly selected full-sib clones. These plants were also grown in the greenhouse and used for DNA isolation.

5.2.2 RFLP analysis and map construction

Total genomic DNA was extracted from approximately 5-10 g of leaf tissue from each of the parental clones and a total of 132 full-sib individuals, using a modified protocol derived from two procedures described by Porebski (Porebski et al., 1997) and Doyle (Doyle and Doyle, 1987). Genomic DNAs were digested with five restriction enzymes including *HindIII*, *EcoRI*, *DraI*, *XbaI* and *TaqI*, and subjected to gel electrophoresis. Genomic blots were prepared and hybridized with 120 genomic or cDNA clones and 10 RGA markers detecting polymorphism between the two parents. Probes were labeled with [α - 32 P] dCTP using the random hexamer procedure (Oligolabelling Kit; Amersham Pharmacia Biotech Inc.). Agarose-gel electrophoresis, Southern blotting, hybridization, and autoradiography were as described in chapter 4. A genetic linkage map was constructed using a total of 132 markers including two morphological characters (flower and tuber skin color). RFLP markers used had known chromosome assignment on the tomato/potato genetic map (Tanksley et al., 1992), and served as anchor markers for the identification and orientation of all 12 potato chromosomes.

5.2.3 Trait evaluation

The entire family, two parental clones and three standard commercial cultivars (Atlantic, Kennebec and Kathadin) were included in the experimental design and evaluated for reaction to late blight under field conditions. Three field experiments were conducted between 1999 and 2002 in Pennsylvania, using a randomized complete block design with two replications. Plots consisted of five plants of a clone planted 22 cm apart within rows, the space between rows was 91 cm with a 1.2 m break between plots within rows. Each treatment plot had an adjacent row of cultivar Russet Burbank that was inoculated and acted as a spreader row. A sporangial suspension of *P. infestans* was inoculated onto spreader rows and allowed to naturally infect the treatment plots. Three isolates of *Phytophthora infestans* US-8 (A2 mating type) were used to inoculate the spreader rows. All isolates were also tested for virulence on a *R* gene differential-set of potato varieties, and comparisons among isolates were made testing them on several common cultivars (see Chapter 3). Equal amounts of the three isolates were pooled together to constitute

the inoculum and subsequently the sporangial concentration was adjusted to 1×10^4 sporangia ml^{-1} . Disease was assessed by estimating the percentage of necrotic tissue observed within each plot. Assessments were made at least once a week for a total of three or four times. Area under the disease progress curve (AUDPC) (Shaner and Finney, 1977) was calculated and appropriate statistics were applied to the data (see Chapter 3).

5.2.4 QTL Analysis

Two analytical approaches were used to identify and validate putative QTLs against late blight segregating in the full-sib family using the established linkage map and the observed trait phenotypes. First, the non-parametric Kruskal-Wallis ‘K-test’: this method can be regarded as the non-parametric equivalent of the one-way analysis of variance (Hollander and Wolfe, 1973; Lehmann and D’Abrera, 1975), which measures the association between marker genotype and disease index. For the K-test, an association was indicated when the mean values of the marker classes were significantly different at $P < 0.01$ (Table 5.1). The second approach employed for QTL mapping was the maximum likelihood interval mapping method (Lander and Botstein, 1989). This method is an extension of one marker analysis, extending the analysis from an individual marker to any genomic location flanked by two markers. The LOD scores, i.e. the likelihood for the presence of a segregating QTL for each position on the genome, is obtained from MapQTL[®] (v. 4.0) software (Van Ooijen et al., 2002). These LOD (\log_{10} of odds ratio) scores were used to construct QTL-likelihood plots of detected QTLs using the computer package MapChart (Voorrips, 2002) (Figure 5.1). In order to determine the significance threshold of the LOD score, the $1000 \times$ permutation test was calculated. This is a resampling method to obtain empirical significance threshold values (Churchill and Doerge, 1994). A five percent genome wide error rate was chosen to identify the LOD interval threshold. A LOD score of 2.4 or above ($P \leq 0.001$), was used to declare the presence of a segregating QTL. LOD peaks were used to determine the estimated position of QTLs on the map. The QTL analysis, with both methods, was implemented using the software package MapQTL, which also provided estimates of the percentage of the total phenotypic variation explained (PVE) by the

most significant marker for each QTL shown in Figure 5.2. Tables of the complete QTL analysis with both methods are reported in Appendix A.

5.3 Results

5.3.1 Phenotypic data

Trait data for late blight were assessed and collected from three replicated field experiments conducted in central and south-east Pennsylvania between 1999 and 2002. For each location, the average AUDPC value for each clone was calculated. The data were square-root transformed to improve the normality of their distributions, and analysis of variance (ANOVA) was performed on individual and combined data sets. Among all genotypes mean AUDPC values ranged between 140 and 820 with an average of 423, and exhibited a continuous and normal distribution consistent with polygenic inheritance characteristic of a quantitative trait (Fig. 3.1). Transgressive segregation, particularly towards resistance to late blight, indicated the presence of positive and negative genetic factors in the parental lines for this character. Association between markers and resistance scores were tested on 132 progenies, separately for each individual location and again on a new data set derived from the three combined experiments. Moreover, an additional analysis was conducted on the combined data after having removed 19 of the 132 selected individuals based on the results of the stability variance test described in more detail in Chapter 3.

5.3.2 Genetic linkage mapping

A genetic linkage map was constructed based on 112 segregating markers on a subset of 132 individuals using the computer program JoinMap[®] (v. 3.0) (Stam, 1993; Van Ooijen and Voorrips, 2001). A total of 126 loci were identified and placed into 14 linkage groups that could be matched to the 12 potato chromosomes (Chromosome X and XII were represented respectively by two separate linkage groups). This map covers in total 855.2 cM, in map units defined as by Kosambi (Kosambi, 1944), with an average interval length of 6.8 cM between markers and with approximately 10 loci per chromosome. Genome coverage by the map is

estimated to be at least 70% based on mapping of subtelomeric repeats (Gebhardt et al., 1995). The length of the map and the order of the markers were in agreement with previously published RFLP maps of potato (Bonierbale et al., 1988; Gebhardt et al., 2001; Tanksley et al., 1992). Skewed segregation ratios (χ^2 test, $P < 0.005$) were observed, the strongest distortion was found on linkage group I and is assumed to be caused, as previously reported, by the activity of the self-incompatibility locus (Gebhardt et al., 1991).

5.3.3 QTL analysis

Analysis on the trait data-set from the estimated multiple locations average

Results from the non-parametric Kruskal-Wallis test suggested the existence of QTLs for late blight resistance on linkage group III and V (Table 5.1; see Appendix A for complete analysis). A P value of < 0.01 was used as a threshold criterion for QTL detection. The QTL on linkage group III is centered in correspondence of marker GP198-1 (P value of 0.00001). The QTL identified on linkage group V appears to be spread across a large number of markers, extending approximately 12 cM along the proximal end of this linkage group. The highest P value (0.00001) was found associated with marker TG69. In the case of linkage group VII and XI, P values of 0.01 indicated the potential presence of two additional, but less statistically supported, QTLs one near the GP179A1–GP193 marker interval on linkage group VII and one located in correspondence of the CP117 marker on the central section of linkage group XI. All of the detected QTLs, with the sole exception of the one present on chromosome XI, were contributed, towards increased resistance, by alleles present in both parents. The QTL on chromosome XI was instead contributed by an allele from the susceptible parent.

The interval-mapping analysis identified three QTLs with LOD scores above the threshold value of 2.4 located on linkage group III, V, and XI (Table 5.2). The QTL on linkage group III had its highest LOD score (4.12) associated with marker GP198-1 with an individual effect of 23.4% of the total phenotypic variation. On linkage group V the QTL had a likelihood peak in the position of marker GP22 with an LOD value of 5.17 and explaining 17.3% of the total phenotypic variation.

Table 5.1. Kruskal-Wallis test on three locations averaged late blight severity data-set and summary of QTLs detected for late blight resistance.

Locus	LG ^a	K ^b	P value ^c	Locus	LG	K	P value
CP15	III	13.829	*****	TG69	V	21.379	*****
GP198-1	III	15.528	*****	GP22	V	11.504	*****
CP167-1	III	14.269	*****	Sol179A1	VII	7.211	***
CP14-1	V	7.248	***	GP193	VII	6.692	***
GP284	V	7.782	***	CP117	XI	6.836	***
CP49	V	10.338	****				

^aLinkage group^bKruskal-Wallis test statistic^cSignificance levels:

*** = 0.01; **** = 0.005; ***** = 0.001; ***** = 0.0005; ***** = 0.00001

Table 5.2. Interval Mapping test on three locations averaged late blight severity data-set and summary of QTLs detected for late blight resistance.

Locus	LG ^a	LOD ^b	Variance	% expl ^c	Locus	LG	LOD	Variance	% expl
CP15	III	2.85	5.84385		GP121	VII	2.21	5.95499	
GP198-1	III	4.12	4.94920	23.4	Sol179A1	VII	2.28	5.90539	8.6
GP167-1	III	3.92	4.97982		CP117-1	XI	2.56	5.84249	
CP49	V	4.14	5.56139		GP232	XI	2.63	5.84904	9.4
TG69	V	4.54	5.50574		GP255-3	XI	2.54	5.76887	
GP22	V	5.17	5.30091	17.9					

^aLinkage group^bLikelihood ratio statistic^cPercentage of the variance explained for by the QTL

The QTL with the smallest effect was found in correspondence with marker GP232 on linkage group XI (LOD = 2.63; PVE = 9.4%). Furthermore, the presence of a QTL in this chromosomal region was found to be not statistically significant in the Kruskal-Wallis test. The LOD values on this linkage group present two significant peaks within a 23 cM interval, one in correspondence of marker GP232 and one centered near GP255-3. In addition to these QTLs, interval-mapping analysis determined relatively high LOD scores associated to marker GP121 (2.21) and GP179A1 (2.28) on linkage group VII. These values fell just below the threshold value of 2.4 for the detection of a QTL, but were considerably high in respect to the overall QTL analysis. The genetic location of QTLs and their correspondent

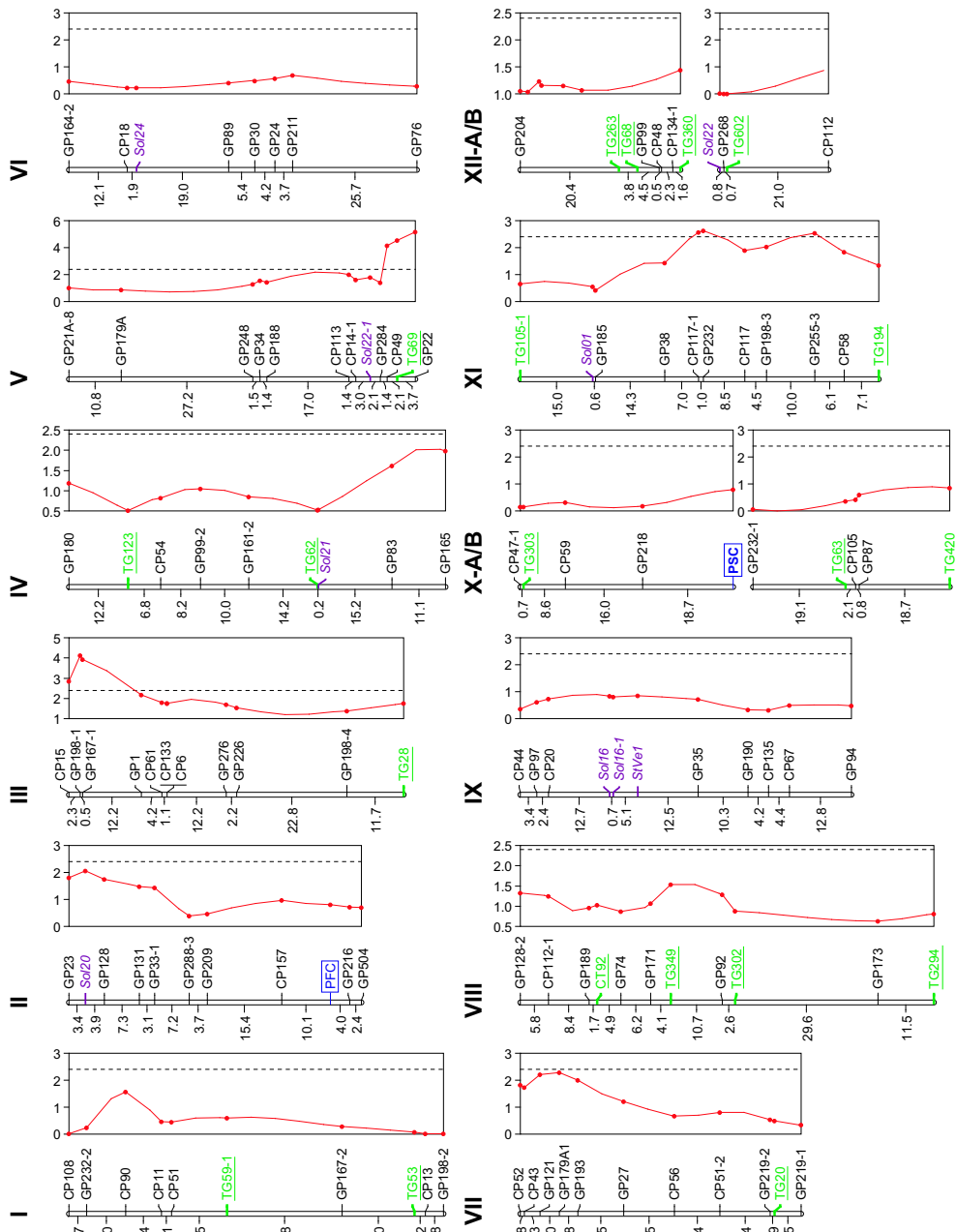


Figure 5.1. QTL analysis based on interval mapping method of trait data-set averaged over three locations. QTL and linkage map of a full-sib family of a cross between clones BDI42-1 and BDI72-1 from a diploid *Solanum phureja* × *S. stenotomum* population. The names of the markers and map distances in cM are shown on right side of chromosome, respectively. QTL likelihood plots are shown on the left side of the chromosome indicating LOD scores for potato late blight resistance. The height of the curve indicates the strength of the evidence for the presence of a QTL at each position. The horizontal dotted line at a height of 2.4 indicates the threshold that the LOD score must cross to allow the presence of a QTL to be inferred. See Fig 4.1 for markers description.

LOD values are shown in Fig.5.1.

Analysis on individual trait data-sets from the three locations

For the QTL analysis conducted on the three separate data sets from the individual locations both types of analysis, Kruskal-Wallis test and interval mapping, revealed similar results. A summary of the QTLs detected from the interval mapping method are presented in Table 5.3. The analysis on the Rock Springs 1999 data set identified two QTLs on linkage group III and V accounting for 19.8 and 13.9% of the total phenotypic variation respectively. These QTLs are mapped in comparable position along the two chromosomes as in the combined analysis. Specifically, on linkage group V the highest LOD value has shifted from marker TG69 to GP22, which are separated on the map by only 3.7 cM. From the Rock Springs 2002 data set analysis, four QTLs were detected on linkage group III, V, XI and XII-A. The QTL with the greater effect (30.6% PVE) is located on the distal section of linkage group III. The LOD values on this linkage group present a significant peak in correspondence of marker GP198-1. QTLs on linkage group V and XI have similar effect and position as in the Rock Springs data set analysis. The QTL with the smallest effect (10.8% PVE), on linkage group XII-A, has the highest LOD score associated with marker GP99. This QTL is also a contribution of alleles present in both parents. Results from the Landisville 2002 experiment shows a single LOD peak (2.49) positioned on linkage group I centered on marker CP90 explaining 8.4% of the total phenotypic variation, and contributed from alleles present in both parents. A potential QTL could be located on linkage group IX where the LOD plot reached its highest peak in proximity of marker GP35 with a LOD value of 2.00 and 7.9% of phenotypic variation explained. This QTL is contributed by an allele only present in the heterozygous state in the male resistant parent.

Analysis on the trait data-set from the three locations combined after removal of selected individuals

The QTL analysis conducted on the combined data set was re-run after removal of 19 selected individuals. The analysis confirmed the presence of the same three

Table 5.3. Interval mapping test on individual location late blight severity data-set and summary of QTLs detected for late blight resistance

Rock Springs 1999									
Locus	LG ^a	LOD ^b	Variance	% expl ^c	Locus	LG	LOD	Variance	% expl
CP15	III	3.56	13.9394		CP49	V	3.27	14.0245	
GP198-1	III	4.93	12.6516	19.8	TG69	V	3.42	14.0087	
GP167-1	III	4.69	12.7201		GP22	V	4.01	13.5824	13.9
GP1	III	2.69	13.9794						
Rock Springs 2002									
Locus	LG	LOD	Variance	% expl.	Locus	LG	LOD	Variance	% expl.
GP198-1	III	2.92	6.62334	30.6	GP22	V	5.49	8.10885	19.6
GP167-1	III	2.72	6.92756		GP255-3	XI	2.87	8.87931	12.0
CP49	V	4.54	8.58905		GP99	XII-A	3.02	8.99282	10.8
TG69	V	5.09	8.43420		CP48	XII-A	2.77	9.07272	
Landisville 2002									
Locus	LG	LOD	Variance	% expl.	Locus	LG	LOD	Variance	% expl.
CP90	I	2.49	5.54035	8.4	GP35	IX	2.00	5.56659	7.9

^aLinkage group^bLikelihood ratio statistic^cPercentage of the variance explained for by the QTL

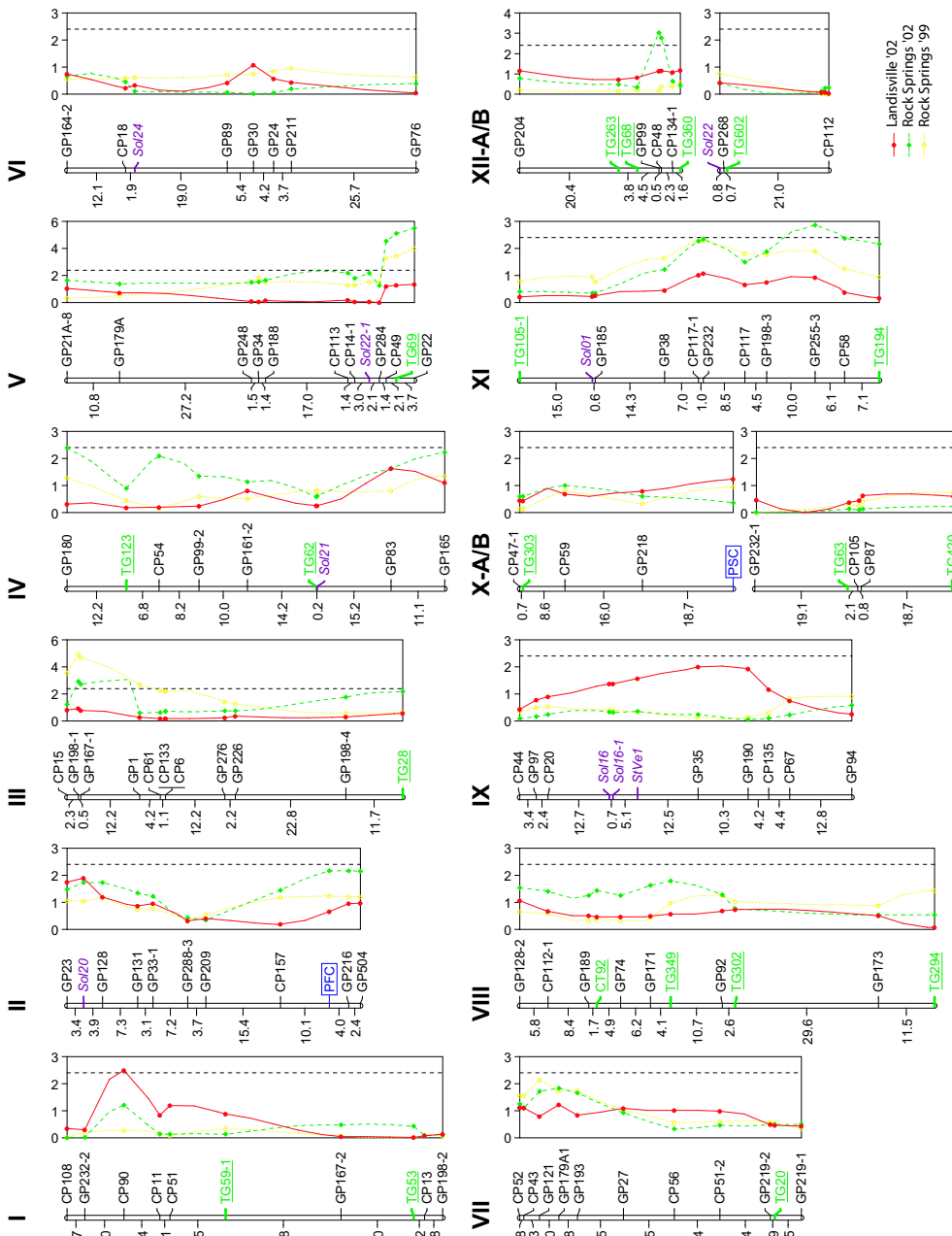


Figure 5.2. QTL analysis based on interval mapping method of trait data-sets from individual locations. QTL and linkage map of a cross between clones BD142-1 and BD172-1 from a diploid *Solanum phureja* X *S. stenotomum* population. The names of the markers and map distances in cM are shown on right side and left side of chromosome, respectively. QTL likelihood plots are shown on the right side of the chromosome indicating LOD scores for potato late blight resistance. The height of the curve indicates the strength of the evidence for the presence of a QTL at each position. The horizontal dotted line at a height of 2.4 indicates the threshold that the LOD score must cross to allow the presence of a QTL to be inferred. See Fig 4.1 for markers description.

QTLs on linkage group III, V and XI as for the combined data set (Table 5.4). A difference was found for the QTL on linkage group XI, where the position of the highest LOD peak shifted towards marker GP255-3 where the total phenotypic variation explained has a value of 12.4%. Moreover, a QTL with LOD values just below the threshold criteria of 2.4, was identified on chromosome I, mapped in the position of marker CP90 (LOD = 2.24) as for the analysis conducted on the Landisville 2002 data set. This potential QTL has an effect on the total phenotypic variation of 8.7%.

Table 5.4. Interval mapping test on three locations averaged late blight severity data-set after removal of 19 clones and summary of QTLs detected for late blight resistance

Locus	LG ^a	LOD ^b	Variance	% expl ^c	Locus	LG	LOD	Variance	% expl
CP90	I	2.24	6.36471	8.7	CP49	V	3.29	6.07344	
CP15	III	2.42	6.31738		TG69	V	3.71	5.99409	
GP198-1	III	3.51	5.33331	11.3	GP22	V	4.20	5.79693	16.9
GP167-1	III	3.32	5.35906		GP255-3	XI	2.59	6.10446	12.4

^aLinkage group

^bLikelihood ratio statistic

^cPercentage of the variance explained for by the QTL

5.4 Discussion

The hybrid population derived from the two diploid potato clones BD142-1 and BD172-1 was evaluated in the field for foliar resistance in three different environments between 1999 and 2002. QTL analyses for this trait were performed on five data sets: (i) on the estimated multiple location average, (ii) separately for each of the three locations, (iii) and again on the same data set as for the first case but with the removal of 19 selected individuals identified as unstable from the variance stability test.

Data-set from the estimated multiple locations average

On the combined data set, the analysis identified three QTLs on chromosomes III, V and XI which together could account for approximately 50% of the total

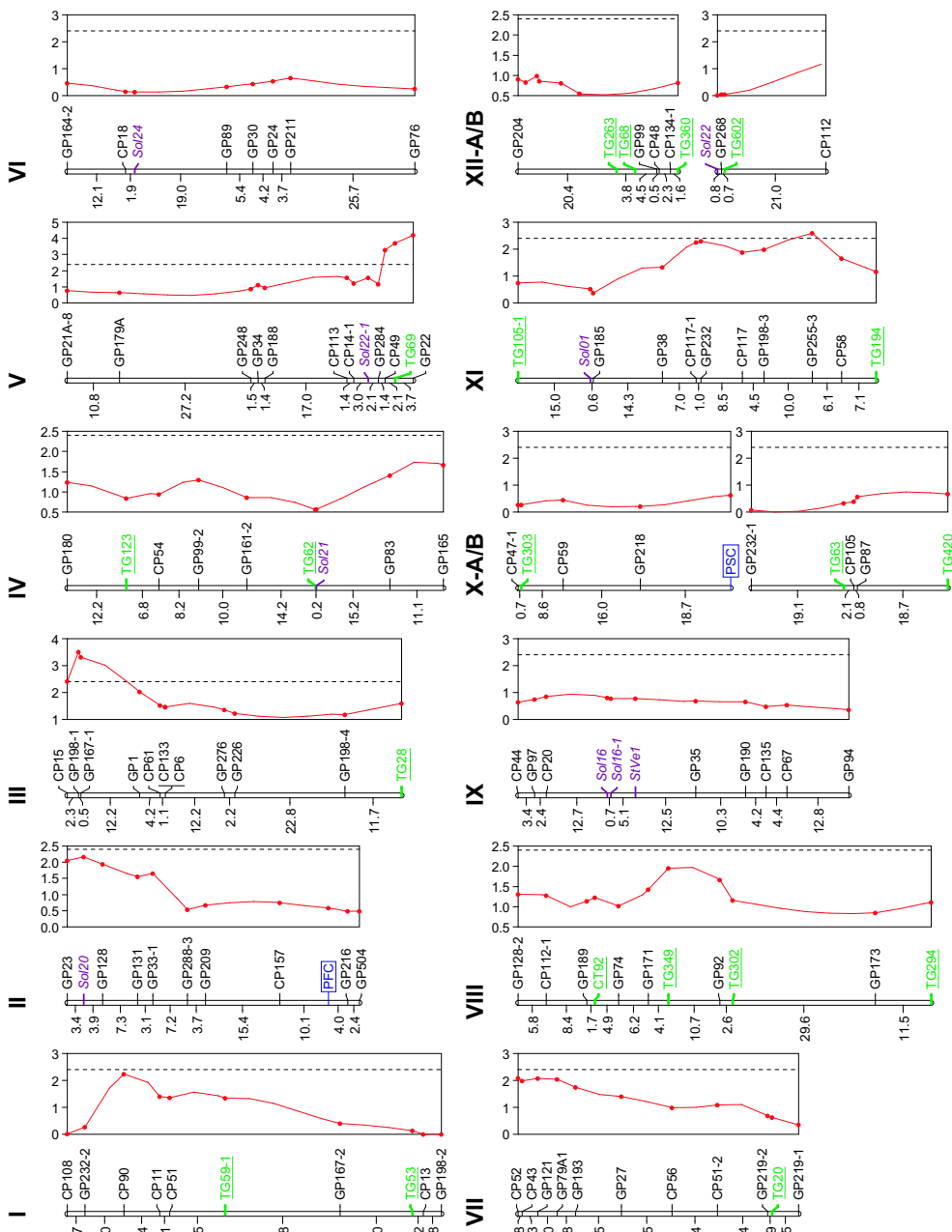


Figure 5.3. QTL analysis based on interval mapping method of trait data-set averaged over three locations after removal of a full-sib family of a cross between clones BD142-1 and BD172-1 from a diploid *Solanum phureja* x *S. stenotomum* population. The names of the markers and map distances in cM are shown on right side and left side of chromosome, respectively. QTL likelihood plots are shown on the right side of the chromosome indicating LOD scores for potato late resistance. The height of the curve indicates the strength of the evidence for the presence of a QTL at each position. The horizontal dotted line at a height of 2.4 indicates the threshold that the LOD score must cross to allow the presence of a QTL to be inferred. See Fig 4.1 for markers description.

phenotypic variation. Furthermore, the smaller effect (8.6% PVE) of a fourth QTL on chromosome VII could also be detected. The most important QTL effect was clearly observed on chromosome III (Figure 5.1). At this chromosome a QTL was segregating, centered on marker GP198-1, with an individual effect on the phenotypic variation of 23.4%. The location and effect of this QTL is in accordance with previous research conducted on different diploid potato populations (Ewing et al., 2000; Leonards-Schippers et al., 1994; Visker et al., 2003). In particular, in a population derived from *Solanum tuberosum* and *Solanum berthaultii*, Ewing et al. (2000) reported the presence of an epistatic interaction between the QTL on chromosome III and those located on chromosome VII and XI, which were mapped in positions close but not coincident to the one detected in this present QTL analysis. In the same study the potential presence at the same locus, of two closely linked QTLs with differential effect on late blight resistance was also suggested .

A second significant QTL located on the proximal section of chromosome V accounts for 17.9% of the total phenotypic variation. Its position, the interval between marker TG69 and GP22, does not coincide with any previously reported resistance locus. QTLs for late blight resistance were identified in the proximal region of chromosome V only in two other studies based on diploid potato populations (Oberhagemann et al., 1999; Sandbrink et al., 2000). Furthermore, the root cyst nematode (*Globodera rostochiensis*) resistance locus *H1* (Gebhardt et al., 1993; Pineda et al., 1992) and *GroV1* (Jacobs et al., 1996) have been mapped in proximity of those same QTLs. This could be indicative of the presence in this region of a cluster of resistance genes involved in the plant defense response mechanism. It should be noticed that this QTL is definitively distinct from the most prominent and consistent QTL identified in the majority of the studies located on chromosome V, and tightly linked to the anchor marker GP179 (Collins et al., 1999; Ewing et al., 2000; Ghislain et al., 2001; Leonards-Schippers et al., 1994; Oberhagemann et al., 1999). This major QTL is known to affect leaf as well as tuber resistance (Collins et al., 1999; Gebhardt and Valkonen, 2001; Oberhagemann et al., 1999). Tightly linked to the same marker GP179, on the distal section of chromosome V, are the *R1* locus conferring race specific resistance to late blight and a major QTL for plant maturity (Collins et al., 1999; Oberhagemann et al.,

1999). Neither QTL mapping method, in the present analysis, found any significant association between marker GP179 and general resistance against late blight present in this population.

The QTL with the smallest effect was identified on chromosome XI (PVE = 9.4%). The likelihood for the presence of a segregating QTL on this linkage group was below the significant threshold criterion in the correspondent Kruskal-Wallis test. On this chromosome, the QTL appeared to extend across a large section in the middle portion of this linkage group (23 cM), and two LOD peaks were identified with values of 2.63 and 2.54 and individual PVE values of 9.4 and 10.7% respectively (see Appendix). The presence of multiple nearby significant likelihood peaks on this chromosome, however, does not necessarily imply the presence of multiple QTLs in this region, but this possibility can not be ruled out from the present study. The location of this complex locus on chromosome XI is comparable with those described by Leonards-Schippers et al. (1994) and Ewing et al. (2000). A previous study also determined that the proximal end of chromosome XI harbors a cluster of three *R* genes (*R3*, *R6* and *R7*) with different pathogen race specificity to *P. infestans* (El-Kharbotly et al., 1994, 1996). Moreover, on the same chromosome the presence of a large number of specific resistance genes for virus, bacteria, nematodes and fungi have been reported (Gebhardt and Valkonen, 2001). From the results of the Kruskal-Wallis analysis it appears that this QTL was contributed by the susceptible parent. Such an observation has been previously reported in potato and other species (De Vicente and Tanksley, 1993; Leonards-Schippers et al., 1994). It is not uncommon, in the case of late blight, to identify QTLs for resistance present in the heterozygous state in the susceptible parent. It has been repeatedly observed that QTL alleles, which increase susceptibility to late blight, are often dominant over alleles that increase resistance, thus explaining why during backcross breeding to susceptible cultivars, field resistance to late blight is frequently lost (Gebhardt and Valkonen, 2001; Ghislain et al., 2001; Leonards-Schippers et al., 1994; Visker et al., 2003). This observation illustrates also the specific feature of QTL marker analysis to identify these type of loci which make a relevant contribution toward resistance that otherwise would have been masked by the overall negative effect of genetic traits possessed by the susceptible parent.

On chromosome VII, the smaller effect (8.6% PVE) of a less significant QTL was identified. This QTL is positioned at the distal end of the chromosome with a LOD plot that has its highest value in correspondence of marker GP179A1 (LOD = 2.28). Despite the relatively low LOD value associated with this QTL, its position and effect is in accord with a QTL of minor effect ($0.05 < P < 0.01$) reported in two studies by Leonards-Schippers *et al.* (1994) and by Ewing *et al.* (2000). Moreover, in a more recent study (Kuhl *et al.*, 2001), a single dominant late blight resistance locus (*Rpi1*) from *S. pinnatisectum* was mapped in the proximity of this region on chromosome VII.

Individual trait data-sets from the three locations

The analysis of the QTL mapping results performed on the three locations separately (Figure 5.2) reveals the presence of similar trends among the LOD plots from the three data sets, which is indicative of common genetic factors acting in concert across environments. Despite this overall agreement, a clear distinction can be made between the two experiments conducted at Rock Springs in 1999 and 2002, and the third one at Landisville in 2002. In this last case, LOD plots with consistently lower values than the other two cases can be observed in at least six of the fourteen linkage groups analyzed. In particular, the linkage groups where significant QTLs have been identified in the two Rock Springs data sets (III; V; and XI) have LOD plots that never reach the threshold of 2.4 for the Landisville data set. Moreover, this trend is completely reversed when we consider the LOD plots of linkage group I and IX. It can be speculated that these differences were caused by the effect of the distinct environmental conditions, in the different locations, on the expression of specific resistance components. Another important factor that most probably has contributed to these differences is also the level of maturity of the plants in the Landisville experiment at the time of inoculation. Due to warmer and dryer weather conditions at this location, the plants were in the field a month longer, compared to field experiments at Rock Springs, before the inoculation of *P. infestans* spores could be applied. Clear evidence has been found that potato plants become more susceptible to infection as the foliage matures (Collins *et al.*, 1999; Hodgson, 1961; Oberhagemann *et al.*, 1999). It is possible that this generalized increase in plant susceptibility may have hampered the ability to clearly

discriminate in the field among levels of resistance consequently effecting the QTL mapping analysis. An additional QTL was identified on linkage group XII-A in the Rock Springs 2002 data set. There are no previous reports indicating the presence of a QTL associated with late blight resistance in the same chromosomal region. Moreover, neither of the two other data sets supported the presence of a QTL in that same position, therefore the authenticity of this QTL remains to be confirmed.

Data-set from the three locations combined after removal of selected individuals

The removal of the 19 selected individuals from the combined data set produced only moderate changes in the position and likelihood values of loci previously identified. In particular, the QTL mapped on chromosome XI, presents now only a single marker (GP255-3) with a LOD value above the significant threshold. Despite this change, the possibility of a second QTL in correspondence of marker GP232 can not be eliminated since the LOD plot for this chromosome continues to show a peak in that position which is just below the set threshold. A considerable increase in LOD values, from 1.56 to 2.16, was instead observed in this data set for marker CP90 on chromosome I, and a minor one for the RGA marker Sol20 on chromosome II. These two loci together with the previously discussed locus on chromosome VII, could potentially correspond to QTLs with smaller effects involved in conferring quantitative resistance against *P. infestans*. This hypothesis is partially supported by a previous study (Leonards-Schippers et al., 1994), with the exception of the locus on chromosome I which could be a specific contribution of the specific population analyzed in the present work.

Conclusion

In the present study, two different approaches of QTL analysis, the non parametric Kruskal-Wallis test and the interval mapping method, were applied. Both methods gave comparable results in identifying several QTLs with significant effect on late blight general resistance in potato. Partial discrepancy between the two method was observed only for the QTL detected on chromosome XI. The combined results suggested the presence in the diploid potato germplasm utilized, of three major

QTLs on chromosome III, V and XI, which accounted for 11.3%, 16.9% and 12.4% of the total phenotypic variation respectively. Furthermore, three additional loci on chromosome I, II and VII, were identified with a potential but more limited effect on the same trait. These results fully support the initial hypothesis suggesting the presence in this population of several loci contributing enhanced general resistance against late blight. Some of these QTLs have been identified in several other studies using different intra- and inter-specific crosses. Common QTLs identified in different species, populations, and environments are ideal targets for marker-assisted selection (MAS) and breeding, and for basic research towards cloning and characterizing genes affecting quantitative traits. This valuable information could be used in any available population to monitor the inheritance of a specific chromosomal segment or to evaluate the variation available in a specific genepool at a particular locus. Moreover, in future studies, the resolution of QTL mapping obtained from this study could be improved by adding more genetic markers and by using a larger population to allow an examination of more recombinant types. These would allow the identification of markers more closely linked to the mapped QTLs. Those markers could then be transformed into PCR-based marker assay to simplify the detection of specific QTL alleles among selected genotypes.

Chapter 6

Conclusions

6.1 Overview

Since its first outbreak in Ireland in the 1880's, late blight has continued to be a serious threat to potato cultivation throughout the world. Sources of resistance against this disease have been found in a number of wild and cultivated potato species. Despite many breeding efforts directed towards the introgression of such resistance into commercially grown potatoes, no cultivar with adequate late blight resistance has yet been developed. A limited understanding of the complex phenomenon of host-pathogen interactions and plant defense mechanisms are probably among the major obstacles that modern breeding programs have to face when trying to improve disease resistance in potato. However, more recently, with the development of DNA-based marker technology, plant breeders were provided with new powerful tools capable of monitoring the whole genome, allowing the dissection of components affecting qualitative as well as quantitative characters. Genetic maps based on several types of molecular markers are becoming available for many economically important plant species, and the application of easy to score markers is now providing the opportunity to precisely determine the number, position, and individual effect of resistance loci showing quantitative inheritance, and to greatly facilitate breeding strategies for incorporating the various resistance components into new varieties.

6.2 General Discussion

In the present study, a diploid hybrid population of *Solanum phureja* \times *S. stenotomum* was utilized to construct a molecular linkage map of potato using RFLP markers, and to search the map for associations between markers and QTLs for late blight resistance. Phenotypic assessments of field resistance in this population were collected under three different environments in Pennsylvania between 1999 and 2002. As expected, the different environmental conditions in the three locations significantly influenced the progression of the disease epidemic. Despite differences between years and locations, all three experiments exhibited continuous variation in the full-sib family, typical of quantitative traits. The result of the stability variance test, allowed the identification of 37 clones among the BD42/72 family which were significantly contributing to the overall variance, and were therefore removed from further analyses. Broad-sense heritability in this population was estimated as 0.67 with a 95% confidence interval of 0.65 to 0.78. Transgressive segregation was observed primarily in the direction of increased resistance. This result could suggest a positive contribution (towards increased resistance) being provided by alleles derived from the susceptible parent.

A genetic linkage map was constructed using 122 RFLP markers (developed in previous studies), 8 RGA markers and 2 morphological characters. This map, composed of 14 linkage groups, covers approximately 855 cM of the potato genome. Despite the introduction of additional, specifically selected, markers, we were unable to join the two linkage groups representing chromosome X and XII. Genome coverage by the map is estimated to be at least 70%. The order and relative distance of the markers was found to be in agreement with those found on previously published potato and tomato maps.

Two methods were used for QTL mapping, the Kruskal-Wallis non-parametric test and the interval mapping method. Both these approaches were effective in identifying several QTLs with significant effects on late blight resistance. The result of this study also confirmed the polygenic nature of this trait which appears to be controlled in this population by few major QTLs which presumably are acting in concert with a number of smaller effect QTLs. The QTL analysis on the multiple location average data set, revealed three loci for *P. infestans* resistance on

chromosome III, V and XI. The position and effect of these QTLs were consistent with those identified from the multi-location data set after the removal of clones which made a significant contribution on the overall variance. This result suggests that these loci represent components of field resistance in this population and that these loci are stable across environments since they were only marginally affected by the removal of the unstable clones from the analysis. Therefore, these three chromosomal regions should be regarded as the main target of further research directed toward the implementation of a MAS breeding program. The mapping precision for these QTLs along the three linkage groups is, however, still limited due to the number of markers utilized and the size of the segregating population.

The components of resistance identified in this population appear to be mainly a contribution of both parental clones. Specifically, QTL alleles conferring increased field resistance to late blight, were found to be often recessive in relation to alleles that increased susceptibility. Furthermore, the segregation ratios at QTLs for late blight resistance were often distorted, with susceptibility alleles being more frequent. This result is in common with previous late blight studies and it is hypothesized that this could be due to the presence of specific resistance gene suppressors (El-Kharbotly et al., 1996; Ordoñez et al., 1997).

6.3 Future Work

The molecular linkage map developed in this study, together with the QTL analysis, provides the first step toward revealing the molecular basis of QTLs controlling partial resistance to late blight in the diploid *Solanum* germplasm used. These results constitute the structural basis for the future implementation of marker assisted selection (MAS) to incorporate the various specific allelic variants into new genotypes which should result in enhanced resistance against *P. infestans*. The ultimate realization of this goal is dependent upon several factors that were only partially addressed in the present study and that still remain to be completed.

A primary objective for future research should be the improvement of marker density and total genome coverage of the present linkage map. Adding other genetic markers to the map will result in a more comprehensive coverage of the 12 potato chromosomes. This should allow a resolution to the problems associated with the

presence of multiple or incomplete linkage groups. Moreover, additional QTLs could potentially be discovered in segments of chromosomes that were initially missing from the linkage map or were scarce in the area of selected RFLP markers.

Additional markers will be required particularly for those chromosomal regions encompassing the identified QTLs for resistance to late blight. The new markers should be used to substantially narrow the gap between the initial RFLP markers and the estimated position of the QTL, consequently generating a high resolution map of those regions. For future large scale MAS breeding schemes, the adoption of less expensive and more user-friendly PCR-based markers would be highly recommended. An increasing number of simple sequence repeats loci (SSR) have now been mapped in diploid potato mapping studies (Ghislain et al., 2001; Milbourne et al., 1998; Sandbrink et al., 2000). They are located on all 12 potato linkage groups and provide a significant and convenient alternative to RFLPs for future linkage studies in potato. By combining SSR-based assays with multiplex assays such as AFLPs, the enrichment of specific QTL regions with more tightly linked markers can quickly be obtained. If necessary, mapped RFLP and AFLP markers could also be converted into a PCR-based type of assay. In addition, high resolution maps of QTL regions will constitute the starting point for tagging, and ultimately cloning the genes controlling this trait.

The quantitative components of late blight resistance, once fully identified and characterized, could be incorporated directly into tetraploid potatoes through the use of $2n$ pollen in $4\times-2\times$ crosses, with efficient reduction of undesirable "linkage drag". MAS may facilitate the simultaneous transfer of genes (QTLs) for this late blight resistance from the diploid population into modern cultivars of tetraploid potato, providing opportunities for a rapid development of cultivars with enhanced characteristics. However, the value of the identified QTLs will require further testing in combination with other desirable horticultural characteristics.

In this direction, a previous study by Christ and Haynes (2001), indicated that the initial random mated population of *S. phureja* \times *S. stenotomum*, from which the BD42/72 was derived, could potentially contribute genes for resistance to early blight, caused by the fungus *Alternaria solani* Souraure. Therefore, for the past three years, in addition to late blight resistance, this mapping family has been evaluated for its resistance against early blight, and QTLs effecting this

trait have also been identified. Consequently, new research will be necessary to combine the results of both studies and plan a MAS strategy that will allow the simultaneous transfer of these desirable traits. This research could potentially identify QTLs with a pleiotropic effect on resistance for both diseases, or the presence of other interactions between loci, thus providing greater insight into the complex mechanism of plant disease response.

Besides disease resistance, other characters affecting the tuber are considered extremely important in potato genetics and breeding. Some of these characters are: tuber yield, content and quality of starch and protein, cooking and chipping quality, flesh and skin color, tuberization and tuber dormancy. Since the majority of these traits are under polygenic control, the present linkage map, could also be used in new QTL mapping studies directed toward the identification of loci regulating these traits.

Appendix A

Data analysis

A.1 Kruskal-Wallis non-parametric Test

A.1.1 Rock Springs 1999 data-set

Significance levels:
 * = 0.1 *** = 0.01 ***** = 0.001 ***** = 0.00001
 ** = 0.05 **** = 0.005 **** = 0.0005

Linkage group (l)		map	locus	inf	k*	(df)	class:	rank	mean	nr	class:	rank	mean	nr
0.0	CP108	132	0.108	(1)	-	nn:	66.2	24.2713	124	np:	70.8	23.9275	8	
3.7	GP232-2	132	0.747	(1)	-	nn:	76.5	25.4304	10	np:	65.7	24.1538	122	
11.7	CP90	132	1.083	(1)	-	nn:	65.0	24.0883	112	np:	74.7	25.1585	20	
19.1	CP11	132	0.671	(1)	-	nn:	72.4	24.9375	23	np:	65.2	24.1055	109	
21.2	CP51	132	0.351	(1)	-	nn:	70.5	24.6874	26	np:	65.5	24.1433	106	
32.7	TG59-1	132	1.382	(1)	-	nn:	72.8	24.9421	37	np:	64.1	23.9811	95	
56.5	GP167-2	132	0.158	(1)	-	nn:	68.1	24.4905	54	np:	65.4	24.0843	78	
71.5	TG53	132	0.093	(1)	-	nn:	65.5	24.1526	64	np:	67.5	24.3426	68	
73.7	CP13	132	0.534	(1)	-	nn:	68.9	24.4582	67	np:	64.0	24.0364	65	

Linkage group (V)		inf	k*	(df)	class:	rank	mean	nr	class:	rank	mean	nr	class:	rank	mean	nr
0.0	GP21A-8	132	0.229	(1)	li:	68.3	24.4329	59	li:	65.1	24.1031	73				
10.8	GP179A	132	1.908	(1)	li:	71.2	24.7297	65	li:	62.0	23.7856	67				
38.0	GP248	132	4.919	(1)	**	75.2	25.1052	55	li:	60.3	23.6400	77				
39.5	GP34	132	6.042	(1)	**	76.2	25.2009	55	li:	59.6	23.5716	77				
40.9	GP188	132	4.929	(1)	**	75.2	25.1210	55	li:	60.3	23.6287	77				
57.9	CP113	132	0.971	(2)	-	68.2	24.5503	46	hk:	68.4	24.4187	55	kk:	60.6	23.5072	31
59.3	CP14-1	132	7.545	(1)	***	78.2	25.3659	50	li:	59.4	23.5703	82				
62.3	Sol22-1	132	4.693	(1)	**	60.8	23.7288	81	li:	75.6	25.0791	51				
64.4	GP284	132	7.758	(1)	***	58.9	23.5469	79	li:	77.8	25.2993	53				
65.8	CP49	132	6.727	(1)	***	74.4	25.1364	72	np:	57.0	23.1874	60				
67.9	TG69	132	16.171	(3)	****	83.7	26.0010	27	ef:	69.0	24.6283	44	eg:	72.5	24.5607	25
71.6	GP22	132	10.757	(1)	****	79.8	25.4848	53	li:	57.6	23.4224	79				
Linkage group (VI)																
map	locus	inf	k*	(df)	class:	rank	mean	nr	class:	rank	mean	nr	class:	rank	mean	nr
0.0	GP164-2	132	0.021	(1)	nn:	67.0	24.3385	61	np:	66.0	24.1749	71				
12.1	CP18	132	0.067	(1)	nn:	67.4	24.2984	66	np:	65.6	24.2026	66				
14.0	Sol24	132	0.113	(1)	nn:	67.6	24.3186	65	np:	65.4	24.1844	67				
33.0	GP89	132	0.274	(1)	nn:	64.7	23.9838	65	np:	68.2	24.5092	67				
38.4	GP30	132	0.176	(1)	nn:	65.2	24.0045	69	np:	68.0	24.5199	63				
42.6	GP24	132	2.509	(3)	ee:	65.7	24.3604	35	ef:	62.5	23.4769	34	eg:	75.5	25.3103	32
46.3	GP211	132	0.844	(1)	nn:	63.6	23.8843	70	np:	69.8	24.6640	62				
72.0	GP76	132	0.095	(1)	nn:	65.4	24.1432	59	np:	67.4	24.3372	73				
Linkage group (VII)																
map	locus	inf	k*	(df)	class:	rank	mean	nr	class:	rank	mean	nr	class:	rank	mean	nr
0.0	CP52	132	5.742	(1)	**	57.9	23.4037	61	np:	73.9	24.9780	71				
0.8	CP43	132	7.082	(3)	*	55.9	23.4595	30	ef:	59.7	23.3114	30	eg:	78.2	25.5212	40
4.1	GP121	132	7.550	(1)	***	75.0	25.0909	71	np:	56.6	23.2723	61				
8.1	GP179A1	132	6.876	(1)	***	57.1	23.4657	61	np:	74.6	24.9248	71				
11.9	GP193	132	7.633	(1)	***	56.4	23.4280	60	np:	74.9	24.9359	72				
21.4	GP27	132	0.008	(1)	-	66.8	24.2869	71	li:	66.2	24.2081	61				
31.9	CP56	132	3.865	(1)	**	58.5	23.5946	53	np:	71.9	24.6905	79				
41.3	CP51-2	132	3.576	(2)	-	72.4	24.5803	39	hk:	68.5	24.5238	59	kk:	56.2	23.3979	34
51.7	GP219-2	132	0.008	(1)	-	66.8	24.1832	61	li:	66.2	24.3083	71				
52.6	TG20	132	3.127	(1)	*	72.3	24.6811	67	np:	60.5	23.8067	65				
58.1	GP219-1	132	1.827	(1)	-	71.0	24.5605	66	np:	62.0	23.9405	66				
Linkage group (VIII)																
map	locus	inf	k*	(df)	class:	rank	mean	nr	class:	rank	mean	nr	class:	rank	mean	nr
0.0	GP128-2	132	1.561	(1)	-	62.4	23.8636	67	np:	70.7	24.6493	65				

map		locus	inf	k*	(df)	class:	rank	mean	nr	class:	rank	mean	nr	class:	rank	mean	nr				
5.8	CP112-1	132	0.168	(1)	-	nn:	65.1	24.1620	63	np:	67.8	24.3312	69								
14.2	GP189	132	0.364	(1)	-	nn:	68.4	24.4905	69	np:	64.4	23.9876	63								
15.9	CT92	132	0.531	(1)	-	nn:	68.9	24.5185	68	np:	64.0	23.9657	64								
20.8	GP74	132	0.674	(2)	-	hh:	65.2	24.1413	34	hk:	71.9	24.8615	27	kk:							
27.0	GP171	132	0.009	(1)	-	li:	66.2	24.1153	68	lim:	66.8	24.3942	64								
31.1	TG349	132	1.146	(1)	-	nn:	70.2	24.7115	63	np:	63.1	23.8296	69								
41.8	GP92	132	2.710	(1)	*	nn:	72.9	24.9305	56	np:	61.8	23.7495	76								
44.4	TG302	132	4.089	(3)	-	ac:	66.6	24.1087	38	ad:	66.8	24.2058	30	bc:	57.2	23.3601	34	bd:	76.6	25.4838	30
74.0	GP173	132	0.879	(1)	-	li:	69.7	24.5967	65	lim:	63.4	23.9146	67								
85.5	TG294	132	0.396	(1)	-	li:	68.5	24.5818	70	lim:	64.3	23.8764	62								
Linkage group (X)																					
map	locus	inf	k*	(df)	class:	rank	mean	nr	class:	rank	mean	nr	class:	rank	mean	nr					
0.0	CP44	132	0.664	(2)	-	hh:	70.1	24.9121	31	hk:	66.6	24.1955	77	kk:	61.6	23.5725	24				
3.4	GP97	132	0.135	(1)	-	nn:	67.7	24.5539	69	np:	65.2	23.9182	63								
5.8	CP20	132	1.326	(1)	-	li:	70.1	24.5788	70	lim:	62.4	23.8798	62								
18.5	Soll6	132	0.981	(1)	-	nn:	69.9	24.7228	64	np:	63.3	23.8060	68								
19.2	Soll6-1	132	0.519	(2)	-	hh:	65.6	23.9023	41	hk:	64.7	24.2345	56	kk:	70.4	24.6839	35				
24.3	StVe1	132	0.103	(1)	-	li:	65.3	24.1955	59	lim:	67.5	24.2949	73								
36.8	GP35	132	0.033	(1)	-	nn:	67.1	24.4696	66	np:	65.9	24.0314	66								
47.1	GP190	132	0.002	(1)	-	li:	66.3	24.3346	54	lim:	66.6	24.1922	78								
51.3	CP135	132	1.014	(1)	-	nn:	69.7	24.5480	69	np:	63.0	23.9246	63								
55.7	CP67	132	2.222	(1)	-	nn:	71.4	24.8444	67	np:	61.5	23.6383	65								
68.5	GP94	132	0.006	(1)	-	li:	66.3	24.1695	76	lim:	66.8	24.3604	56								
Linkage group (X-A)																					
map	locus	inf	k*	(df)	class:	rank	mean	nr	class:	rank	mean	nr	class:	rank	mean	nr					
0.0	CP47-1	37	0.000	(0)	-	hh:	19.0	24.5317	37	hk:	—	—	0	(?)							
0.7	TG303	132	1.495	(1)	-	nn:	62.3	23.9781	64	np:	70.4	24.5069	68								
9.3	CP59	132	3.159	(1)	*	nn:	60.7	23.7074	67	np:	72.5	24.8103	65								
25.3	GP218	132	1.930	(1)	-	nn:	61.4	23.7987	59	np:	70.7	24.6156	73								
44.0	PSC	131	3.121	(1)	*	nn:	61.2	23.8012	79	np:	73.2	24.8338	52								
Linkage group (X-B)																					
map	locus	inf	k*	(df)	class:	rank	mean	nr	class:	rank	mean	nr	class:	rank	mean	nr					
0.0	GP232-1	132	0.104	(1)	-	li:	65.1	24.1872	49	lim:	67.3	24.2879	83								
19.1	TG63	132	2.323	(1)	-	li:	71.1	24.6073	72	lim:	60.9	23.8223	60								
21.2	CP105	132	1.893	(1)	-	li:	70.9	24.6076	69	lim:	61.7	23.8593	63								
22.0	GP87	132	2.680	(1)	-	li:	71.8	24.7137	68	lim:	60.9	23.7583	64								
40.7	TG420	132	4.157	(1)	**	li:	73.3	24.8884	66	lim:	59.7	23.6126	66								

Linkage group (X1)		inf	k*	(df)	class:	rank	mean	nr	class:	rank	mean	nr	class:	rank	mean	nr
map	locus															
0.0	TG105-1	132	3.006	(2)	hh:	67.2	24.6775	34	hk:	74.0	24.8635	42	kk:	60.5	23.5314	56
15.0	So101	132	3.453	(1)	li:	59.6	23.4556	59	lm:	72.1	24.8930	73				
15.6	GP185	132	3.082	(3)	ee:	59.6	23.6330	29	ef:	73.8	24.8832	42	eg:	61.2	23.4304	29
29.9	GP38	132	4.280	(1)	li:	58.8	23.3376	59	lm:	72.7	24.9883	73				
36.9	CP117-1	132	0.174	(1)	nn:	65.2	24.1221	70	np:	68.0	24.3954	62				
37.9	GP232	38	0.000	(0)	hh:	19.5	24.9178	38	hk:	—	—	0	kk:	—	—	0
46.4	CP117	132	5.888	(1)	li:	73.4	25.0671	76	lm:	57.1	23.1422	56				
50.9	GP198-3	132	0.039	(1)	nn:	67.3	24.2468	56	np:	65.9	24.2532	76				
60.9	GP255-3	132	1.350	(1)	nn:	71.7	24.7977	47	np:	63.6	23.9479	85				
67.0	CP58	132	0.266	(1)	nn:	65.0	24.1316	74	np:	68.4	24.4022	58				
74.1	TG194	132	3.653	(1)	li:	72.6	24.9246	69	lm:	59.8	23.5122	63				
Linkage group (X1I-A)																
map	locus	inf	k*	(df)	class:	rank	mean	nr	class:	rank	mean	nr	class:	rank	mean	nr
0.0	GP204	132	0.220	(1)	nn:	65.1	24.1176	73	np:	68.2	24.4149	59				
20.4	TG263	31	0.000	(0)	hh:	16.0	24.4952	31	hk:	—	—	0	kk:	—	—	0
24.2	TG68	132	0.972	(3)	ee:	62.0	23.9835	31	ef:	69.6	24.6303	31	eg:	64.4	23.8762	33
28.7	GP99	132	0.035	(1)	nn:	67.2	24.3414	63	np:	65.9	24.1675	69				
29.2	CP48	132	0.236	(1)	nn:	65.0	23.9801	70	np:	68.2	24.5558	62				
31.5	CP134-1	132	0.672	(2)	hh:	64.9	23.9913	37	hk:	69.0	24.4943	69	kk:	62.3	23.9723	26
33.1	TG360	132	0.854	(1)	nn:	63.6	23.8540	71	np:	69.8	24.7120	61				
Linkage group (X1I-B)																
map	locus	inf	k*	(df)	class:	rank	mean	nr	class:	rank	mean	nr	class:	rank	mean	nr
0.0	So122	132	0.054	(1)	li:	65.7	24.2170	65	lm:	67.3	24.2830	67				
0.8	GP268	132	0.143	(1)	li:	67.8	24.3224	66	lm:	65.2	24.1786	66				
1.5	TG602	132	0.201	(1)	li:	68.0	24.3450	67	lm:	65.0	24.1531	65				
22.5	CP112	132	3.288	(1)	li:	72.3	24.8638	69	lm:	60.2	23.5788	63				
Linkage group (I)																
map	locus	inf	k*	(df)	class:	rank	mean	nr	class:	rank	mean	nr	class:	rank	mean	nr
0.0	CP108	131	0.000	(1)	nn:	66.0	19.9271	123	np:	65.8	19.8180	8				
3.7	GP232-2	131	0.236	(1)	nn:	71.6	20.2471	10	np:	65.5	19.8934	121				
11.7	CP90	131	5.682	(1)	nn:	62.6	19.6454	111	np:	84.6	21.4466	20				
19.1	CP11	131	0.978	(1)	nn:	73.1	20.4072	23	np:	64.5	19.8167	108				
21.2	CP51	131	1.002	(1)	nn:	72.7	20.3585	26	np:	64.3	19.8119	105				
32.7	TG59-1	131	1.014	(1)	nn:	71.3	20.2673	37	np:	63.9	19.7839	94				

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map	locus	inf	k*	(df)	class:	rank	mean	nr	class:	rank	mean	nr	class:	rank	mean	nr					
56.5	GP167-2	131	2.281	(1)	-	nn:	72.0	20.4134	54	np:	61.8	19.5747	77								
71.5	TG53	131	2.070	(1)	-	nn:	70.9	20.3166	64	np:	61.3	19.5419	67								
73.7	CP13	131	0.835	(1)	-	nn:	63.0	19.7429	66	np:	69.1	20.1006	65								
77.5	GP198-2	131	1.097	(1)	-	nn:	69.4	20.1283	66	np:	62.5	19.7093	65								
Linkage group (II)																					
map	locus	inf	k*	(df)	class:	rank	mean	nr	class:	rank	mean	nr	class:	rank	mean	nr					
0.0	GP23	131	3.638	(1)	*	li:	61.1	19.5238	82	lm:	74.2	20.5842	49								
3.4	SoI20	131	4.151	(1)	**	li:	61.0	19.5078	85	lm:	75.2	20.6828	46								
7.3	GP128	131	3.796	(1)	*	li:	61.3	19.5249	86	lm:	74.9	20.6762	45								
14.6	GP131	131	2.380	(1)	-	li:	73.9	20.5934	39	lm:	62.7	19.6351	92								
17.7	GP33-1	131	3.827	(1)	*	nn:	74.5	20.6060	48	np:	61.1	19.5239	83								
24.9	GP288-3	131	1.236	(2)	-	hh:	84.2	21.8489	5	hk:	65.9	19.7858	71	kk:	64.5	19.9189	55				
28.6	GP209	131	0.009	(1)	-	li:	65.8	19.9140	91	lm:	66.5	19.9349	40								
44.0	CP157	131	2.505	(1)	-	nn:	61.7	19.6539	78	np:	72.4	20.3127	53								
54.1	PFC	39	0.000	(0)	-	hh:	20.0	19.4777	39	hk:	—	—	0	kk:	—	0	(?)				
58.1	GP216	131	1.052	(1)	-	li:	63.6	19.7516	87	lm:	70.8	20.2541	44								
60.5	GP504	131	2.012	(1)	-	nn:	62.1	19.6270	78	np:	71.7	20.3522	53								
Linkage group (III)																					
map	locus	inf	k*	(df)	class:	rank	mean	nr	class:	rank	mean	nr	class:	rank	mean	nr					
0.0	CP15	131	4.219	(1)	**	nn:	60.4	19.4117	78	np:	74.3	20.6691	53								
2.3	GP198-1	131	4.874	(1)	**	nn:	59.7	19.3505	75	np:	74.5	20.6837	56								
2.8	GP167-1	131	4.713	(1)	**	nn:	59.9	19.3658	76	np:	74.5	20.6868	55								
15.0	GP1	131	1.766	(1)	-	nn:	70.7	20.3716	61	np:	61.9	19.5272	70								
19.2	CP61	131	1.906	(1)	-	nn:	61.7	19.5193	69	np:	70.8	20.3668	62								
20.3	CP133	131	1.176	(1)	-	nn:	62.5	19.5787	67	np:	69.7	20.2782	64								
20.3	CP6	131	1.176	(1)	-	nn:	62.5	19.5787	67	np:	69.7	20.2782	64								
32.5	GP276	131	8.104	(3)	**	ee:	70.9	20.3000	32	ef:	51.1	18.6721	34	eg:	75.4	20.6724	38	fg:	65.7	19.9841	27
34.7	GP226	131	2.769	(1)	*	nn:	60.5	19.4802	66	np:	71.6	20.3674	65								
57.5	GP198-4	131	1.079	(1)	-	nn:	69.6	20.2054	63	np:	62.7	19.6564	68								
69.2	TG28	131	4.227	(1)	**	nn:	73.0	20.5361	64	np:	59.3	19.3323	67								
Linkage group (IV)																					
map	locus	inf	k*	(df)	class:	rank	mean	nr	class:	rank	mean	nr	class:	rank	mean	nr					
0.0	GP180	131	8.753	(2)	**	hh:	54.6	18.9984	39	hk:	65.5	19.7796	62	kk:	81.9	21.4100	30				
12.2	TG123	131	3.356	(3)	-	ee:	74.2	20.7839	33	ef:	69.2	20.0124	33	eg:	58.7	19.3050	25	fg:	61.2	19.5168	40
19.0	CP54	131	6.112	(2)	**	hh:	59.8	19.3697	46	hk:	63.7	19.6465	59	kk:	82.1	21.5164	26				
27.2	GP99-2	131	5.127	(1)	**	nn:	74.8	20.6319	55	np:	59.6	19.4055	76								
37.2	GP161-2	131	4.885	(1)	**	nn:	73.2	20.5210	67	np:	58.5	19.2916	64								
51.4	TG62	131	2.468	(1)	-	nn:	60.6	19.4866	63	np:	71.0	20.3223	68								
51.6	SoI21	131	1.003	(1)	-	li:	62.4	19.7506	61	lm:	69.1	20.0684	70								
66.8	GP83	131	6.905	(1)	***	nn:	74.3	20.6247	69	np:	56.8	19.1366	62								
77.9	GP165	131	3.946	(2)	-	hh:	59.5	19.3816	23	hk:	62.5	19.5622	69	kk:	76.0	20.8719	39				

Linkage group (V)		inf	k*	(df)	class:	rank	mean	nr	class:	rank	mean	nr	class:	rank	mean	nr	
map	locus																
0.0	GP21A-8	131	1.595	(1)	li:	61.4	19.5177	59	li:	69.8	20.2504	72					
10.8	GP179A	131	0.835	(1)	li:	62.9	19.6300	65	li:	69.0	20.2064	66					
38.0	GP248	131	0.034	(1)	li:	66.7	19.8388	54	li:	65.5	19.9776	77					
39.5	GP34	131	0.325	(1)	li:	68.3	19.9491	54	li:	64.4	19.9003	77					
40.9	GP188	131	0.143	(1)	li:	67.5	19.8794	54	li:	64.9	19.9492	77					
57.9	CP113	131	8.124	(2)	hh:	77.0	20.8999	46	hk:	64.5	19.8852	55	kk:	51.8	18.4830	30	
59.3	CP14-1	131	2.843	(1)	li:	73.2	20.3985	49	li:	61.7	19.6347	82					
62.3	So22-1	131	2.925	(1)	li:	61.5	19.6183	81	li:	73.2	20.4099	50					
64.4	GP284	131	2.634	(1)	li:	61.6	19.6205	79	li:	72.6	20.3760	52					
65.8	CP49	131	17.037	(1)	nn:*****	78.6	20.9848	71	np:	51.1	18.6609	60					
67.9	TG69	131	23.518	(3)	ee:*****	82.3	21.2626	26	ef:	77.7	20.9137	44	eg:	63.0	19.3974	25	
71.6	GP22	131	4.889	(1)	li:	75.0	20.5506	52	li:	60.1	19.5056	79			42.0	18.1002	36
Linkage group (VI)																	
map	locus	inf	k*	(df)	class:	rank	mean	nr	class:	rank	mean	nr	class:	rank	mean	nr	
0.0	GP164-2	131	0.289	(1)	nn:	67.9	20.1662	61	np:	64.3	19.7062	70					
12.1	CP18	131	0.392	(1)	nn:	63.9	19.6907	65	np:	68.1	20.1467	66					
14.0	So24	131	0.210	(1)	nn:	64.4	19.7338	64	np:	67.5	20.0986	67					
33.0	GP89	131	0.002	(1)	nn:	66.2	19.8429	64	np:	65.8	19.9944	67					
38.4	GP30	131	0.017	(1)	nn:	65.6	19.8794	68	np:	66.5	19.9647	63					
42.6	GP24	131	0.450	(3)	ee:	65.2	19.8414	34	ef:	65.0	19.8420	34	eg:	69.8	20.1560	32	
46.3	GP211	131	0.314	(1)	nn:	64.2	19.7952	69	np:	68.0	20.0598	62			64.0	19.8499	31
72.0	GP76	131	0.011	(1)	nn:	65.6	19.8219	59	np:	66.3	20.0011	72					
Linkage group (VII)																	
map	locus	inf	k*	(df)	class:	rank	mean	nr	class:	rank	mean	nr	class:	rank	mean	nr	
0.0	CP52	131	1.401	(1)	nn:	61.8	19.5883	61	np:	69.7	20.2098	70					
0.8	CP43	131	7.045	(3)	ee:	62.8	19.6031	30	ef:	61.7	19.6323	30	eg:	79.1	20.8606	39	
4.1	GP121	131	1.891	(1)	nn:	70.3	20.2503	70	np:	61.1	19.5419	61			57.0	19.3420	32
8.1	GP179A1	131	3.280	(1)	nn:	59.6	19.3980	61	np:	71.6	20.3756	70					
11.9	GP193	131	2.743	(1)	nn:	60.0	19.4134	60	np:	71.0	20.3489	71					
21.4	GP27	131	0.004	(1)	li:	66.2	19.8118	70	li:	65.8	20.0450	61					
31.9	CP56	131	0.828	(1)	nn:	62.3	19.5985	53	np:	68.5	20.1391	78					
41.3	CP51-2	131	0.680	(2)	hh:	66.2	19.8434	38	hk:	68.4	20.0910	59	kk:	61.7	19.7105	34	
51.7	GP219-2	131	1.371	(1)	li:	61.8	19.5481	60	li:	69.6	20.2350	71					
52.6	TG20	131	0.193	(1)	nn:	67.4	20.0028	66	np:	64.5	19.8367	65					
58.1	GP219-1	131	0.080	(1)	nn:	65.1	19.7997	65	np:	66.9	20.0393	66					

Linkage group (VIII)												
map	locus	inf	k*	(df)	class:	rank	mean	nr	class:	rank	mean	nr
0.0	GP128-2	131	0.020	(1)	nn:	66.5	19.9292	67	np:	65.5	19.9112	64
5.8	CP112-1	131	0.080	(1)	nn:	67.0	19.9453	63	np:	65.1	19.8973	68
14.2	GP189	131	2.522	(1)	nn:	71.0	20.3281	69	np:	60.4	19.4667	62
15.9	CT92	131	3.016	(1)	nn:	71.5	20.3791	68	np:	60.0	19.4253	63
20.8	GP74	131	0.592	(2)	hh:	66.7	19.8803	34	hk:	64.0	19.8026	71
27.0	GP171	131	3.200	(1)	li:	60.2	19.4016	67	lim:	72.1	20.4635	64
31.1	TG349	131	4.940	(1)	nn:	73.7	20.5446	63	np:	58.9	19.3421	68
41.8	GP92	131	5.282	(1)	nn:	74.8	20.6169	56	np:	59.4	19.4003	75
44.4	TG302	131	3.863	(3)	ac:	59.1	19.3673	37	ad:	67.0	20.0331	30
74.0	GP173	131	0.113	(1)	li:	67.1	19.9508	64	lim:	64.9	19.8913	67
85.5	TG294	131	0.504	(1)	li:	68.2	20.0114	69	lim:	63.5	19.8192	62
Linkage group (IX)												
map	locus	inf	k*	(df)	class:	rank	mean	nr	class:	rank	mean	nr
0.0	CP44	131	0.369	(2)	hh:	66.0	19.9044	31	hk:	67.3	20.0341	77
3.4	GP97	131	0.186	(1)	nn:	67.4	20.0246	69	np:	64.5	19.8045	62
5.8	CP20	131	0.559	(1)	li:	68.3	20.0987	70	lim:	63.3	19.7158	61
18.5	Soll6	131	0.240	(1)	nn:	67.7	20.1537	64	np:	64.4	19.6976	67
19.2	Soll6-1	131	0.368	(2)	hh:	66.0	19.8877	41	hk:	64.1	19.6587	55
24.3	StVel1	131	0.067	(1)	li:	67.0	19.9529	58	lim:	65.2	19.8946	73
36.8	GP35	131	0.424	(1)	nn:	68.1	20.1875	66	np:	63.8	19.6492	65
47.1	GP190	131	0.040	(1)	li:	65.2	19.8029	53	lim:	66.5	20.0002	78
51.3	CP135	131	0.188	(1)	nn:	67.4	19.9326	68	np:	64.5	19.9072	63
55.7	CP67	131	0.584	(1)	nn:	68.5	20.0534	66	np:	63.4	19.7854	65
68.5	GP94	131	2.043	(1)	li:	70.0	20.2845	76	lim:	60.4	19.4174	55
Linkage group (X-A)												
map	locus	inf	k*	(df)	class:	rank	mean	nr	class:	rank	mean	nr
0.0	CP47-1	37	0.000	(0)	hh:	19.0	19.8084	37	hk:	—	—	0
0.7	TG303	131	1.885	(1)	nn:	70.7	20.3395	63	np:	61.6	19.5321	68
9.3	CP59	131	2.618	(1)	nn:	71.3	20.4582	66	np:	60.6	19.3744	65
25.3	GP218	131	1.186	(1)	nn:	70.1	20.3688	58	np:	62.8	19.5641	73
44.0	P5C	131	0.371	(1)	nn:	67.6	20.1607	79	np:	63.5	19.5554	52
Linkage group (X-B)												
map	locus	inf	k*	(df)	class:	rank	mean	nr	class:	rank	mean	nr
0.0	GP232-1	131	0.025	(1)	li:	66.7	19.9810	49	lim:	65.6	19.8842	82
19.1	TG63	131	0.871	(1)	li:	68.8	20.1178	71	lim:	62.6	19.6868	60
21.2	CP105	131	0.689	(1)	li:	68.6	20.1027	69	lim:	63.1	19.7175	62
22.0	GP87	131	0.892	(1)	li:	69.0	20.1292	68	lim:	62.7	19.6951	63
40.7	TG420	131	0.970	(1)	li:	69.2	20.1948	66	lim:	62.7	19.6418	65

Linkage group (XI)												
map	locus	inf	k*	(df)	class:	rank	mean	nr	class:	rank	mean	nr
0.0	TG105-1	131	2.674	(2)	-	71.9	20.3805	33	hh:	69.6	20.1012	42
15.0	So101	131	1.036	(1)	-	62.3	19.6211	59	lm:	69.1	20.1656	72
15.6	GP185	131	1.919	(3)	-	60.6	19.5515	29	ef:	65.4	19.9156	42
29.9	GP38	131	4.972	(1)	**	57.8	19.2380	59	lm:	72.7	20.4796	72
36.9	CP117-1	131	0.157	(1)	-	67.2	20.0453	69	np:	64.6	19.7814	62
37.9	GP232	37	0.000	(0)	-	19.0	20.9015	37	hk:	—	—	0
46.4	CP117	131	7.257	(1)	***	73.7	20.5172	75	lm:	55.7	19.1211	56
50.9	GP198-3	131	0.060	(1)	-	65.1	19.8040	56	np:	66.7	20.0073	75
60.9	GP255-3	131	1.621	(1)	-	71.7	20.3996	46	np:	62.9	19.6611	85
67.0	CP58	131	0.007	(1)	-	65.8	19.8670	74	np:	66.3	19.9898	57
74.1	TG194	131	7.858	(1)	***	74.9	20.6855	68	lm:	56.3	19.0946	63
Linkage group (XII-B)												
map	locus	inf	k*	(df)	class:	rank	mean	nr	class:	rank	mean	nr
0.0	GP204	131	2.070	(1)	-	70.3	20.2999	72	np:	60.7	19.4573	59
20.4	TG263	31	0.000	(0)	-	16.0	20.3025	31	hk:	—	—	0
24.2	TG68	131	11.702	(3)	***	48.6	18.2907	31	ef:	70.8	20.4987	31
28.7	GP99	131	4.034	(1)	**	59.1	19.3337	63	np:	72.4	20.4640	68
29.2	CP48	131	2.996	(1)	*	71.4	20.3772	69	np:	59.9	19.4121	62
31.5	CP134-1	131	7.898	(2)	**	74.8	20.6527	37	hk:	68.0	20.1570	68
33.1	TG360	131	1.083	(1)	-	69.2	20.1838	70	np:	62.3	19.6182	61
Linkage group (XIII-B)												
map	locus	inf	k*	(df)	class:	rank	mean	nr	class:	rank	mean	nr
0.0	So122	131	1.059	(1)	-	69.5	20.2190	64	lm:	62.7	19.6352	67
0.8	GP268	131	0.904	(1)	-	62.9	19.6468	66	lm:	69.2	20.1983	65
1.5	TG602	131	0.474	(1)	-	63.8	19.7233	67	lm:	68.3	20.1268	64
22.5	CP112	131	2.507	(1)	-	71.0	20.2742	69	lm:	60.5	19.5266	62
Linkage group (I)												
map	locus	inf	k*	(df)	class:	rank	mean	nr	class:	rank	mean	nr
0.0	CP108	131	1.889	(1)	-	64.8	17.4222	123	np:	83.9	18.5368	8
3.7	GP232-2	131	1.421	(1)	-	79.8	18.3612	10	np:	64.9	17.4182	121
11.7	CP90	131	9.318	(1)	****	61.7	17.1883	111	np:	89.8	19.1659	20
19.1	CP11	131	3.057	(1)	*	78.6	18.3986	23	np:	63.3	17.2968	108
21.2	CP51	131	4.962	(1)	**	80.8	18.4898	26	np:	62.3	17.2427	105

A.1.3 Landisville 2002 data-set

77.9	GP165	131	3.607	(2)	-	hh:	58.0	17.0396	23	hk:	63.5	17.2405	69	kk:	75.2	18.1977	39				
Linkage group (V)		map	locus	inf	k*	(df)	class:	rank	mean	nr	class:	rank	mean	nr	class:	rank	mean	nr			
0.0	GP21A-8	131	1.430	(1)	-	li:	61.6	17.1542	59	li:	69.6	17.7655	72								
10.8	GP179A	131	0.000	(1)	-	li:	66.0	17.4180	65	li:	66.0	17.5614	66								
38.0	GP248	131	0.914	(1)	-	li:	69.8	17.6618	54	li:	63.3	17.3699	77								
39.5	GP34	131	1.400	(1)	-	li:	70.7	17.7094	54	li:	62.7	17.3365	77								
40.9	GP188	131	0.736	(1)	-	li:	69.4	17.6300	54	li:	63.6	17.3922	77								
57.9	CP113	131	0.989	(2)	-	hh:	62.8	17.3297	46	hk:	65.6	17.4358	55	kk:	71.7	17.8361	30				
59.3	CP14-1	131	3.056	(1)	*	li:	73.5	17.9825	49	li:	61.5	17.1961	82								
62.3	Sol22-1	131	2.829	(1)	*	li:	61.6	17.2195	81	li:	73.1	17.9288	50								
64.4	GP284	131	4.373	(1)	**	li:	60.4	17.1476	79	li:	74.5	18.0108	52								
65.8	CP49	131	0.199	(1)	-	nn:	67.4	17.6198	71	np:	64.4	17.3370	60								
67.9	TG69	131	6.597	(3)	*	ee:	74.3	18.0513	26	ef:	63.6	17.3789	44	eg:	77.3	18.0918	25	fg:	55.1	16.8034	36
71.6	GP22	131	5.802	(1)	**	li:	75.8	18.0851	52	li:	59.5	17.0987	79								
Linkage group (VI)		map	locus	inf	k*	(df)	class:	rank	mean	nr	class:	rank	mean	nr	class:	rank	mean	nr			
0.0	GP164-2	131	0.133	(1)	-	nn:	64.7	17.4790	61	np:	67.1	17.5000	70								
12.1	CP18	131	1.389	(1)	-	nn:	69.9	17.6446	65	np:	62.1	17.3382	66								
14.0	Sol24	131	1.461	(1)	-	nn:	70.1	17.6663	64	np:	62.1	17.3220	67								
33.0	GP89	131	1.216	(1)	-	nn:	62.3	17.1953	64	np:	69.6	17.7719	67								
38.4	GP30	131	1.853	(1)	-	nn:	61.7	17.1853	68	np:	70.7	17.8194	63								
42.6	GP24	131	2.595	(3)	-	ee:	60.3	17.0543	34	ef:	64.4	17.3866	34	eg:	74.8	18.0136	32	fg:	64.9	17.5419	31
46.3	GP211	131	0.658	(1)	-	nn:	63.4	17.2969	69	np:	68.8	17.7054	62								
72.0	GP76	131	0.181	(1)	-	nn:	67.6	17.5352	59	np:	64.7	17.4534	72								
Linkage group (VII)		map	locus	inf	k*	(df)	class:	rank	mean	nr	class:	rank	mean	nr	class:	rank	mean	nr			
0.0	CP52	131	3.711	(1)	*	nn:	59.2	17.0377	61	np:	72.0	17.8846	70								
0.8	CP43	131	5.328	(3)	-	ee:	56.7	16.7935	30	ef:	61.5	17.2749	30	eg:	76.7	18.0765	39	fg:	65.9	17.6307	32
4.1	GP121	131	2.653	(1)	-	nn:	71.0	17.8410	70	np:	60.2	17.0878	61								
8.1	GP179A1	131	3.882	(1)	**	nn:	59.0	16.9715	61	np:	72.1	17.9422	70								
11.9	GP193	131	2.743	(1)	*	nn:	60.0	17.0540	60	np:	71.0	17.8588	71								
21.4	GP27	131	0.121	(1)	-	li:	64.9	17.3204	70	li:	67.2	17.6851	61								
31.9	CP56	131	1.700	(1)	-	nn:	60.8	17.0655	53	np:	69.6	17.7788	78								
41.3	CP51-2	131	3.290	(2)	-	hh:	64.4	17.3570	38	hk:	72.0	17.9395	59	kk:	57.4	16.8596	34				
51.7	GP219-2	131	0.845	(1)	-	li:	69.3	17.7374	60	li:	63.2	17.2813	71								
52.6	TG20	131	0.553	(1)	-	nn:	68.4	17.6423	66	np:	63.5	17.3358	65								
58.1	GP219-1	131	0.229	(1)	-	nn:	67.6	17.5967	65	np:	64.4	17.3853	66								

Linkage group (VIII)												
map	locus	inf	k*	(df)	class:	rank	mean	nr	class:	rank	mean	nr
0.0	GP128-2	131	0.001	(1)	nn:	65.9	17.4356	67	np:	66.1	17.5474	64
5.8	CP112-1	131	0.013	(1)	nn:	65.6	17.4069	63	np:	66.4	17.5675	68
14.2	GP189	131	0.596	(1)	nn:	68.4	17.6392	69	np:	63.3	17.3245	62
15.9	CT92	131	0.348	(1)	nn:	67.9	17.6084	68	np:	64.0	17.3627	63
20.8	GP74	131	1.182	(2)	hh:	63.8	17.3386	34	hk:	64.4	17.4029	71
27.0	GP171	131	2.401	(1)	li:	61.0	17.2081	67	lim:	71.3	17.7856	64
31.1	TG349	131	0.390	(1)	nn:	68.2	17.6557	63	np:	64.0	17.3369	68
41.8	GP92	131	0.327	(1)	nn:	68.2	17.7038	56	np:	64.4	17.3307	75
44.4	TG302	131	4.268	(3)	ac:	56.5	16.9010	37	ad:	66.9	17.6414	30
74.0	GP173	131	1.384	(1)	li:	62.0	17.1775	64	lim:	69.8	17.7890	67
85.5	TG294	131	0.291	(1)	li:	67.7	17.5020	69	lim:	64.1	17.4772	62
Linkage group (IX)												
map	locus	inf	k*	(df)	class:	rank	mean	nr	class:	rank	mean	nr
0.0	CP44	131	1.335	(2)	hh:	72.8	17.9955	31	hk:	63.5	17.3627	77
3.4	GP97	131	1.453	(1)	nn:	69.8	17.7142	69	np:	61.8	17.2410	62
5.8	CP20	131	1.017	(1)	li:	69.1	17.7330	70	lim:	62.4	17.2117	61
18.5	Soll16	131	2.538	(1)	nn:	71.4	17.8998	64	np:	60.8	17.0990	67
19.2	Soll16-1	131	0.086	(2)	hh:	64.6	17.3816	41	hk:	66.6	17.5139	55
24.3	StVe1	131	0.624	(1)	li:	63.1	17.1725	56	lim:	68.3	17.7427	73
36.8	GP35	131	2.854	(1)	nn:	71.6	17.9174	68	np:	60.4	17.0564	65
47.1	GP190	131	2.210	(1)	li:	60.0	17.1216	53	lim:	70.1	17.7407	78
51.3	CP135	131	0.474	(1)	nn:	63.8	17.3161	68	np:	68.4	17.6781	63
55.7	CP67	131	0.002	(1)	nn:	65.9	17.4465	66	np:	66.1	17.5346	65
68.5	GP94	131	0.467	(1)	li:	64.1	17.4083	76	lim:	68.7	17.6035	55
Linkage group (X-A)												
map	locus	inf	k*	(df)	class:	rank	mean	nr	class:	rank	mean	nr
0.0	CP47-1	37	0.000	(0)	hh:	19.0	17.7703	37	hk:	—	—	0
0.7	TG303	131	0.250	(1)	nn:	67.7	17.5879	63	np:	64.4	17.3998	68
9.3	CP59	131	0.020	(1)	nn:	65.5	17.5105	66	np:	66.5	17.4696	65
25.3	GP218	131	0.009	(1)	nn:	65.6	17.6042	58	np:	66.3	17.3997	73
44.0	PSC	131	1.028	(1)	nn:	63.3	17.4160	79	np:	70.1	17.6030	52
Linkage group (X-B)												
map	locus	inf	k*	(df)	class:	rank	mean	nr	class:	rank	mean	nr
0.0	GP232-1	131	1.896	(1)	li:	71.9	17.8913	49	lim:	62.5	17.2506	82
19.1	TG63	131	1.632	(1)	li:	69.9	17.7462	71	lim:	61.4	17.1874	60
21.2	CP105	131	2.016	(1)	li:	70.5	17.7638	69	lim:	61.0	17.1635	62
22.0	GP87	131	2.827	(1)	li:	71.4	17.8417	68	lim:	60.2	17.1109	63
40.7	TG420	131	2.435	(1)	li:	71.1	17.8389	66	lim:	60.8	17.1362	65

Linkage group (XI)												
map	locus	inf	k*	(df)	class:	rank	mean	nr	class:	rank	mean	nr
0.0	TG105-1	131	1.318	(2)	-	67.1	17.6060	33	hh:	70.6	17.7073	42
15.0	Sol01	131	0.059	(1)	-	65.1	17.4258	59	lm:	66.7	17.5430	72
15.6	GP185	131	1.316	(3)	-	60.2	17.1262	29	ef:	65.8	17.4579	42
29.9	GP38	131	0.725	(1)	-	62.9	17.3115	59	lm:	68.6	17.6367	72
36.9	CP117-1	131	1.404	(1)	-	69.7	17.7391	69	np:	61.9	17.2132	62
37.9	GP232	37	0.000	(0)	-	19.0	18.2230	37	hk:	—	—	0
46.4	CP117	131	1.833	(1)	-	69.9	17.7219	75	lm:	60.8	17.1799	56
50.9	GP198-3	131	0.175	(1)	-	64.4	17.3743	56	np:	67.2	17.5768	75
60.9	GP255-3	131	1.442	(1)	-	71.4	17.8785	46	np:	63.1	17.2801	85
67.0	CP58	131	0.038	(1)	-	66.6	17.4608	74	np:	65.3	17.5284	57
74.1	TG194	131	0.003	(1)	-	66.2	17.5723	68	lm:	65.8	17.4016	63
Linkage group (XII-A)												
map	locus	inf	k*	(df)	class:	rank	mean	nr	class:	rank	mean	nr
0.0	GP204	131	0.655	(1)	-	63.6	17.3251	72	np:	69.0	17.6917	59
20.4	TG263	31	0.000	(0)	-	16.0	17.9240	31	hk:	—	—	0
24.2	TG68	131	4.143	(3)	-	66.2	17.5290	31	ef:	72.7	17.9910	31
28.7	GP99	131	1.617	(1)	-	70.4	17.8184	63	np:	61.9	17.1862	68
29.2	CP48	131	1.631	(1)	-	62.0	17.1881	69	np:	70.5	17.8265	62
31.5	CP134-1	131	0.319	(2)	-	68.9	17.6540	37	hk:	65.2	17.4293	68
33.1	TG360	131	2.173	(1)	-	61.4	17.1689	70	np:	71.2	17.8590	61
Linkage group (XII-B)												
map	locus	inf	k*	(df)	class:	rank	mean	nr	class:	rank	mean	nr
0.0	Sol22	131	0.264	(1)	-	64.3	17.4148	64	lm:	67.7	17.5623	67
0.8	GP268	131	0.580	(1)	-	68.5	17.6128	66	lm:	63.5	17.3658	65
1.5	TG602	131	0.474	(1)	-	68.2	17.5993	67	lm:	63.7	17.3760	64
22.5	CP112	131	2.321	(1)	-	70.8	17.7709	69	lm:	60.7	17.1778	62
Linkage group (I)												
map	locus	inf	k*	(df)	class:	rank	mean	nr	class:	rank	mean	nr
0.0	CP108	131	0.311	(1)	-	65.5	20.5263	123	np:	73.2	20.7608	8
3.7	GP232-2	131	1.064	(1)	-	77.9	21.3462	10	np:	65.0	20.4740	121
11.7	CP90	131	6.552	(1)	**	62.4	20.2914	111	np:	86.0	21.9237	20
19.1	CP11	131	2.269	(1)	-	76.8	21.2478	23	np:	63.7	20.3900	108

A.1.4 Locations averaged data-set

21.2	CP51	131	2.115	(1)	-	nn:	75.7	21.1786	26	np:	63.6	20.3826	105			
32.7	TG59-1	131	2.512	(1)	*	nn:	74.4	21.1277	37	np:	62.7	20.3095	94			
56.5	GP167-2	131	0.955	(1)	-	nn:	69.9	20.8384	54	np:	63.3	20.3317	77			
71.5	TG53	131	0.280	(1)	-	nn:	67.8	20.6751	64	np:	64.3	20.4121	67			
73.7	CP13	131	0.001	(1)	-	nn:	66.1	20.5782	66	np:	65.9	20.5024	65			
77.5	GP198-2	131	0.018	(1)	-	nn:	66.4	20.4954	66	np:	65.6	20.5865	65			
Linkage group (II)																
map	locus	inf	k*	(df)	class:	rank	mean	nr	class:	rank	mean	nr	class:	rank	mean	nr
0.0	GP23	131	2.677	(1)	-	li:	61.8	20.3083	82	lim:	73.0	20.9292	49			
3.4	So/20	131	3.518	(1)	*	li:	61.4	20.2899	85	lim:	74.5	21.0038	46			
7.3	GP128	131	1.868	(1)	-	li:	62.7	20.3585	86	lim:	72.3	20.8886	45			
14.6	GP131	131	2.311	(1)	-	li:	73.7	21.0151	39	lim:	62.7	20.3394	92			
17.7	GP33-1	131	4.083	(1)	**	nn:	74.8	21.1481	48	np:	60.9	20.1892	83			
24.9	GP288-3	131	1.023	(2)	-	hh:	82.8	21.9809	5	hk:	65.5	20.4414	71			
28.6	GP209	131	0.004	(1)	-	li:	65.9	20.5331	91	lim:	66.3	20.5577	40			
44.0	CP157	131	0.419	(1)	-	nn:	64.2	20.4268	78	np:	68.6	20.7080	53			
54.1	PFC	39	0.000	(0)	-	hh:	20.0	20.3340	39	hk:	—	—	0			
58.1	GP216	131	0.210	(1)	-	li:	64.9	20.5080	87	lim:	68.1	20.6050	44			
60.5	GP504	131	1.498	(1)	-	nn:	62.7	20.3380	78	np:	70.9	20.8387	53			
Linkage group (III)																
map	locus	inf	k*	(df)	class:	rank	mean	nr	class:	rank	mean	nr	class:	rank	mean	nr
0.0	CP15	131	13.829	(1)	*****	nn:	55.8	19.8940	78	np:	81.0	21.4922	53			
2.3	GP198-1	131	15.528	(1)	*****	nn:	54.7	19.8149	75	np:	81.1	21.5124	56			
2.8	GP167-1	131	14.269	(1)	*****	nn:	55.3	19.8511	76	np:	80.7	21.4933	55			
15.0	GP1	131	6.185	(1)	**	nn:	74.8	21.1134	61	np:	58.3	20.0414	70			
19.2	CP61	131	3.417	(1)	*	nn:	60.2	20.1427	69	np:	72.5	20.9834	62			
20.3	CP133	131	2.642	(1)	-	nn:	60.7	20.1699	67	np:	71.5	20.9287	64			
20.3	CP6	131	2.642	(1)	-	nn:	60.7	20.1699	67	np:	71.5	20.9287	64			
32.5	GP276	131	8.037	(3)	**	ee:	67.1	20.5876	32	ef:	51.1	19.5705	34			
34.7	GP226	131	3.408	(1)	*	nn:	59.9	20.1437	66	np:	72.2	20.9436	65			
57.5	GP198-4	131	0.564	(1)	-	nn:	68.6	20.7330	63	np:	63.6	20.3623	68			
69.2	TG28	131	2.672	(1)	-	nn:	71.5	20.9534	64	np:	60.7	20.1462	67			
Linkage group (IV)																
map	locus	inf	k*	(df)	class:	rank	mean	nr	class:	rank	mean	nr	class:	rank	mean	nr
0.0	GP180	131	3.868	(2)	-	hh:	57.4	19.8983	39	hk:	66.9	20.5646	62			
12.2	TG123	131	1.212	(3)	-	ee:	71.8	21.0665	33	ef:	66.0	20.5705	33			
19.0	CP54	131	2.177	(2)	-	hh:	61.7	20.1713	46	hk:	65.3	20.4811	59			
27.2	GP99-2	131	2.866	(1)	*	nn:	72.6	21.0522	55	np:	61.2	20.1703	76			
37.2	GP161-2	131	2.509	(1)	-	nn:	71.1	20.9053	67	np:	60.6	20.1587	64			
51.4	TG62	131	1.369	(1)	-	nn:	62.0	20.2035	63	np:	69.7	20.8529	68			

map	locus	inf	k*	(df)	class:	rank	mean	nr	class:	rank	mean	nr	class:	rank	mean	nr
51.6	Sol21	131	0.000	(1)	-	66.0	20.5815	61	lm:	66.0	20.5049	70				
66.8	GP83	131	3.695	(1)	*	72.0	21.0130	69	np:	59.3	20.0149	62				
77.9	GP165	131	6.145	(2)	**	64.7	20.2372	23	hk:	59.5	20.1103	69	kk:	78.3	21.4807	39
Linkage group (V)																
map	locus	inf	k*	(df)	class:	rank	mean	nr	class:	rank	mean	nr	class:	rank	mean	nr
0.0	GP21A-8	131	0.438	(1)	-	63.6	20.3683	59	lm:	68.0	20.6818	72				
10.8	GP179A	131	0.087	(1)	-	67.0	20.5925	65	lm:	65.0	20.4894	66				
38.0	GP248	131	2.061	(1)	-	71.7	20.8420	54	lm:	62.0	20.3292	77				
39.5	GP34	131	3.258	(1)	*	73.1	20.9271	54	lm:	61.0	20.2695	77				
40.9	GP188	131	2.197	(1)	-	71.9	20.8503	54	lm:	61.9	20.3234	77				
57.9	CP113	131	2.190	(2)	-	70.3	20.9266	46	hk:	67.1	20.5799	55	kk:	57.4	19.8765	30
59.3	CP14-1	131	7.248	(1)	***	77.6	21.2215	49	lm:	59.1	20.1337	82				
62.3	Sol22-1	131	5.930	(1)	**	59.7	20.1888	81	lm:	76.3	21.1104	50				
64.4	GP284	131	7.782	(1)	***	58.5	20.1050	79	lm:	77.4	21.2023	52				
65.8	CP49	131	10.338	(1)	****	75.8	21.2269	71	np:	54.4	19.7284	60				
67.9	TG69	131	21.379	(3)	*****	85.0	21.7279	26	ef:	71.1	20.9736	44	eg:	71.0	20.6833	25
71.6	GP22	131	11.504	(1)	*****	79.9	21.3483	52	lm:	56.9	20.0089	79				
Linkage group (VI)																
map	locus	inf	k*	(df)	class:	rank	mean	nr	class:	rank	mean	nr	class:	rank	mean	nr
0.0	GP164-2	131	0.161	(1)	-	67.4	20.6612	61	np:	64.8	20.4354	70				
12.1	CP18	131	0.001	(1)	-	66.1	20.5183	65	np:	65.9	20.5625	66				
14.0	Sol24	131	0.023	(1)	-	66.5	20.5464	64	np:	65.5	20.5350	67				
33.0	GP89	131	0.563	(1)	-	63.5	20.3124	64	np:	68.4	20.7585	67				
38.4	GP30	131	0.711	(1)	-	63.3	20.3299	68	np:	68.9	20.7680	63				
42.6	GP24	131	2.609	(3)	-	63.5	20.3692	34	ef:	62.1	20.2352	34	eg:	75.4	21.1600	32
46.3	GP211	131	1.095	(1)	-	62.7	20.2987	69	np:	69.7	20.8097	62				
72.0	GP76	131	0.025	(1)	-	65.4	20.5001	59	np:	66.5	20.5738	72				
Linkage group (VII)																
map	locus	inf	k*	(df)	class:	rank	mean	nr	class:	rank	mean	nr	class:	rank	mean	nr
0.0	CP52	131	5.217	(1)	**	57.9	20.0099	61	np:	73.1	21.0030	70				
0.8	CP43	131	8.210	(3)	**	55.6	19.9520	30	ef:	60.4	20.0729	30	eg:	79.9	21.4529	39
4.1	GP121	131	6.301	(1)	***	73.8	21.0401	70	np:	57.1	19.9673	61				
8.1	GP179A1	131	7.211	(1)	***	56.5	19.9451	61	np:	74.3	21.0595	70				
11.9	GP193	131	6.692	(1)	***	56.7	19.9651	60	np:	73.9	21.0269	71				
21.4	GP27	131	0.140	(1)	-	64.8	20.4487	70	lm:	67.3	20.6461	61				
31.9	CP56	131	2.978	(1)	*	59.1	20.0862	53	np:	70.7	20.8493	78				
41.3	CP51-2	131	2.682	(2)	-	67.6	20.5512	38	hk:	70.1	20.8514	59	kk:	57.0	19.9893	34
51.7	GP219-2	131	0.114	(1)	-	64.8	20.4605	60	lm:	67.0	20.6082	71				
52.6	TG20	131	1.673	(1)	-	70.3	20.7515	66	np:	61.7	20.3264	65				
58.1	GP219-1	131	0.509	(1)	-	68.4	20.6274	65	np:	63.7	20.4551	66				

Linkage group (VIII)												
map	locus	inf	k*	(df)	class:	rank	mean	nr	class:	rank	mean	nr
0.0	GP128-2	131	0.392	(1)	nn:	64.0	20.4095	67	np:	68.1	20.6778	64
5.8	CP112-1	131	0.026	(1)	nn:	65.4	20.5047	63	np:	66.5	20.5738	68
14.2	GP189	131	1.607	(1)	nn:	70.0	20.8192	69	np:	61.6	20.2304	62
15.9	CT92	131	1.834	(1)	nn:	70.3	20.8353	68	np:	61.3	20.2224	63
20.8	GP74	131	1.358	(2)	hh:	65.5	20.4534	34	hk:	63.5	20.4253	71
27.0	GP171	131	1.833	(1)	li:	61.6	20.2153	67	lim:	70.6	20.8811	64
31.1	TG349	131	3.585	(1)	nn:	72.5	20.9706	63	np:	60.0	20.1422	68
41.8	GP92	131	4.721	(1)	nn:	74.3	21.0837	56	np:	59.8	20.1350	75
44.4	TG302	131	3.760	(3)	ac:	58.7	20.0779	37	ad:	67.8	20.6268	30
74.0	GP173	131	0.001	(1)	li:	65.9	20.5499	64	lim:	66.1	20.5316	67
85.5	TG294	131	0.172	(1)	li:	67.3	20.6750	69	lim:	64.5	20.3909	62
Linkage group (IX)												
map	locus	inf	k*	(df)	class:	rank	mean	nr	class:	rank	mean	nr
0.0	CP44	131	1.296	(2)	hh:	71.4	20.9373	31	hk:	65.7	20.5307	77
3.4	GP97	131	0.735	(1)	nn:	68.7	20.7642	69	np:	63.0	20.2917	62
5.8	CP20	131	2.277	(1)	li:	70.7	20.8035	70	lim:	60.6	20.2389	61
18.5	Soll6	131	1.722	(1)	nn:	70.5	20.9254	64	np:	61.7	20.1730	67
19.2	Soll6-1	131	0.234	(2)	hh:	65.0	20.3905	41	hk:	65.0	20.4377	55
24.3	StVel1	131	0.198	(1)	li:	64.3	20.4103	58	lim:	67.3	20.6441	73
36.8	GP35	131	1.111	(1)	nn:	69.5	20.8582	66	np:	62.5	20.2181	65
47.1	GP190	131	0.317	(1)	li:	63.7	20.3878	53	lim:	67.5	20.6444	78
51.3	CP135	131	0.095	(1)	nn:	67.0	20.5751	68	np:	64.9	20.5033	63
55.7	CP67	131	0.839	(1)	nn:	69.0	20.7584	66	np:	62.9	20.3194	65
68.5	GP94	131	0.273	(1)	li:	67.5	20.6207	76	lim:	64.0	20.4298	55
Linkage group (X-A)												
map	locus	inf	k*	(df)	class:	rank	mean	nr	class:	rank	mean	nr
0.0	CP47-1	37	0.000	(0)	hh:	19.0	20.7035	37	hk:	—	—	0
0.7	TG303	131	0.037	(1)	nn:	65.3	20.6064	63	np:	66.6	20.4796	68
9.3	CP59	131	0.275	(1)	nn:	64.3	20.5299	66	np:	67.8	20.5514	65
25.3	GP218	131	0.219	(1)	nn:	64.3	20.5583	58	np:	67.4	20.5265	73
44.0	P5C	131	0.833	(1)	nn:	63.5	20.4593	79	np:	69.7	20.6641	52
Linkage group (X-B)												
map	locus	inf	k*	(df)	class:	rank	mean	nr	class:	rank	mean	nr
0.0	GP232-1	131	0.160	(1)	li:	67.7	20.6865	49	lim:	65.0	20.4534	82
19.1	TG63	131	2.240	(1)	li:	70.6	20.8012	71	lim:	60.6	20.2322	60
21.2	CP105	131	2.708	(1)	li:	71.2	20.8314	69	lim:	60.2	20.2169	62
22.0	GP87	131	3.672	(1)	li:	72.1	20.8949	68	lim:	59.4	20.1582	63
40.7	TG420	131	4.349	(1)	li:	72.9	20.9740	66	lim:	59.0	20.1005	65

Linkage group (XI)												
map	locus	inf	k*	(df)	class:	rank	mean	nr	class:	rank	mean	nr
0.0	TG105-1	131	3.092	(2)	-	69.4	20.8402	33	hh:	72.2	20.8907	42
15.0	So101	131	2.667	(1)	-	60.0	20.1675	59	li:	70.9	20.8463	72
15.6	GP185	131	2.607	(3)	-	56.9	20.1036	29	ee:	70.1	20.7522	42
29.9	GP38	131	5.096	(1)	**	57.7	19.9624	59	li:	72.8	21.0144	72
36.9	CP117-1	131	0.157	(1)	-	67.2	20.6100	69	nn:	64.6	20.4633	62
37.9	GP232	37	0.000	(0)	-	19.0	21.3069	37	hh:	—	—	0
46.4	CP117	131	6.836	(1)	***	73.5	21.0828	75	li:	56.0	19.8144	56
50.9	GP198-3	131	0.015	(1)	-	65.5	20.4750	56	nn:	66.3	20.5895	75
60.9	GP255-3	131	2.411	(1)	-	73.0	20.9918	46	nn:	62.2	20.2964	85
67.0	CP58	131	0.009	(1)	-	65.7	20.4865	74	nn:	66.4	20.6108	57
74.1	TG194	131	5.585	(1)	**	73.5	21.0388	68	li:	57.9	20.0028	63

Linkage group (XII-A)												
map	locus	inf	k*	(df)	class:	rank	mean	nr	class:	rank	mean	nr
0.0	GP204	131	0.014	(1)	-	66.4	20.5564	72	nn:	65.6	20.5213	59
20.4	TG263	31	0.000	(0)	-	16.0	20.9072	31	hh:	—	—	0
24.2	TG68	131	6.096	(3)	-	56.2	19.9344	31	ee:	72.7	21.0400	31
28.7	GP99	131	0.031	(1)	-	65.4	20.4978	63	nn:	66.6	20.5802	68
29.2	CP48	131	0.014	(1)	-	65.6	20.4889	69	nn:	66.4	20.5981	62
31.5	CP134-1	131	2.636	(2)	-	69.5	20.7660	37	hh:	68.2	20.6694	68
33.1	TG360	131	0.573	(1)	-	63.7	20.3758	70	nn:	68.7	20.7297	61

Linkage group (XII-B)												
map	locus	inf	k*	(df)	class:	rank	mean	nr	class:	rank	mean	nr
0.0	So122	131	0.025	(1)	-	66.5	20.5899	64	li:	65.5	20.4935	67
0.8	GP268	131	0.001	(1)	-	66.1	20.5273	66	li:	65.9	20.5540	65
1.5	TG602	131	0.031	(1)	-	66.6	20.5559	67	li:	65.4	20.5246	64
22.5	CP112	131	4.095	(1)	**	72.4	20.9697	69	li:	58.9	20.0630	62

Linkage group (I)												
map	locus	inf	k*	(df)	class:	rank	mean	nr	class:	rank	mean	nr
0.0	CP108	113	0.461	(1)	-	56.5	20.5210	106	nn:	65.1	20.8401	7
3.7	GP232-2	113	1.288	(1)	-	68.9	21.4730	9	nn:	56.0	20.4601	104
11.7	CP90	113	9.742	(1)	****	53.1	20.2242	97	nn:	80.7	22.4598	16
19.1	CP11	113	7.097	(1)	***	75.3	21.9253	19	nn:	53.3	20.2609	94
21.2	CP51	113	6.905	(1)	***	74.0	21.8248	21	nn:	53.1	20.2477	92

A.1.5 Locations averaged with 19 clones removal data-set

map	locus	inf	k*	(df)	class:	rank	mean	nr	class:	rank	mean	nr	class:	rank	mean	nr					
32.7	TG59-1	113	6.430	(1)	**	nn:	70.0	21.5554	30	np:	52.3	20.1740	83								
56.5	GP167-2	113	1.550	(1)	-	nn:	61.6	20.9519	46	np:	53.8	20.2585	67								
71.5	TG53	113	0.525	(1)	-	nn:	59.3	20.7422	54	np:	54.9	20.3563	59								
73.7	CP13	113	0.016	(1)	-	nn:	56.6	20.5444	58	np:	57.4	20.5369	55								
77.5	GP198-2	113	0.058	(1)	-	nn:	57.7	20.5224	57	np:	56.2	20.5594	56								
Linkage group (II)																					
map	locus	inf	k*	(df)	class:	rank	mean	nr	class:	rank	mean	nr	class:	rank	mean	nr					
0.0	GP23	113	1.384	(1)	-	li:	54.2	20.3679	71	lm:	61.7	20.8330	42								
3.4	SoI20	113	1.841	(1)	-	li:	53.9	20.3462	73	lm:	62.6	20.8958	40								
7.3	GP128	113	0.685	(1)	-	li:	55.1	20.4251	74	lm:	60.5	20.7601	39								
14.6	GP131	113	0.958	(1)	-	li:	61.7	20.8863	33	lm:	55.1	20.3982	80								
17.7	GP33-1	113	5.907	(1)	**	nn:	66.6	21.3130	43	np:	51.1	20.0664	70								
24.9	GP288-3	113	1.118	(2)	-	hh:	71.4	21.9809	5	hk:	55.4	20.3451	59	kk:	57.5	20.6294	49				
28.6	GP209	113	0.098	(1)	-	li:	57.6	20.5885	81	lm:	55.5	20.4198	32								
44.0	CP157	113	0.758	(1)	-	nn:	54.8	20.3619	67	np:	60.2	20.8013	46								
54.1	PFC	36	0.000	(0)	-	hh:	18.5	20.4027	36	hk:	—	—	0	kk:	—	0	(?)				
58.1	GP216	113	0.079	(1)	-	li:	57.5	20.6117	81	lm:	55.6	20.3611	32								
60.5	GP504	113	1.291	(1)	-	nn:	54.2	20.3284	69	np:	61.4	20.8737	44								
Linkage group (III)																					
map	locus	inf	k*	(df)	class:	rank	mean	nr	class:	rank	mean	nr	class:	rank	mean	nr					
0.0	CP15	113	11.893	(1)	*****	nn:	48.0	19.8579	66	np:	69.6	21.4997	47								
2.3	GP198-1	113	13.602	(1)	*****	nn:	46.9	19.7621	63	np:	69.8	21.5219	50								
2.8	GP167-1	113	12.449	(1)	*****	nn:	47.5	19.8058	64	np:	69.4	21.5006	49								
15.0	GP1	113	6.614	(1)	**	nn:	65.4	21.1834	53	np:	49.5	19.9730	60								
19.2	CP61	113	3.485	(1)	*	nn:	51.4	20.0884	58	np:	62.9	21.0178	55								
20.3	CP133	113	2.831	(1)	*	nn:	51.9	20.1204	57	np:	62.2	20.9686	56								
20.3	CP6	113	2.831	(1)	*	nn:	51.9	20.1204	57	np:	62.2	20.9686	56								
32.5	GP276	113	6.589	(3)	*	ee:	58.1	20.5970	27	ef:	44.9	19.5928	30	eg:	66.0	21.2042	32	fg:	58.8	20.7778	24
34.7	GP226	113	2.870	(1)	*	nn:	51.7	20.1286	56	np:	62.2	20.9456	57								
57.5	GP198-4	113	0.647	(1)	-	nn:	59.5	20.7685	55	np:	54.6	20.3248	58								
69.2	TG28	113	2.045	(1)	-	nn:	61.4	20.9513	56	np:	52.6	20.1374	57								
Linkage group (IV)																					
map	locus	inf	k*	(df)	class:	rank	mean	nr	class:	rank	mean	nr	class:	rank	mean	nr					
0.0	GP180	113	4.392	(2)	-	hh:	47.9	19.7463	34	hk:	58.8	20.6424	50	kk:	64.7	21.2969	29				
12.2	TG123	113	2.603	(3)	-	ee:	63.1	21.1514	30	ef:	59.2	20.7459	29	eg:	56.0	20.3984	21	fg:	50.2	19.8959	33
19.0	CP54	113	2.766	(2)	-	hh:	50.9	19.9791	38	hk:	57.8	20.5826	51	kk:	65.0	21.3411	24				
27.2	GP99-2	113	4.302	(1)	**	nn:	64.3	21.1879	49	np:	51.4	20.0452	64								
37.2	GP161-2	113	2.622	(1)	-	nn:	61.9	20.9584	57	np:	52.0	20.1157	56								
51.4	TG62	113	1.625	(1)	-	nn:	53.0	20.1593	56	np:	60.9	20.9155	57								
51.6	SoI21	113	0.001	(1)	-	li:	56.9	20.5763	52	lm:	57.1	20.5104	61								
66.8	GP83	113	2.697	(1)	-	nn:	62.0	21.0254	57	np:	51.9	20.0474	56								

77.9	GP165	113	5.099	(2)	*	hh:	54.2	20.1151	21	hk:	52.0	20.1258	59	kk:	67.8	21.5536	33
Linkage group (V)		map	locus	inf	k*	(df)	class:	rank	nr	class:	rank	mean	nr	class:	rank	mean	nr
0.0	GP21A-8	113	0.316	(1)	-	ll:	55.0	20.3650	49	lm:	58.5	20.6753	64				
10.8	GP179A	113	0.233	(1)	-	ll:	58.6	20.6329	54	lm:	55.6	20.4565	59				
38.0	GP248	113	3.263	(1)	*	ll:	63.5	20.9714	48	lm:	52.2	20.2227	65				
39.5	GP34	113	4.821	(1)	**	ll:	64.9	21.0672	48	lm:	51.2	20.1520	65				
40.9	GP188	113	3.433	(1)	*	ll:	63.6	20.9807	48	lm:	52.1	20.2158	65				
57.9	CP113	113	0.953	(2)	-	hh:	58.8	20.8285	36	hk:	58.5	20.6194	52	kk:	51.4	19.9629	25
59.3	CP14-1	113	6.531	(1)	**	ll:	66.9	21.2349	44	lm:	50.7	20.0981	69				
62.3	So122-1	113	5.033	(1)	**	ll:	51.5	20.1789	69	lm:	65.7	21.1082	44				
64.4	GP284	113	7.056	(1)	***	ll:	50.1	20.0621	66	lm:	66.7	21.2129	47				
65.8	CP49	113	8.227	(1)	****	nn:	65.5	21.2597	59	np:	47.8	19.7553	54				
67.9	TG69	113	17.710	(3)	*****	ee:	73.1	21.7530	23	ef:	61.1	20.9902	35	eg:	62.0	20.7259	22
71.6	GP22	113	10.794	(1)	****	ll:	69.0	21.3744	47	lm:	48.5	19.9471	66				
Linkage group (VI)		map	locus	inf	k*	(df)	class:	rank	nr	class:	rank	mean	nr	class:	rank	mean	nr
0.0	GP164-2	113	0.037	(1)	-	nn:	57.7	20.6267	48	np:	56.5	20.4773	65				
12.1	CP18	113	0.038	(1)	-	nn:	57.5	20.5565	62	np:	56.3	20.5216	51				
14.0	So124	113	0.100	(1)	-	nn:	57.9	20.5866	61	np:	55.9	20.4870	52				
33.0	GP89	113	0.568	(1)	-	nn:	54.8	20.3203	60	np:	59.5	20.7903	53				
38.4	GP30	113	0.486	(1)	-	nn:	55.2	20.3676	65	np:	59.5	20.7752	48				
42.6	GP24	113	2.612	(3)	-	ee:	54.0	20.3165	33	ef:	54.6	20.3009	31	eg:	66.8	21.3065	23
46.3	GP211	113	1.040	(1)	-	nn:	54.2	20.3068	64	np:	60.6	20.8464	49				
72.0	GP76	113	0.100	(1)	-	nn:	55.9	20.4494	52	np:	57.9	20.6187	61				
Linkage group (VII)		map	locus	inf	k*	(df)	class:	rank	nr	class:	rank	mean	nr	class:	rank	mean	nr
0.0	CP52	113	6.498	(1)	**	nn:	48.0	19.8372	49	np:	63.9	21.0794	64				
0.8	CP43	113	9.149	(3)	**	ee:	49.1	20.0097	26	ef:	46.8	19.6325	22	eg:	69.8	21.5376	36
4.1	GP121	113	6.980	(1)	***	nn:	64.1	21.0900	64	np:	47.7	19.8234	49				
8.1	GP179A1	113	7.773	(1)	***	nn:	47.0	19.7872	48	np:	64.4	21.0972	65				
11.9	GP193	113	7.243	(1)	***	nn:	47.2	19.8094	47	np:	64.0	21.0615	66				
21.4	GP27	113	0.003	(1)	-	ll:	57.2	20.5199	62	lm:	56.8	20.5661	51				
31.9	CP56	113	3.961	(1)	**	nn:	49.0	19.9201	42	np:	61.7	20.9079	71				
41.3	CP51-2	113	4.825	(2)	*	hh:	59.7	20.6463	37	hk:	61.4	20.9321	50	kk:	44.7	19.6379	26
51.7	GP219-2	113	0.038	(1)	-	ll:	57.6	20.5758	53	lm:	56.4	20.5098	60				
52.6	TG20	113	2.255	(1)	-	nn:	61.4	20.8103	60	np:	52.1	20.2357	53				
58.1	GP219-1	113	1.216	(1)	-	nn:	60.3	20.7236	58	np:	53.5	20.3479	55				

Linkage group (VIII)												
map	locus	inf	k*	(df)	class:	rank	mean	nr	class:	rank	mean	nr
0.0	GP128-2	113	0.330	(1)	nn:	55.3	20.4184	59	np:	58.9	20.6744	54
5.8	CP112-1	113	0.003	(1)	nn:	57.2	20.5569	54	np:	56.8	20.5260	59
14.2	GP189	113	2.413	(1)	nn:	61.5	20.9134	60	np:	51.9	20.1189	53
15.9	CT92	113	2.522	(1)	nn:	61.6	20.9214	60	np:	51.8	20.1098	53
20.8	GP74	113	0.816	(2)	hh:	57.0	20.4825	30	hk:	55.0	20.4396	61
27.0	GP171	113	2.248	(1)	li:	52.3	20.1220	55	lm:	61.5	20.9378	58
31.1	TG349	113	4.671	(1)	nn:	64.0	21.0896	54	np:	50.6	20.0384	59
41.8	GP92	113	5.968	(1)	nn:	66.1	21.2517	46	np:	50.8	20.0526	67
44.4	TG302	113	5.067	(3)	ac:	49.4	19.9716	32	ad:	59.3	20.6718	24
74.0	GP173	113	0.153	(1)	li:	58.3	20.6530	52	lm:	55.9	20.4451	61
85.5	TG294	113	1.104	(1)	li:	60.2	20.8266	57	lm:	53.7	20.2497	56
Linkage group (IX)												
map	locus	inf	k*	(df)	class:	rank	mean	nr	class:	rank	mean	nr
0.0	CP44	113	2.538	(2)	hh:	63.1	21.0492	29	hk:	56.9	20.5443	66
3.4	GP97	113	1.405	(1)	nn:	60.4	20.8415	60	np:	53.1	20.2002	53
5.8	CP20	113	1.909	(1)	li:	60.8	20.7934	63	lm:	52.2	20.2224	50
18.5	Sol16	113	1.837	(1)	nn:	61.1	20.9517	57	np:	52.8	20.1225	56
19.2	Sol16-1	113	0.216	(2)	hh:	55.0	20.3121	37	hk:	57.8	20.5451	45
24.3	StVe1	113	0.191	(1)	li:	55.4	20.3793	47	lm:	58.1	20.6557	66
36.8	GP35	113	0.887	(1)	nn:	59.9	20.8627	56	np:	54.1	20.2244	57
47.1	GP190	113	0.677	(1)	li:	53.6	20.2583	40	lm:	58.9	20.6955	73
51.3	CP135	113	0.131	(1)	nn:	58.1	20.5934	59	np:	55.8	20.4832	54
55.7	CP67	113	1.010	(1)	nn:	60.1	20.8062	57	np:	53.9	20.2705	56
68.5	GP94	113	0.124	(1)	li:	57.9	20.6082	68	lm:	55.7	20.4389	45
Linkage group (X-A)												
map	locus	inf	k*	(df)	class:	rank	mean	nr	class:	rank	mean	nr
0.0	CP47-1	33	0.000	(0)	hh:	17.0	20.7493	33	hk:	—	—	0
0.7	TG303	113	0.001	(1)	nn:	56.9	20.6606	53	np:	57.1	20.4348	60
9.3	CP59	113	0.228	(1)	nn:	55.6	20.5467	59	np:	58.5	20.5342	54
25.3	GP218	113	0.257	(1)	nn:	55.3	20.5590	52	np:	58.4	20.5252	61
44.0	PSC	113	1.017	(1)	nn:	54.7	20.4516	73	np:	61.2	20.7034	40
Linkage group (X-B)												
map	locus	inf	k*	(df)	class:	rank	mean	nr	class:	rank	mean	nr
0.0	GP232-1	113	0.280	(1)	li:	59.1	20.7350	42	lm:	55.7	20.4258	71
19.1	TG63	113	1.982	(1)	li:	60.9	20.8162	62	lm:	52.2	20.2059	51
21.2	CP105	113	2.431	(1)	li:	61.5	20.8514	60	lm:	51.9	20.1891	53
22.0	GP87	113	3.404	(1)	li:	62.4	20.9249	59	lm:	51.1	20.1210	54
40.7	TG420	113	3.140	(1)	li:	62.1	20.9471	60	lm:	51.2	20.0807	53

Linkage group (XI)													
map	locus	inf	k*	(df)	class:	rank	mean	nr	class:	rank	mean	nr	class:
0.0	TG105-1	113	3.281	(2)	-	59.3	20.8019	30	hh:	63.4	20.9804	36	kk:
15.0	Sol01	113	2.676	(1)	-	51.3	20.1229	50	ll:	61.5	20.8724	63	
15.6	GP185	113	2.085	(3)	-	51.0	20.2298	24	ee:	61.4	20.8136	36	eg:
29.9	GP38	113	5.089	(1)	**	49.3	19.9091	51	ll:	63.3	21.0603	62	fg:
36.9	CP117-1	113	0.001	(1)	-	57.1	20.5439	60	nn:	56.9	20.5372	53	
37.9	GP232	32	0.000	(0)	-	16.5	21.2437	32	hh:	—	—	0	kk:
46.4	CP117	113	7.014	(1)	***	64.4	21.1765	62	ll:	48.0	19.7679	51	
50.9	GP198-3	113	0.001	(1)	-	56.9	20.4888	47	nn:	57.1	20.5777	66	
60.9	GP255-3	113	3.032	(1)	*	64.2	21.0919	40	nn:	53.0	20.2388	73	
67.0	CP58	113	0.012	(1)	-	56.7	20.4788	65	nn:	57.4	20.6246	48	
74.1	TG194	113	4.483	(1)	**	63.1	21.0458	60	ll:	50.1	19.9690	53	
Linkage group (XII-A)													
map	locus	inf	k*	(df)	class:	rank	mean	nr	class:	rank	mean	nr	class:
0.0	GP204	113	0.163	(1)	-	55.9	20.4502	62	nn:	58.4	20.6508	51	
20.4	TG263	27	0.000	(0)	-	14.0	20.8030	27	hh:	—	—	0	kk:
24.2	TG68	113	4.326	(3)	-	49.7	20.0325	26	ee:	63.2	21.0926	27	eg:
28.7	GP99	113	0.022	(1)	-	57.5	20.5834	54	nn:	56.6	20.5017	59	fg:
29.2	CP48	113	0.217	(1)	-	55.6	20.3980	60	nn:	58.5	20.7023	53	
31.5	CP134-1	113	1.506	(2)	-	59.1	20.7011	31	hh:	58.6	20.6482	61	kk:
33.1	TG360	113	0.826	(1)	-	54.4	20.3104	60	nn:	60.0	20.8015	53	
Linkage group (XII-B)													
map	locus	inf	k*	(df)	class:	rank	mean	nr	class:	rank	mean	nr	class:
0.0	Sol22	113	0.162	(1)	-	55.8	20.4728	57	ll:	58.2	20.6099	56	
0.8	GP268	113	0.343	(1)	-	58.9	20.6526	55	ll:	55.2	20.4347	58	
1.5	TG602	113	0.343	(1)	-	58.9	20.6526	55	ll:	55.2	20.4347	58	
22.5	CP112	113	5.718	(1)	**	64.1	21.0939	59	ll:	49.3	19.9364	54	

A.2 Interval Mapping Analysis

A.2.1 Rock Springs 1999 data-set

Linkage group (I)									
map	lod	iter	$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$	var	%expl	locus
0.0	0.01	4	24.2713	23.9275	24.2713	23.9275	15.7747	0.0	CP108
3.7	0.21	4	24.1538	25.4304	24.1538	25.4304	15.6673	0.7	GP232-2
8.7	0.27	6	24.0943	25.3514	24.0943	25.3514	15.6095	1.1	
11.7	0.27	4	24.0883	25.1585	24.0883	25.1585	15.6342	0.9	CP90
16.7	0.25	6	24.0672	25.1689	24.0672	25.1689	15.6131	1.1	
19.1	0.18	4	24.1055	24.9375	24.1055	24.9375	15.6819	0.6	CP11
21.2	0.09	4	24.1433	24.6874	24.1433	24.6874	15.7346	0.3	CP51
26.2	0.21	6	24.0444	24.9145	24.0444	24.9145	15.6446	0.9	
31.2	0.32	5	23.9872	24.9590	23.9872	24.9590	15.5949	1.2	
32.7	0.34	4	23.9811	24.9421	23.9811	24.9421	15.5952	1.2	TG59-1
37.7	0.30	6	23.9515	24.9169	23.9515	24.9169	15.5822	1.3	
42.7	0.24	7	23.9531	24.8343	23.9531	24.8343	15.6078	1.1	
47.7	0.17	6	23.9876	24.7090	23.9876	24.7090	15.6609	0.8	
52.7	0.11	5	24.0419	24.5761	24.0419	24.5761	15.7136	0.4	
56.5	0.07	4	24.0843	24.4905	24.0843	24.4905	15.7416	0.3	GP167-2
61.5	0.02	5	24.1414	24.3925	24.1414	24.3925	15.7660	0.1	
66.5	0.00	3	24.2472	24.2544	24.2472	24.2544	15.7814	0.0	
71.5	0.02	4	24.3415	24.1537	24.3415	24.1537	15.7727	0.1	
71.5	0.02	4	24.3426	24.1526	24.3426	24.1526	15.7724	0.1	TG53
73.7	0.08	4	24.4582	24.0364	24.4582	24.0364	15.7370	0.3	CP13
77.5	0.08	4	24.4616	24.0393	24.4616	24.0393	15.7369	0.3	GP198-2

Linkage group (II)									
map	lod	iter	$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$	var	%expl	locus
0.0	1.06	11	24.2508	23.8698	23.1976	26.1552	14.9086	5.5	GP23
3.4	1.05	8	24.1571	24.0174	23.2682	26.2483	14.9690	5.1	Sol20
7.3	1.18	7	24.3068	24.1448	23.0180	26.2345	14.9401	5.3	GP128
12.3	0.83	6	24.0109	24.2931	23.5950	26.1274	15.2618	3.3	
14.6	0.75	5	23.8796	24.3599	23.9200	26.0589	15.3418	2.8	GP131
17.7	0.78	6	24.0469	24.3651	23.6126	26.1349	15.3321	2.8	GP33-1
22.7	0.49	6	24.4009	24.2632	23.4909	25.9770	15.4566	2.1	
24.9	0.35	4	24.5014	24.2625	23.6067	25.5446	15.5890	1.2	GP288-3
28.6	0.53	6	24.5318	24.1726	23.4580	25.7409	15.4550	2.1	GP209
33.6	0.79	7	24.6324	24.1085	23.2191	26.0478	15.2209	3.6	
38.6	1.02	8	24.7137	24.0730	23.0692	26.2400	15.0305	4.8	
43.6	1.17	8	24.7318	24.0747	23.0667	26.3683	14.9652	5.2	
44.0	1.18	8	24.7297	24.0763	23.0735	26.3755	14.9671	5.2	CP157
49.0	1.21	8	24.4726	24.2443	23.1366	26.6398	14.9415	5.3	
54.0	1.24	6	24.1955	24.4250	23.2738	26.6655	14.9997	5.0	
54.1	1.24	6	24.1892	24.4293	23.2773	26.6630	15.0019	4.9	PFC
58.1	1.21	5	24.0882	24.5361	23.3009	26.4735	15.0919	4.4	GP216
60.5	1.21	5	24.0985	24.5327	23.2811	26.3455	15.0959	4.3	GP504

Linkage group (III)									
map	lod	iter	$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$	var	%expl	locus
0.0	3.56	4	23.1212	25.8817	23.1212	25.8817	13.9394	11.7	CP15
2.3	4.93	21	24.1153	26.4787	21.7224	25.3849	12.6516	19.8	GP198-1
2.8	4.69	21	24.2309	26.4078	21.7112	25.4033	12.7201	19.4	GP167-1
7.8	4.13	18	24.2182	26.2063	21.6375	25.4215	12.8233	18.7	
12.8	3.16	13	24.3760	25.6750	21.8154	25.3287	13.5396	14.2	
15.0	2.69	11	24.5197	25.3561	21.9861	25.2151	13.9794	11.4	GP1
19.2	2.26	10	24.6155	25.1285	22.1389	25.1295	14.2779	9.5	CP61
20.3	2.20	10	24.7116	24.9757	22.1320	25.1479	14.3041	9.4	CP133
20.3	2.20	10	24.7114	24.9757	22.1322	25.1479	14.3044	9.4	CP6
25.3	2.20	9	24.4374	25.1179	22.2031	25.3473	14.2362	9.8	
30.3	1.71	8	24.1572	25.2458	22.6249	25.0702	14.6636	7.1	
32.5	1.41	4	24.0643	25.2793	23.0017	24.6420	15.0235	4.8	GP276
34.7	1.27	5	24.2315	25.1715	22.9777	24.6285	15.0804	4.4	GP226
39.7	1.03	7	24.2464	25.2919	23.0220	24.4145	15.0880	4.4	
44.7	0.79	11	24.3230	25.3994	23.1723	24.0392	15.1308	4.1	
49.7	0.62	15	24.4598	25.4784	23.4117	23.5665	15.1086	4.3	
54.7	0.57	16	24.6266	25.5016	23.6375	23.1620	14.9899	5.0	
57.5	0.57	17	24.7165	25.4908	23.7285	22.9991	14.9137	5.5	GP198-4
62.5	0.61	21	24.5576	25.6751	23.6468	23.0862	14.8551	5.9	
67.5	0.64	32	24.5452	25.7297	23.4722	23.2252	14.8309	6.0	
69.2	0.64	40	24.6143	25.7276	23.3591	23.2622	14.7914	6.3	TG28

Linkage group (IV)									
map	lod	iter	$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$	var	%expl	locus
0.0	1.28	6	24.9575	25.0515	24.3624	23.0451	15.0829	4.4	GP180
5.0	0.99	7	24.8501	24.9591	24.5040	23.0549	15.1491	4.0	
10.0	0.60	6	24.6979	24.7469	24.4992	23.3458	15.4223	2.3	
12.2	0.45	4	24.6257	24.6399	24.4758	23.5060	15.5365	1.6	TG123
17.2	0.22	5	24.6199	24.4763	24.4212	23.7625	15.6538	0.8	
19.0	0.16	4	24.5917	24.4375	24.3812	23.8622	15.6932	0.6	CP54
24.0	0.40	6	24.9380	24.1305	24.6709	23.6883	15.5337	1.6	
27.2	0.60	7	25.0965	23.9816	24.7279	23.6513	15.4462	2.1	GP99-2
32.2	0.53	8	25.1518	23.7974	24.5489	23.7244	15.4522	2.1	
37.2	0.50	8	25.1835	23.5577	24.2119	24.0574	15.4671	2.0	GP161-2
42.2	0.64	8	25.2250	23.4083	24.4766	23.8396	15.3441	2.8	
47.2	0.76	7	25.1963	23.3223	24.6046	23.7750	15.2839	3.2	
51.4	0.80	4	25.1244	23.3227	24.5540	23.8765	15.3455	2.8	TG62
51.6	0.80	4	25.1242	23.3182	24.5580	23.8744	15.3426	2.8	Sol21
56.6	0.77	8	25.2453	23.3149	24.4761	23.8361	15.2752	3.2	
61.6	0.76	10	25.3823	23.3349	24.2439	23.9180	15.2222	3.5	
66.6	0.80	10	25.4257	23.4040	23.9464	24.1236	15.2074	3.6	
66.8	0.80	10	25.4237	23.4080	23.9368	24.1323	15.2087	3.6	GP83
71.8	1.23	9	25.5796	23.0866	23.8137	24.4084	14.8878	5.7	
76.8	1.36	7	25.4236	23.0786	23.9023	24.5189	14.9793	5.1	
77.9	1.35	7	25.3725	23.1056	23.9408	24.5038	15.0340	4.7	GP165

Linkage group (V)									
map	lod	iter	$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$	var	%expl	locus
0.0	0.33	53	26.7937	24.5206	27.1700	24.2610	12.3910	10.3	GP21A-8
5.0	0.36	50	26.9858	24.5061	26.8092	24.2130	12.5170	9.5	
10.0	0.49	48	27.1144	24.4498	26.3127	24.2925	12.6946	8.3	
10.8	0.52	47	27.1245	24.4343	26.2304	24.3157	12.7207	8.2	GP179A
15.8	0.63	46	27.1614	24.3458	25.9222	24.3519	12.7904	7.7	
20.8	0.76	44	27.2010	24.2202	25.5391	24.4233	12.8348	7.4	
25.8	0.95	41	27.2304	24.0627	25.1199	24.5117	12.8259	7.5	
30.8	1.17	35	27.2358	23.8920	24.7479	24.5598	12.7774	7.8	
35.8	1.42	29	27.2114	23.7218	24.5344	24.4874	12.7625	7.9	
38.0	1.53	27	27.1918	23.6497	24.5086	24.4140	12.7846	7.8	GP248
39.5	1.86	25	27.2089	23.1730	24.1505	23.8953	12.5185	9.4	GP34
40.9	1.53	22	27.1058	23.2666	24.5124	23.9227	12.7346	8.1	GP188
45.9	1.55	16	27.0664	22.9028	24.3317	23.9389	12.7032	8.3	
50.9	1.52	10	26.9680	22.6680	24.2707	24.0218	12.8216	7.5	
55.9	1.38	6	26.7708	22.7521	24.4796	24.1243	13.1993	5.1	
57.9	1.29	3	26.6607	22.8668	24.6965	24.1783	13.3896	3.9	CP113
59.3	1.29	6	26.6134	22.2909	23.9069	23.1522	13.2957	4.5	CP14-1
62.3	1.52	6	26.5625	21.0545	24.6871	24.1750	13.0524	6.1	Sol22-1
64.4	1.53	7	26.4241	21.2795	22.5124	23.9399	13.0680	6.0	GP284
65.8	3.27	4	26.2065	24.3316	24.3992	22.4473	14.0245	11.1	CP49
67.9	3.42	2	26.0010	24.5607	24.6283	22.2604	14.0087	11.2	TG69
71.6	4.01	5	26.4282	24.5047	24.4664	22.1329	13.5824	13.9	GP22

Linkage group (VI)									
map	lod	iter	$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$	var	%expl	locus
0.0	0.56	27	25.1435	25.6250	23.1751	23.0030	14.4600	8.4	GP164-2
5.0	0.54	25	25.2431	25.3319	23.1982	23.1596	14.6716	7.0	
10.0	0.57	21	25.3785	25.0154	23.2129	23.3480	14.8448	5.9	
12.1	0.60	19	25.4288	24.9042	23.2214	23.4200	14.8959	5.6	CP18
14.0	0.61	18	25.4268	24.8367	23.2076	23.4932	14.9419	5.3	Sol24
19.0	0.59	15	25.2149	24.9256	23.2049	23.6159	15.0650	4.5	
24.0	0.61	12	24.9718	25.0508	23.2232	23.7090	15.1532	4.0	
29.0	0.66	10	24.7322	25.1783	23.3177	23.7171	15.2129	3.6	
33.0	0.72	8	24.5702	25.2460	23.4098	23.7120	15.2486	3.4	GP89
38.0	0.74	6	24.5945	25.1676	23.3498	23.8988	15.3167	2.9	
38.4	0.74	6	24.6056	25.1506	23.3521	23.9060	15.3255	2.9	GP30
42.6	0.85	4	24.3604	25.3103	23.4769	23.8808	15.3197	2.9	GP24
46.3	0.95	6	24.3161	25.4830	23.4284	23.8425	15.2096	3.6	GP211
51.3	0.84	9	24.4110	25.5033	23.4230	23.7237	15.1631	3.9	
56.3	0.74	14	24.5317	25.5063	23.5083	23.4849	15.1117	4.2	
61.3	0.68	19	24.6672	25.5104	23.6674	23.1280	14.9894	5.0	
66.3	0.65	19	24.8323	25.4727	23.7092	22.9060	14.8621	5.8	
71.3	0.64	18	25.0150	25.3924	23.6332	22.8474	14.7851	6.3	
72.0	0.64	18	25.0400	25.3805	23.6182	22.8459	14.7752	6.4	GP76

Linkage group (VII)									
map	lod	iter	$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$	var	%expl	locus
0.0	1.55	5	23.4942	25.5573	23.3102	24.2740	14.9421	5.3	CP52
0.8	1.55	4	23.4595	25.5212	23.3114	24.2839	14.9493	5.3	CP43
4.1	2.13	6	23.1295	25.8076	23.4234	24.2330	14.6186	7.4	GP121
8.1	1.73	7	23.1676	25.7847	23.7701	23.8695	14.7222	6.7	GP179A1
11.9	1.75	9	23.0844	25.8367	23.7864	23.8682	14.6371	7.3	GP193
16.9	1.31	11	23.0430	25.5601	23.5672	24.3877	14.8259	6.1	
21.4	1.03	8	23.2027	25.1302	23.3212	24.8648	15.0190	4.8	GP27
26.4	0.82	7	23.4472	24.9778	23.2680	24.7875	15.2105	3.6	
31.4	0.59	5	23.7840	24.7630	23.3214	24.6523	15.4485	2.1	
31.9	0.57	5	23.8153	24.7430	23.3309	24.6380	15.4678	2.0	CP56
36.9	0.57	5	23.9336	24.6763	23.3459	24.7749	15.4510	2.1	
41.3	0.59	4	24.0923	24.5803	23.3979	24.8854	15.4590	2.0	CP51-2
46.3	0.63	7	24.0577	24.4466	23.4034	25.1546	15.3662	2.6	
51.3	0.58	5	24.0386	24.3009	23.5881	25.1659	15.4393	2.2	
51.7	0.58	5	24.0375	24.2913	23.6081	25.1553	15.4513	2.1	GP219-2
52.6	0.54	4	24.0458	24.2776	23.6461	25.1216	15.4812	1.9	TG20
57.6	0.36	7	24.1598	24.1465	23.7606	25.0538	15.5525	1.5	
58.1	0.34	7	24.1721	24.1325	23.7818	25.0360	15.5653	1.4	GP219-1

Linkage group (VIII)									
map	lod	iter	$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$	var	%expl	locus
0.0	0.66	12	23.5756	23.8456	24.1493	25.6254	15.1991	3.7	GP128-2
5.0	0.58	11	24.1500	23.4223	24.0865	25.5376	15.1906	3.7	
5.8	0.59	11	24.2154	23.3829	24.1090	25.4911	15.1980	3.7	CP112-1
10.8	0.33	9	24.1384	23.5405	24.5632	24.9540	15.5049	1.8	
14.2	0.33	7	24.1106	23.6326	24.8319	24.5100	15.5621	1.4	GP189
15.9	0.37	6	24.2323	23.5550	24.7794	24.5618	15.5479	1.5	CT92
20.8	0.33	5	24.1413	23.6731	24.4974	24.8615	15.5933	1.2	GP74
25.8	0.31	6	24.0711	24.0686	25.0122	23.8302	15.5785	1.3	
27.0	0.44	6	24.0725	24.1536	25.1103	23.6474	15.5019	1.8	GP171
31.1	0.97	6	23.9327	24.2427	25.4705	23.3564	15.2031	3.7	TG349
36.1	1.24	7	23.9258	24.2282	25.7178	23.2026	14.9764	5.1	
41.1	1.27	6	24.0803	24.1518	25.7113	23.2717	15.0453	4.7	
41.8	1.25	5	24.1125	24.1392	25.6909	23.2970	15.0753	4.5	GP92
44.4	1.03	4	24.2058	24.1087	25.4838	23.3601	15.2253	3.5	TG302
49.4	0.99	8	24.2034	24.2485	25.5478	23.1640	15.0891	4.4	
54.4	0.95	13	24.2661	24.4063	25.5644	22.9399	14.9250	5.4	
59.4	0.92	16	24.4442	24.5077	25.5304	22.7190	14.7503	6.5	
64.4	0.91	18	24.6892	24.4843	25.4833	22.5716	14.6095	7.4	
69.4	0.90	17	24.9094	24.3334	25.4432	22.5563	14.5663	7.7	
74.0	0.88	19	25.0830	24.1340	25.4147	22.6107	14.5616	7.7	GP173
79.0	1.29	21	24.8193	24.6367	25.8311	21.8622	13.6063	13.8	
84.0	1.44	20	24.7458	24.5317	26.0484	21.6948	13.3586	15.4	
85.5	1.44	22	24.7522	24.4197	26.0983	21.7257	13.3984	15.1	TG294

Linkage group (IX)									
map	lod	iter	$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$	var	%expl	locus
0.0	0.35	5	23.5725	24.0935	24.2921	24.9121	15.5876	1.2	CP44
3.4	0.49	6	23.6341	24.0163	24.1403	25.0849	15.5013	1.8	GP97
5.8	0.53	5	23.6916	24.0477	24.0119	25.1294	15.4794	1.9	CP20
10.8	0.47	6	23.4891	24.3855	23.9936	25.0556	15.4641	2.0	
15.8	0.43	6	23.5186	24.6311	23.9490	24.8793	15.5099	1.7	
18.5	0.41	4	23.6300	24.6716	23.9231	24.7839	15.5594	1.4	Sol16
19.2	0.40	4	23.6628	24.6839	23.9023	24.7667	15.5648	1.4	Sol16-1
24.2	0.35	6	23.5327	24.7065	23.9716	24.7202	15.5516	1.5	
24.3	0.35	6	23.5309	24.7064	23.9734	24.7186	15.5519	1.5	StVe1
29.3	0.24	7	23.6390	24.6408	24.0068	24.6394	15.6164	1.0	
34.3	0.15	7	23.7286	24.6060	24.1181	24.4489	15.6847	0.6	
36.8	0.13	6	23.7485	24.6073	24.1884	24.3324	15.7018	0.5	GP35
41.8	0.08	7	23.9234	24.5821	24.3759	24.0140	15.7165	0.4	
46.8	0.14	6	24.2246	24.4213	24.5277	23.7651	15.6883	0.6	
47.1	0.15	5	24.2432	24.4088	24.5336	23.7556	15.6857	0.6	GP190
51.3	0.30	6	24.3892	24.3369	24.6390	23.5640	15.6060	1.1	CP135
55.7	0.85	7	24.6941	24.1612	24.9294	23.1661	15.2898	3.1	CP67
60.7	0.89	8	24.6691	24.1885	25.0424	23.0244	15.1578	4.0	
65.7	0.91	9	24.6761	24.1443	25.1388	22.9468	15.0538	4.6	
68.5	0.91	9	24.6951	24.0920	25.1830	22.9296	15.0109	4.9	GP94

Linkage group (X-A)									
map	lod	iter	$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$	var	%expl	locus
0.0	0.13	4	23.9770	24.5317	23.9770	24.4828	15.7103	0.5	CP47-1
0.7	0.13	4	23.9781	24.5321	23.9781	24.4764	15.7112	0.4	TG303
5.7	0.57	32	22.7233	25.0409	24.7638	24.4732	14.9475	5.3	
9.3	0.79	28	22.7513	25.1218	24.7152	24.4708	14.9363	5.4	CP59
14.3	0.67	32	22.9034	25.1294	24.3590	24.5560	15.0971	4.3	
19.3	0.50	30	23.3818	24.9449	23.8798	24.6502	15.3953	2.4	
24.3	0.35	24	24.0840	24.5395	23.4455	24.7634	15.5375	1.5	
25.3	0.33	23	24.1796	24.4574	23.4114	24.7881	15.5355	1.6	GP218
30.3	0.56	43	24.6939	24.1798	22.7075	25.4219	14.8147	6.1	
35.3	0.79	51	25.0700	23.9191	22.3233	25.8603	14.0052	11.3	
40.3	0.91	50	25.2183	23.6959	22.3099	26.0715	13.6795	13.3	
44.0	0.96	48	25.2678	23.5397	22.3916	26.1587	13.6171	13.7	PSC

Linkage group (X-B)									
map	lod	iter	$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$	var	%expl	locus
0.0	0.00	3	24.2879	24.2879	24.1872	24.1872	15.7791	0.0	GP232-1
5.0	0.04	5	24.3816	24.3816	24.0499	24.0499	15.7552	0.2	
10.0	0.11	6	24.4877	24.4877	23.9205	23.9205	15.7032	0.5	
15.0	0.21	5	24.5707	24.5707	23.8415	23.8415	15.6505	0.8	
19.1	0.28	4	24.6073	24.6073	23.8223	23.8223	15.6287	1.0	TG63
21.2	0.25	4	24.6076	24.6076	23.8593	23.8593	15.6418	0.9	CP105
22.0	0.42	4	24.7137	24.7137	23.7583	23.7583	15.5534	1.4	GP87
27.0	0.59	6	24.8581	24.8581	23.6104	23.6104	15.3925	2.5	
32.0	0.72	7	24.9410	24.9410	23.5336	23.5336	15.2864	3.1	

37.0	0.76	6	24.9359	24.9359	23.5534	23.5534	15.3037	3.0	
40.7	0.75	4	24.8884	24.8884	23.6126	23.6126	15.3745	2.6	TG420
Linkage group (XI)									
map	lod	iter	$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$	var	%expl	locus
0.0	0.77	7	25.1701	24.6775	23.5314	24.3791	15.3483	2.7	TG105-1
5.0	0.93	10	25.3225	24.7606	23.2736	24.0472	15.0969	4.3	
10.0	0.97	10	25.1796	24.8499	23.3230	23.5603	15.1151	4.2	
15.0	0.96	4	24.8827	24.9068	23.6210	23.2904	15.2584	3.3	Sol01
15.6	0.76	4	24.8832	24.7228	23.6330	23.4304	15.3685	2.6	GP185
20.6	1.24	9	25.4026	24.6365	23.1096	23.4175	14.9031	5.6	
25.6	1.56	8	25.6392	24.4861	22.9928	23.4926	14.7432	6.6	
29.9	1.64	7	25.6669	24.3740	23.0547	23.6363	14.8396	6.0	GP38
34.9	2.17	7	25.6459	24.8769	22.8744	23.1282	14.4610	8.4	
36.9	2.29	6	25.6235	24.9187	22.8302	23.1370	14.4439	8.5	CP117-1
37.9	2.29	6	25.5930	24.9178	22.8088	23.1863	14.4765	8.3	GP232
42.9	2.05	6	25.4212	24.9462	22.7112	23.2859	14.6047	7.5	
46.4	1.81	6	25.2436	24.9047	22.6757	23.4312	14.8027	6.2	CP117
50.9	1.78	6	25.1900	25.1013	22.6565	23.3301	14.6943	6.9	GP198-3
55.9	1.93	9	25.1170	25.2807	22.3413	23.8013	14.4383	8.5	
60.9	1.90	8	24.9782	25.5583	22.6553	23.9516	14.5292	7.9	
60.9	1.90	8	24.9781	25.5585	22.6557	23.9516	14.5294	7.9	GP255-3
65.9	1.29	7	25.0359	25.1779	23.3001	23.2332	14.9332	5.4	
67.0	1.25	7	25.1114	25.0633	23.4508	23.1869	14.9735	5.1	CP58
72.0	1.03	5	25.0753	24.8901	23.5760	23.3506	15.1858	3.8	
74.1	0.94	6	25.0552	24.8095	23.6310	23.4246	15.2709	3.2	TG194
Linkage group (XII-A)									
map	lod	iter	$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$	var	%expl	locus
0.0	0.20	14	23.8587	23.7196	25.0007	24.4508	15.5406	1.5	GP204
5.0	0.18	12	23.9669	23.7110	24.8662	24.4633	15.5925	1.2	
10.0	0.16	11	24.0400	23.7179	24.7268	24.4978	15.6310	1.0	
15.0	0.15	9	24.0708	23.7565	24.5995	24.5333	15.6616	0.8	
20.0	0.15	6	24.0726	23.8179	24.5022	24.5521	15.6861	0.6	
20.4	0.15	6	24.0721	23.8238	24.4952	24.5527	15.6880	0.6	TG263
24.2	0.19	4	23.9835	23.8762	24.6303	24.4898	15.6798	0.6	TG68
28.7	0.16	5	23.9681	23.8909	24.6317	24.4344	15.6836	0.6	GP99
29.2	0.38	5	23.9503	23.9185	25.0322	24.0381	15.5615	1.4	CP48
31.5	0.38	4	23.9723	23.9627	25.0108	23.9913	15.5728	1.3	CP134-1
33.1	0.55	5	24.0582	23.9082	25.1147	23.7953	15.4751	1.9	TG360
Linkage groupLinkage group (XII-B)									
map	lod	iter	$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$	var	%expl	locus
0.0	0.00	3	24.2830	24.2830	24.2170	24.2170	15.7804	0.0	Sol22
0.8	0.01	3	24.3224	24.3224	24.1786	24.1786	15.7763	0.0	GP268
1.5	0.02	4	24.3450	24.3450	24.1531	24.1531	15.7723	0.1	TG602
6.5	0.11	6	24.5272	24.5272	23.9617	23.9617	15.7015	0.5	
11.5	0.31	7	24.7250	24.7250	23.7487	23.7487	15.5434	1.5	
16.5	0.54	7	24.8427	24.8427	23.6148	23.6148	15.4050	2.4	

21.5 0.73 5 24.8673 24.8673 23.5773 23.5773 15.3662 2.6 CP112

A.2.2 Rock Springs 2002 data-set

map	lod	iter	Linkage group (I)				var	%expl	locus
			$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$			
0.0	0.00	3	19.9271	19.8180	19.9271	19.8180	10.0851	0.0	CP108
3.7	0.02	4	19.8934	20.2471	19.8934	20.2471	10.0770	0.1	GP232-2
8.7	0.97	8	19.6537	21.7176	19.6537	21.7176	9.60641	4.8	
11.7	1.21	4	19.6454	21.4466	19.6454	21.4466	9.66609	4.2	CP90
16.7	0.46	7	19.7186	20.9401	19.7186	20.9401	9.88005	2.0	
19.1	0.14	4	19.8167	20.4072	19.8167	20.4072	10.0353	0.5	CP11
21.2	0.13	4	19.8119	20.3585	19.8119	20.3585	10.0383	0.5	CP51
26.2	0.15	5	19.7831	20.3629	19.7831	20.3629	10.0250	0.6	
31.2	0.14	5	19.7804	20.2947	19.7804	20.2947	10.0334	0.5	
32.7	0.13	4	19.7839	20.2673	19.7839	20.2673	10.0384	0.5	TG59-1
37.7	0.24	7	19.6957	20.4187	19.6957	20.4187	9.97380	1.1	
42.7	0.36	8	19.6105	20.5296	19.6105	20.5296	9.89698	1.9	
47.7	0.45	8	19.5644	20.5437	19.5644	20.5437	9.86386	2.2	
52.7	0.48	6	19.5604	20.4809	19.5604	20.4809	9.88402	2.0	
56.5	0.48	4	19.5747	20.4134	19.5747	20.4134	9.91535	1.7	GP167-2
61.5	0.51	5	19.5240	20.4288	19.5240	20.4288	9.88427	2.0	
66.5	0.49	6	19.5113	20.3941	19.5113	20.3941	9.89196	1.9	
71.5	0.43	4	19.5412	20.3180	19.5412	20.3180	9.93499	1.5	
71.5	0.43	4	19.5419	20.3166	19.5419	20.3166	9.93583	1.5	TG53
73.7	0.09	4	19.7429	20.1006	19.7429	20.1006	10.0538	0.3	CP13
77.5	0.12	4	19.7093	20.1283	19.7093	20.1283	10.0419	0.4	GP198-2

map	lod	iter	Linkage group (II)				var	%expl	locus
			$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$			
0.0	1.48	14	19.0708	20.2382	19.8110	21.5786	9.33235	7.5	GP23
3.4	1.73	11	19.1246	20.1094	19.8705	21.7992	9.30321	7.8	Sol20
7.3	1.73	9	19.0853	20.1964	20.0018	21.7581	9.34247	7.4	GP128
12.3	1.50	7	19.1471	20.2777	20.1498	21.5305	9.48235	6.0	
14.6	1.35	6	19.2054	20.3447	20.1481	21.3586	9.57821	5.0	GP131
17.7	1.22	6	19.2730	20.3245	20.0912	21.3887	9.64300	4.4	GP33-1
22.7	0.50	6	19.6822	19.9799	19.8414	21.6716	9.87889	2.1	
24.9	0.43	4	19.9189	19.7671	19.8078	21.8489	9.93380	1.5	GP288-3
28.6	0.35	9	19.9313	19.8893	19.5354	21.5626	9.88683	2.0	GP209
33.6	0.71	10	19.8909	19.8165	19.4370	22.1402	9.66818	4.1	
38.6	1.07	10	19.8402	19.7500	19.4318	22.4374	9.50413	5.8	
43.6	1.42	8	19.7795	19.7075	19.4881	22.5794	9.41488	6.7	
44.0	1.45	8	19.7747	19.7054	19.4940	22.5856	9.41128	6.7	CP157
49.0	1.87	9	19.5967	19.7635	19.4486	22.9647	9.13931	9.4	
54.0	2.16	8	19.5288	19.8282	19.4400	22.9532	9.13048	9.5	
54.1	2.16	8	19.5281	19.8300	19.4401	22.9495	9.13311	9.4	PFC
58.1	2.17	5	19.7144	19.7905	19.3809	22.6984	9.31159	7.7	GP216

60.5	2.15	6	19.8128	19.6462	19.3645	22.5956	9.28931	7.9	GP504
Linkage group (III)									
map	lod	iter	$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$	var	%expl	locus
0.0	1.23	55	20.8382	17.9837	20.6460	25.9889	6.92757	18.4	CP15
2.3	2.92	58	20.8299	23.5294	19.2525	17.4910	6.62334	30.6	GP198-1
2.8	2.72	55	20.8382	22.6190	17.9879	16.5747	6.92756	27.5	GP167-1
7.8	2.97	31	20.8369	22.1117	17.6978	17.0093	6.52743	31.5	
12.8	3.06	42	20.8181	21.3477	17.7143	17.2055	6.59946	30.8	
15.0	0.61	63	20.7672	20.7243	17.5933	17.2569	6.61162	3.1	GP1
19.2	0.64	72	20.7191	20.7517	17.9336	17.8788	6.78383	1.4	CP61
20.3	0.72	67	20.8385	20.3097	17.9145	17.8165	6.77469	1.5	CP133
20.3	0.72	67	20.8383	20.3098	17.9156	17.8175	6.77527	1.5	CP6
25.3	0.68	88	20.7245	20.5722	18.3713	18.4788	7.04258	-1.1	
30.3	0.72	106	20.6140	20.8672	18.8332	19.0774	7.16809	-2.4	
32.5	0.76	115	20.5813	20.9445	18.9928	19.2644	7.18700	-2.6	GP276
34.7	0.75	98	20.6178	20.9380	18.9559	19.2255	7.11843	-1.9	GP226
39.7	0.87	167	20.5531	21.3073	18.8524	18.8990	6.87357	0.5	
44.7	1.11	109	20.4895	21.7961	19.0315	18.7936	6.49200	4.3	
49.7	1.40	78	20.4810	22.2049	19.3756	18.8814	6.14826	7.7	
54.7	1.64	62	20.5214	22.4488	19.6196	18.9311	5.89798	10.2	
57.5	1.75	57	20.5613	22.5238	19.6974	18.9340	5.80210	11.2	GP198-4
62.5	2.10	55	20.3307	22.9348	19.9777	19.4441	5.39126	15.2	
67.5	2.15	71	20.3821	22.7298	19.5364	19.5759	5.64290	12.7	
69.2	2.17	86	20.4658	22.6221	19.2457	19.5326	5.71036	12.1	TG28
Linkage group (IV)									
map	lod	iter	$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$	var	%expl	locus
0.0	2.39	7	21.4100	19.3940	20.1193	18.9984	9.25318	8.3	GP180
5.0	1.89	7	21.3823	19.2732	20.0213	19.1789	9.33944	7.4	
10.0	1.18	6	21.0084	19.2617	19.9926	19.4222	9.63502	4.5	
12.2	0.89	4	20.7839	19.3050	20.0124	19.5168	9.77378	3.1	TG123
17.2	1.88	6	21.4246	19.1908	20.0292	19.3862	9.39361	6.9	
19.0	2.09	5	21.5164	19.2421	20.0554	19.3697	9.36547	7.1	CP54
24.0	1.84	8	21.5878	19.1751	20.1190	19.3848	9.31004	7.7	
27.2	1.35	8	21.2593	19.3956	20.0725	19.4123	9.57208	5.1	GP99-2
32.2	1.33	8	21.0134	19.3484	20.4231	19.1973	9.53483	5.5	
37.2	1.13	9	20.4841	19.5714	20.5521	19.0680	9.67696	4.1	GP161-2
42.2	1.18	10	20.4490	19.3041	20.7719	19.0415	9.53006	5.5	
47.2	0.91	8	20.3040	19.2230	20.7262	19.2930	9.66229	4.2	
51.4	0.58	4	20.1139	19.3263	20.5186	19.6148	9.88031	2.0	TG62
51.6	0.61	4	20.1211	19.3136	20.5320	19.6046	9.87037	2.1	Sol21
56.6	1.01	7	20.3494	19.0985	20.7026	19.4005	9.65673	4.3	
61.6	1.38	8	20.5364	18.9809	20.7165	19.3080	9.52211	5.6	
66.6	1.62	7	20.6439	18.9732	20.6075	19.3129	9.51796	5.6	
66.8	1.63	7	20.6464	18.9743	20.6019	19.3146	9.51978	5.6	GP83
71.8	1.98	8	20.8600	18.7004	20.5667	19.3601	9.28270	8.0	
76.8	2.20	9	20.8853	18.5728	20.5764	19.3822	9.16663	9.1	
77.9	2.22	9	20.8719	18.5629	20.5797	19.3816	9.16220	9.2	GP165

Linkage group (V)									
map	lod	iter	$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$	var	%expl	locus
0.0	1.64	46	21.9396	19.0728	22.7643	20.6513	6.70615	17.1	GP21A-8
5.0	1.53	43	21.8177	19.2754	22.8594	20.5738	6.82768	15.9	
10.0	1.39	39	21.7420	19.5131	22.9158	20.3810	6.95904	14.6	
10.8	1.37	38	21.7368	19.5522	22.9217	20.3442	6.97800	14.4	GP179A
15.8	1.42	35	21.7409	19.3917	22.9471	20.4017	6.91059	15.1	
20.8	1.43	33	21.7609	19.2246	22.9017	20.4293	6.89442	15.3	
25.8	1.42	31	21.7940	19.0646	22.7418	20.3931	6.96458	14.6	
30.8	1.40	30	21.8367	18.9172	22.4260	20.2883	7.13501	12.9	
35.8	1.43	27	21.8738	18.7856	21.9976	20.1504	7.34910	10.8	
38.0	1.48	24	21.8814	18.7317	21.8152	20.0839	7.43063	10.0	GP248
39.5	1.53	23	21.9130	18.6622	21.4724	20.0199	7.51045	9.2	GP34
40.9	1.65	20	21.8849	18.5411	21.6305	20.0011	7.41704	10.1	GP188
45.9	2.10	16	21.8551	18.0486	21.3727	20.2715	7.27990	11.4	
50.9	2.34	10	21.8186	17.7568	21.0869	20.1615	7.32922	11.0	
55.9	2.27	7	21.7595	17.7073	20.8751	19.6797	7.63527	7.9	
57.9	2.18	3	21.7213	17.7770	20.8506	19.4084	7.80691	6.2	CP113
59.3	1.79	6	21.7529	17.4833	20.3470	18.4889	7.85220	5.8	CP14-1
62.3	2.18	11	21.8105	16.8555	18.9098	18.5370	7.69048	7.4	Sol22-1
64.4	1.24	11	21.6183	17.3279	18.9065	19.4517	7.88324	5.5	GP284
65.8	4.54	4	21.3064	19.2948	20.7734	18.2499	8.58905	14.8	CP49
67.9	5.09	2	21.2626	19.3974	20.9137	18.1002	8.43420	16.4	TG69
71.6	5.49	6	21.8079	19.2871	20.7264	18.0319	8.10885	19.6	GP22

Linkage group (VI)									
map	lod	iter	$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$	var	%expl	locus
0.0	0.67	41	19.7967	22.1437	19.6157	18.0997	8.12587	19.4	GP164-2
5.0	0.76	43	19.6497	22.2903	19.6788	17.9183	7.73590	23.3	
10.0	0.59	52	19.6728	22.1416	19.6781	17.9418	7.85198	22.1	
12.1	0.45	62	19.7157	21.9974	19.6677	18.0252	8.05535	20.1	CP18
14.0	0.11	40	19.8268	20.3605	19.6441	19.8229	10.0115	0.7	Sol24
19.0	0.09	10	19.8693	20.1404	19.5961	20.0608	10.0414	0.4	
24.0	0.08	13	19.9391	20.0446	19.5737	20.1186	10.0419	0.4	
29.0	0.07	9	20.0100	19.9810	19.5997	20.0932	10.0498	0.4	
33.0	0.06	6	20.0530	19.9460	19.6432	20.0466	10.0583	0.3	GP89
38.0	0.03	5	19.9904	20.0124	19.7517	19.9288	10.0753	0.1	
38.4	0.02	5	19.9858	20.0168	19.7670	19.9140	10.0765	0.1	GP30
42.6	0.05	4	19.8414	20.1560	19.8420	19.8499	10.0678	0.2	GP24
46.3	0.20	6	19.6579	20.3892	19.9362	19.7303	10.0068	0.8	GP211
51.3	0.24	10	19.5876	20.4873	20.0820	19.5532	9.94225	1.4	
56.3	0.30	15	19.5085	20.5551	20.2875	19.3425	9.83307	2.5	
61.3	0.35	19	19.4290	20.5553	20.4834	19.2058	9.72509	3.6	
66.3	0.38	23	19.3519	20.4908	20.6307	19.1843	9.66366	4.2	
71.3	0.39	28	19.2564	20.3913	20.7553	19.2447	9.62147	4.6	
72.0	0.39	28	19.2400	20.3762	20.7733	19.2572	9.61386	4.7	GP76

Linkage group (VII)									
map	lod	iter	$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$	var	%expl	locus
0.0	1.25	5	19.5448	20.9532	19.6333	19.3280	9.63849	4.4	CP52
0.8	1.11	4	19.6031	20.8606	19.6323	19.3420	9.69884	3.8	CP43
4.1	1.71	6	19.2137	21.1026	19.8933	19.2580	9.45529	6.3	GP121
8.1	1.84	7	18.9462	21.1395	19.8691	19.4585	9.37452	7.1	GP179A1
11.9	1.66	7	18.8541	21.0189	20.0132	19.5588	9.42798	6.5	GP193
16.9	1.26	8	18.7865	20.8255	20.0636	19.8134	9.53183	5.5	
21.4	0.92	7	18.8596	20.5771	20.0408	20.0480	9.68288	4.0	GP27
26.4	0.61	8	18.9733	20.3896	20.0552	20.1052	9.80227	2.8	
31.4	0.35	6	19.2229	20.1122	20.0168	20.1844	9.94527	1.4	
31.9	0.33	6	19.2473	20.0855	20.0136	20.1914	9.95475	1.3	CP56
36.9	0.37	7	19.2811	19.9603	19.8336	20.4464	9.92166	1.6	
41.3	0.47	7	19.4025	19.8434	19.7105	20.6548	9.88471	2.0	CP51-2
46.3	0.43	7	19.4049	19.7330	19.8318	20.6486	9.88948	1.9	
51.3	0.48	5	19.6105	19.5064	19.9393	20.5861	9.91286	1.7	
51.7	0.49	5	19.6264	19.4884	19.9440	20.5850	9.91132	1.7	GP219-2
52.6	0.49	4	19.6502	19.4614	19.9620	20.5774	9.91055	1.7	TG20
57.6	0.49	6	19.9023	19.2181	20.1047	20.4650	9.87736	2.1	
58.1	0.50	6	19.9204	19.1978	20.1209	20.4514	9.87193	2.1	GP219-1

Linkage group (VIII)									
map	lod	iter	$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$	var	%expl	locus
0.0	1.54	14	19.7831	18.5790	20.0742	21.5782	8.98989	10.9	GP128-2
5.0	1.44	12	19.7861	18.7108	20.0952	21.4029	9.15497	9.2	
5.8	1.41	12	19.7749	18.7470	20.1148	21.3533	9.20193	8.8	CP112-1
10.8	1.15	10	19.8172	18.8504	20.5143	20.7789	9.51151	5.7	
14.2	1.26	7	19.8380	18.9147	20.7691	20.3083	9.56716	5.1	GP189
15.9	1.44	7	19.9945	18.8190	20.7302	20.3363	9.52298	5.6	CT92
20.8	1.26	5	19.8803	18.9611	20.7090	20.2946	9.63664	4.5	GP74
25.8	1.55	6	19.9464	18.8816	20.9929	19.9414	9.50669	5.7	
27.0	1.62	6	19.9429	18.8998	21.0558	19.8526	9.48833	5.9	GP171
31.1	1.79	6	19.8301	19.0281	21.2297	19.6961	9.43172	6.5	TG349
36.1	1.64	7	19.9880	19.0424	21.2408	19.6618	9.43882	6.4	
41.1	1.33	6	20.2458	19.1172	20.9846	19.6930	9.60233	4.8	
41.8	1.28	6	20.2812	19.1344	20.9294	19.7042	9.63244	4.5	GP92
44.4	0.76	4	20.0331	19.3673	20.7585	19.6834	9.82104	2.6	TG302
49.4	0.71	7	20.0684	19.3405	20.8242	19.6135	9.77732	3.1	
54.4	0.66	10	20.1540	19.3141	20.8429	19.5355	9.74080	3.4	
59.4	0.60	11	20.2976	19.2808	20.8056	19.4566	9.70679	3.8	
64.4	0.56	14	20.4787	19.2350	20.7381	19.3808	9.65648	4.3	
69.4	0.54	17	20.6620	19.1752	20.6790	19.3090	9.57688	5.0	
74.0	0.54	21	20.8133	19.1086	20.6527	19.2445	9.47815	6.0	GP173
79.0	0.54	27	20.8404	19.1463	20.7617	19.0812	9.37220	7.1	
84.0	0.54	35	20.8821	19.1563	20.8430	18.9453	9.26068	8.2	
85.5	0.54	39	20.9044	19.1411	20.8627	18.9151	9.22074	8.6	TG294

Linkage group (IX)									
map	lod	iter	$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$	var	%expl	locus
0.0	0.09	5	19.5615	20.0517	20.0173	19.9044	10.0554	0.3	CP44
3.4	0.16	8	19.3855	19.9619	20.1203	20.0866	10.0090	0.8	GP97
5.8	0.24	6	19.3242	20.0506	20.0950	20.1023	9.98826	1.0	CP20
10.8	0.39	8	19.1232	20.3730	20.0948	19.9530	9.88955	1.9	
15.8	0.39	6	19.2350	20.4148	19.9960	19.8849	9.92321	1.6	
18.5	0.33	4	19.3654	20.3744	19.9108	19.8901	9.96917	1.2	Sol16
19.2	0.31	4	19.3984	20.3701	19.8877	19.8920	9.97716	1.1	Sol16-1
24.2	0.36	7	19.2369	20.4725	19.8366	19.9656	9.91786	1.7	
24.3	0.36	7	19.2353	20.4681	19.8350	19.9737	9.91865	1.7	StVe1
29.3	0.26	9	19.3216	20.3325	19.7407	20.1674	9.95231	1.3	
34.3	0.24	7	19.5208	20.0830	19.6829	20.3401	9.98852	1.0	
36.8	0.24	7	19.5898	19.9914	19.6809	20.3830	9.99312	0.9	GP35
41.8	0.14	7	19.6418	19.9257	19.7662	20.3062	10.0263	0.6	
46.8	0.05	5	19.7405	19.8512	19.8868	20.1476	10.0652	0.2	
47.1	0.05	5	19.7470	19.8465	19.8940	20.1377	10.0667	0.2	GP190
51.3	0.10	6	19.5888	19.7573	20.1200	20.0383	10.0427	0.4	CP135
55.7	0.23	8	19.5685	19.5325	20.3113	20.0124	9.97633	1.1	CP67
60.7	0.40	9	19.3414	19.4943	20.4430	20.0436	9.89062	1.9	
65.7	0.53	9	19.2855	19.4911	20.4908	20.0440	9.86054	2.2	
68.5	0.58	8	19.3141	19.4974	20.4891	20.0333	9.86936	2.1	GP94

Linkage group (X-A)									
map	lod	iter	$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$	var	%expl	locus
0.0	0.59	4	20.3409	19.8084	20.3409	19.1921	9.87222	2.1	CP47-1
0.7	0.60	4	20.3395	19.8118	20.3395	19.1952	9.87417	2.1	TG303
5.7	0.91	19	20.4924	19.7194	20.4615	18.9875	9.71499	3.7	
9.3	1.00	23	20.3329	19.7957	20.5928	18.9170	9.68802	3.9	CP59
14.3	0.92	29	20.7140	19.7625	20.2887	18.9329	9.65034	4.3	
19.3	0.80	30	20.9615	19.7856	20.0009	19.0228	9.61700	4.6	
24.3	0.63	27	21.0239	19.8669	19.7532	19.1773	9.65861	4.2	
25.3	0.59	26	21.0205	19.8855	19.7082	19.2122	9.67240	4.1	GP218
30.3	0.57	29	21.0343	19.7842	19.6582	19.2155	9.63675	4.5	
35.3	0.51	36	20.9717	19.7073	19.6129	19.2660	9.65663	4.3	
40.3	0.43	37	20.8611	19.6049	19.5654	19.4260	9.72114	3.6	
44.0	0.36	116	20.7748	19.2632	19.5277	19.8615	9.72818	3.5	PSC

Linkage group (X-B)									
map	lod	iter	$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$	var	%expl	locus
0.0	0.01	3	19.8842	19.8842	19.9810	19.9810	10.0836	0.0	GP232-1
5.0	0.00	4	19.9422	19.9422	19.8874	19.8874	10.0851	0.0	
10.0	0.03	6	20.0184	20.0184	19.7851	19.7851	10.0725	0.1	
15.0	0.08	5	20.0850	20.0850	19.7123	19.7123	10.0515	0.3	
19.1	0.13	4	20.1178	20.1178	19.6868	19.6868	10.0397	0.5	TG63
21.2	0.10	4	20.1027	20.1027	19.7175	19.7175	10.0488	0.4	CP105
22.0	0.13	4	20.1292	20.1292	19.6951	19.6951	10.0387	0.5	GP87
27.0	0.18	6	20.1844	20.1844	19.6406	19.6406	10.0119	0.7	
32.0	0.21	6	20.2172	20.2172	19.6110	19.6110	9.99397	0.9	

37.0	0.22	5	20.2149	20.2149	19.6182	19.6182	9.99679	0.9	
40.7	0.22	4	20.1948	20.1948	19.6418	19.6418	10.0094	0.8	TG420

Linkage group (XI)									
map	lod	iter	$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$	var	%expl	locus
0.0	0.40	6	19.9775	20.3805	19.5137	20.2965	9.94352	1.4	TG105-1
5.0	0.41	9	20.0784	20.4246	19.3732	20.1444	9.90200	1.8	
10.0	0.37	9	20.0212	20.4716	19.3876	19.9015	9.92732	1.6	
15.0	0.35	4	19.9175	20.5114	19.5370	19.7052	9.96205	1.2	Sol01
15.6	0.34	4	19.9156	20.4926	19.5515	19.6847	9.96587	1.2	GP185
20.6	0.69	8	20.2294	20.5717	19.0441	19.6476	9.76124	3.2	
25.6	1.09	9	20.4730	20.5308	18.8227	19.6085	9.60261	4.8	
29.9	1.23	6	20.5076	20.4536	18.8975	19.6005	9.64819	4.3	GP38
34.9	2.03	7	20.6348	20.8158	18.6857	19.1434	9.25299	8.3	
36.9	2.27	7	20.6281	20.8829	18.6854	19.0500	9.19013	8.9	CP117-1
37.9	2.35	7	20.6115	20.9015	18.6596	19.0603	9.18231	9.0	GP232
42.9	1.95	8	20.4477	20.8742	18.6454	19.1746	9.31130	7.7	
46.4	1.50	6	20.2793	20.7461	18.8411	19.2976	9.55645	5.2	CP117
50.9	1.88	8	20.3213	21.0376	18.9338	18.9433	9.25558	8.2	GP198-3
55.9	2.59	10	20.1820	21.6727	18.8275	18.8718	8.83657	12.4	
60.9	2.87	9	20.3234	21.8132	18.8467	18.9245	8.87910	12.0	
60.9	2.87	9	20.3236	21.8131	18.8467	18.9246	8.87931	12.0	GP255-3
65.9	2.54	10	20.2807	21.3982	19.3547	18.5460	8.91251	11.6	
67.0	2.38	8	20.4809	21.1293	19.3480	18.6277	9.06122	10.2	CP58
72.0	2.24	7	20.3738	21.0501	19.5125	18.6921	9.22470	8.5	
74.1	2.16	7	20.3268	20.9929	19.5776	18.7389	9.31410	7.7	TG194

Linkage group (XII-A)									
map	lod	iter	$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$	var	%expl	locus
0.0	0.77	28	17.1783	18.5153	20.0164	19.3355	8.30463	7.6	GP204
5.0	0.64	21	17.3797	18.6122	19.7564	19.3756	8.55876	5.1	
10.0	0.54	16	17.5756	18.6347	19.4943	19.4960	8.74392	3.3	
15.0	0.48	13	17.7504	18.5937	19.2701	19.6880	8.85189	2.2	
20.0	0.48	11	17.9002	18.4353	19.1100	19.8495	8.91648	1.5	
20.4	0.48	11	17.9120	18.4096	19.0984	19.8549	8.92200	1.5	TG263
24.2	0.33	8	18.1306	18.1139	19.5322	19.7656	9.02914	0.4	TG68
28.7	3.02	5	18.0902	19.8448	20.3238	21.0299	8.99284	10.8	GP99
29.2	2.77	5	18.1002	19.8671	20.4721	20.8337	9.07274	10.0	CP48
31.5	0.63	11	18.1975	12.9292	16.3498	11.9950	8.76074	3.1	CP134-1
33.1	0.41	16	18.4676	16.5662	16.0865	15.4721	8.76743	3.0	TG360

Linkage group (XII-B)									
map	lod	iter	$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$	var	%expl	locus
0.0	0.24	4	19.6352	19.6352	20.2190	20.2190	10.0006	0.8	Sol22
0.8	0.22	4	19.6468	19.6468	20.1983	20.1983	10.0097	0.8	GP268
1.5	0.11	4	19.7233	19.7233	20.1268	20.1268	10.0451	0.4	TG602
6.5	0.01	5	19.8454	19.8454	20.0000	20.0000	10.0798	0.1	
11.5	0.02	6	20.0075	20.0075	19.8269	19.8269	10.0777	0.1	
16.5	0.15	6	20.1608	20.1608	19.6590	19.6590	10.0229	0.6	

21.5	0.35	4	20.2617	20.2617	19.5422	19.5422	9.95672	1.3	CP112
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A.2.3 Landisville 2002 data-set

map	lod	iter	Linkage group (I)				var	%expl	locus
			$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$			
0.0	0.34	4	17.4222	18.5368	17.4222	18.5368	5.97502	1.2	CP108
3.7	0.30	4	17.4182	18.3612	17.4182	18.3612	5.98357	1.0	GP232-2
8.7	2.16	8	17.2058	19.4900	17.2058	19.4900	5.47748	9.4	
11.7	2.49	4	17.1883	19.1659	17.1883	19.1659	5.54035	8.4	CP90
16.7	1.47	6	17.2196	18.8130	17.2196	18.8130	5.68824	5.9	
19.1	0.84	4	17.2968	18.3986	17.2968	18.3986	5.87054	2.9	CP11
21.2	1.19	4	17.2427	18.4898	17.2427	18.4898	5.79884	4.1	CP51
26.2	1.18	6	17.1940	18.4572	17.1940	18.4572	5.75977	4.7	
31.2	0.96	5	17.2085	18.2483	17.2085	18.2483	5.83269	3.5	
32.7	0.88	4	17.2212	18.1738	17.2212	18.1738	5.86233	3.0	TG59-1
37.7	0.73	7	17.1961	18.1487	17.1961	18.1487	5.85262	3.2	
42.7	0.50	8	17.2152	18.0352	17.2152	18.0352	5.89640	2.5	
47.7	0.28	7	17.2753	17.8660	17.2753	17.8660	5.96549	1.3	
52.7	0.12	6	17.3529	17.7028	17.3529	17.7028	6.01706	0.5	
56.5	0.05	4	17.4054	17.6113	17.4054	17.6113	6.03599	0.2	GP167-2
61.5	0.04	5	17.3977	17.6088	17.3977	17.6088	6.03529	0.2	
66.5	0.03	5	17.4063	17.5875	17.4063	17.5875	6.03810	0.1	
71.5	0.02	4	17.4271	17.5564	17.4271	17.5564	6.04208	0.1	
71.5	0.02	4	17.4275	17.5559	17.4275	17.5559	6.04214	0.1	TG53
73.7	0.07	4	17.6086	17.3701	17.6086	17.3701	6.03205	0.2	CP13
77.5	0.14	4	17.6645	17.3185	17.6645	17.3185	6.01634	0.5	GP198-2

map	lod	iter	Linkage group (II)				var	%expl	locus
			$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$			
0.0	1.75	14	17.2209	17.4207	16.7271	19.2914	5.37865	11.0	GP23
3.4	1.90	12	17.1652	17.4065	16.9275	19.3517	5.44010	10.0	Sol20
7.3	1.19	9	17.1659	17.6753	17.0098	18.9013	5.68774	5.9	GP128
12.3	0.93	7	17.0959	17.7976	17.2817	18.5808	5.80770	3.9	
14.6	0.86	6	17.0861	17.8713	17.3728	18.3885	5.84567	3.3	GP131
17.7	0.96	6	17.1173	17.7636	17.3759	18.6414	5.83376	3.5	GP33-1
22.7	0.56	6	17.1923	17.6354	17.5228	18.7791	5.90151	2.4	
24.9	0.31	4	17.2820	17.5420	17.6179	18.5493	5.98041	1.1	GP288-3
28.6	0.40	6	17.3414	17.3728	17.5965	18.5938	5.95485	1.5	GP209
33.6	0.33	9	17.4540	17.1865	17.5963	18.5863	5.93065	1.9	
38.6	0.24	13	17.5659	17.0930	17.6159	18.3018	5.94056	1.7	
43.6	0.18	14	17.6435	17.1913	17.6549	17.5085	6.00263	0.7	
44.0	0.19	13	17.6476	17.2089	17.6575	17.4214	6.00482	0.7	CP157
49.0	0.33	11	17.5680	17.4953	17.7393	16.4157	5.92921	1.9	
54.0	0.65	7	17.4894	17.6019	17.7835	16.1624	5.86502	3.0	
54.1	0.66	7	17.4880	17.6035	17.7839	16.1597	5.86418	3.0	PFC
58.1	0.96	5	17.4323	17.6148	17.8898	16.1267	5.83691	3.5	GP216
60.5	0.97	6	17.4313	17.6505	17.9038	16.1437	5.81878	3.8	GP504

Linkage group (III)									
map	lod	iter	$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$	var	%expl	locus
0.0	0.82	4	17.1490	17.9924	17.1490	17.9924	5.87494	2.8	CP15
2.3	0.94	64	17.0092	18.9064	17.2670	16.9653	5.46407	9.6	GP198-1
2.8	0.77	88	17.0769	18.7791	17.2583	17.0601	5.58416	7.6	GP167-1
7.8	0.72	82	16.9440	18.7391	17.2725	17.1864	5.57274	7.8	
12.8	0.39	18	17.1470	17.8952	17.2703	17.7573	5.94557	1.7	
15.0	0.28	11	17.2502	17.6983	17.2813	17.8032	5.98653	1.0	GP1
19.2	0.17	12	17.6029	17.1828	17.3012	17.8986	5.97285	1.2	CP61
20.3	0.17	11	17.6112	17.2051	17.3029	17.8827	5.97754	1.1	CP133
20.3	0.17	11	17.6112	17.2053	17.3029	17.8825	5.97760	1.1	CP6
25.3	0.19	8	17.5381	17.3523	17.2375	17.8971	5.98826	1.0	
30.3	0.22	5	17.4365	17.4854	17.2215	17.8893	5.99354	0.9	
32.5	0.24	4	17.3984	17.5275	17.2260	17.8793	5.99450	0.9	GP276
34.7	0.36	5	17.7176	17.2465	17.2199	17.8976	5.96305	1.4	GP226
39.7	0.30	10	17.6676	17.2505	17.1560	17.9716	5.94380	1.7	
44.7	0.24	13	17.5298	17.3669	17.1272	17.9829	5.95440	1.5	
49.7	0.24	13	17.3541	17.5677	17.1504	17.9185	5.96890	1.3	
54.7	0.28	10	17.2630	17.7052	17.2083	17.8179	5.97595	1.2	
57.5	0.31	6	17.2435	17.7486	17.2469	17.7610	5.98138	1.1	GP198-4
62.5	0.43	13	17.2248	17.7889	17.1447	17.8330	5.94824	1.6	
67.5	0.53	17	17.2367	17.8000	17.0675	17.8750	5.92669	2.0	
69.2	0.56	19	17.2477	17.7969	17.0493	17.8813	5.92369	2.0	TG28

Linkage group (IV)									
map	lod	iter	$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$	var	%expl	locus
0.0	0.32	5	17.6098	17.2466	17.2120	17.8148	5.97899	1.1	GP180
5.0	0.36	7	17.7846	17.1254	17.1804	17.7841	5.94745	1.6	
10.0	0.24	6	17.8089	17.1786	17.2987	17.5966	5.98925	0.9	
12.2	0.18	4	17.7898	17.2412	17.3728	17.4957	6.00834	0.6	TG123
17.2	0.20	5	17.8793	17.2823	17.4150	17.4303	6.00214	0.7	
19.0	0.19	4	17.8790	17.3122	17.4627	17.4025	6.00624	0.7	CP54
24.0	0.22	7	17.9771	17.3057	17.3574	17.4171	5.98524	1.0	
27.2	0.24	7	17.9891	17.3525	17.2818	17.4262	5.98092	1.1	GP99-2
32.2	0.48	10	18.1769	17.2312	17.0669	17.5483	5.88344	2.7	
37.2	0.80	9	18.2739	17.1464	16.9469	17.6639	5.78806	4.3	GP161-2
42.2	0.57	10	18.1566	17.2664	16.9702	17.6264	5.84975	3.3	
47.2	0.34	8	17.8971	17.5173	17.0513	17.5482	5.95207	1.6	
51.4	0.26	4	17.7043	17.6941	17.1246	17.4914	5.99010	0.9	TG62
51.6	0.26	4	17.7119	17.6824	17.1254	17.4924	5.99042	0.9	Sol21
56.6	0.51	9	18.0809	17.4269	17.0160	17.4473	5.89566	2.5	
61.6	1.07	10	18.4476	17.2078	16.8942	17.3864	5.69207	5.9	
66.6	1.61	9	18.5940	17.1702	16.8183	17.3198	5.57305	7.8	
66.8	1.63	9	18.5947	17.1716	16.8170	17.3174	5.57196	7.8	GP83
71.8	1.52	9	18.5344	17.2075	16.8783	17.2215	5.61091	7.2	
76.8	1.17	7	18.2683	17.3648	17.0410	17.0690	5.77876	4.4	
77.9	1.10	6	18.1977	17.4119	17.0738	17.0396	5.81369	3.8	GP165

Linkage group (V)									
map	lod	iter	$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$	var	%expl	locus
0.0	1.03	32	17.5330	17.9195	19.4311	17.4853	5.13292	10.7	GP21A-8
5.0	0.89	33	17.5131	18.1524	19.4940	17.3778	5.07665	11.6	
10.0	0.74	27	17.6410	18.3002	19.4152	17.2546	5.13133	10.7	
10.8	0.72	25	17.6743	18.3108	19.3873	17.2357	5.15147	10.4	GP179A
15.8	0.71	29	17.7321	18.1319	19.4931	17.1694	5.07974	11.6	
20.8	0.65	34	17.8045	17.9431	19.5325	17.1127	5.04400	12.2	
25.8	0.52	37	17.8947	17.7627	19.4529	17.0852	5.09343	11.4	
30.8	0.33	41	17.9993	17.6198	19.2061	17.1277	5.26585	8.5	
35.8	0.15	41	18.0982	17.5616	18.7808	17.3099	5.53054	4.1	
38.0	0.09	38	18.1293	17.5687	18.5701	17.4369	5.63157	2.5	GP248
39.5	0.06	33	18.1570	17.6212	18.3515	17.5737	5.70538	1.2	GP34
40.9	0.16	27	18.0764	17.6768	18.6932	17.6213	5.65132	2.1	GP188
45.9	0.10	23	18.0603	17.7399	18.6204	17.6540	5.69335	1.4	
50.9	0.06	16	18.1319	17.7127	18.0866	17.5436	5.75325	0.5	
55.9	0.15	7	18.2100	17.5627	17.4193	17.3241	5.73814	0.7	
57.9	0.19	3	18.2010	17.5438	17.3555	17.2996	5.74182	0.6	CP113
59.3	0.07	4	18.0520	17.9637	18.3906	17.7120	5.76432	0.3	CP14-1
62.3	0.06	5	18.0439	17.8286	18.5366	18.1579	5.76732	0.2	Sol22-1
64.4	0.00	3	18.0530	18.1106	17.9773	17.9381	5.78004	0.0	GP284
65.8	1.19	4	17.9920	18.1287	17.3727	16.8317	5.79334	4.2	CP49
67.9	1.28	2	18.0513	18.0918	17.3789	16.8034	5.78094	4.4	TG69
71.6	1.35	5	18.1121	18.0581	17.3682	16.7658	5.75894	4.8	GP22

Linkage group (VI)									
map	lod	iter	$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$	var	%expl	locus
0.0	0.75	29	17.1955	18.8314	17.8046	16.0819	5.11678	15.4	GP164-2
5.0	0.54	32	17.3153	18.6377	17.8113	16.0901	5.23179	13.5	
10.0	0.30	45	17.5007	18.2809	17.7437	16.3168	5.54291	8.3	
12.1	0.22	56	17.5783	18.0133	17.7056	16.5780	5.76219	4.7	CP18
14.0	0.33	48	17.5294	18.1131	17.7985	16.4704	5.66323	6.3	Sol24
19.0	0.15	44	17.3941	17.9753	17.7328	16.8147	5.85483	3.2	
24.0	0.10	20	17.2740	17.8549	17.5422	17.2548	5.98547	1.0	
29.0	0.24	11	17.1758	17.8623	17.3505	17.5327	5.98070	1.1	
33.0	0.42	7	17.1308	17.8831	17.2567	17.6522	5.95446	1.5	GP89
38.0	1.03	7	16.8664	18.2461	17.5077	17.4120	5.80511	4.0	
38.4	1.07	6	16.8654	18.2524	17.5233	17.3977	5.80196	4.0	GP30
42.6	0.57	4	17.0543	18.0136	17.3866	17.5419	5.92661	2.0	GP24
46.3	0.43	6	17.1019	17.9800	17.4973	17.4306	5.94837	1.6	GP211
51.3	0.35	9	17.0883	17.9808	17.5358	17.4082	5.94424	1.7	
56.3	0.26	13	17.0964	17.9484	17.5757	17.3909	5.95122	1.6	
61.3	0.17	16	17.1338	17.8790	17.6082	17.3822	5.97038	1.3	
66.3	0.10	19	17.1997	17.7833	17.6235	17.3837	5.99611	0.8	
71.3	0.05	22	17.2822	17.6851	17.6158	17.3934	6.01931	0.4	
72.0	0.04	23	17.2940	17.6726	17.6130	17.3951	6.02195	0.4	GP76

Linkage group (VII)									
map	lod	iter	$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$	var	%expl	locus
0.0	1.12	5	16.8040	18.1018	17.2790	17.6272	5.81167	3.9	CP52
0.8	1.10	4	16.7935	18.0765	17.2749	17.6307	5.81732	3.8	CP43
4.1	0.79	5	16.8951	17.9664	17.2926	17.6932	5.87682	2.8	GP121
8.1	1.22	7	16.7442	17.9677	17.2046	17.9110	5.78672	4.3	GP179A1
11.9	0.84	6	16.8614	17.7960	17.2550	17.9352	5.86515	3.0	GP193
16.9	0.95	7	16.9268	17.6717	17.0590	18.1532	5.80992	3.9	
21.4	1.09	7	17.0130	17.5670	16.9237	18.2477	5.77322	4.5	GP27
26.4	1.01	8	17.1734	17.5084	16.7935	18.1963	5.78850	4.3	
31.4	1.01	8	17.3923	17.4431	16.6626	18.1195	5.79769	4.1	
31.9	1.02	7	17.4114	17.4385	16.6544	18.1103	5.79900	4.1	CP56
36.9	1.01	7	17.6035	17.3917	16.7015	18.1481	5.78383	4.3	
41.3	0.99	6	17.7783	17.3570	16.8596	18.0738	5.83725	3.5	CP51-2
46.3	0.88	9	17.8660	17.4521	16.7520	18.0483	5.79048	4.2	
51.3	0.50	5	17.8137	17.6712	16.9760	17.6515	5.93269	1.9	
51.7	0.49	5	17.8059	17.6851	16.9961	17.6242	5.93998	1.8	GP219-2
52.6	0.47	5	17.8147	17.6847	17.0142	17.5974	5.94540	1.7	TG20
57.6	0.44	7	17.9214	17.6394	17.0073	17.5641	5.93153	1.9	
58.1	0.43	7	17.9325	17.6349	17.0100	17.5554	5.93082	1.9	GP219-1

Linkage group (VIII)									
map	lod	iter	$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$	var	%expl	locus
0.0	1.06	14	17.5988	16.7429	17.2738	18.5685	5.62834	6.9	GP128-2
5.0	0.72	10	17.3675	16.9602	17.4560	18.3353	5.79991	4.1	
5.8	0.67	10	17.3264	16.9973	17.4869	18.2944	5.82158	3.7	CP112-1
10.8	0.51	10	17.3784	16.9909	17.6682	18.0967	5.88788	2.6	
14.2	0.51	7	17.4072	16.9927	17.8478	17.8311	5.91653	2.1	GP189
15.9	0.47	6	17.3748	17.0377	17.8215	17.8525	5.92879	1.9	CT92
20.8	0.47	4	17.3386	17.1031	17.7253	17.9268	5.94596	1.7	GP74
25.8	0.47	6	17.2305	17.1642	17.9681	17.6253	5.93892	1.8	
27.0	0.49	5	17.2394	17.1790	17.9898	17.5708	5.94102	1.7	GP171
31.1	0.57	6	17.2328	17.1168	18.0678	17.5846	5.90878	2.3	TG349
36.1	0.56	7	17.3955	17.0000	17.9986	17.6652	5.90603	2.3	
41.1	0.66	5	17.6443	16.9140	17.7735	17.7945	5.89774	2.5	
41.8	0.68	5	17.6636	16.9136	17.7412	17.8107	5.89693	2.5	GP92
44.4	0.73	4	17.6414	16.9010	17.5717	17.9261	5.89216	2.5	TG302
49.4	0.75	8	17.6241	16.7943	17.6170	18.0034	5.83525	3.5	
54.4	0.74	12	17.5817	16.7251	17.6979	18.0275	5.79889	4.1	
59.4	0.70	15	17.5254	16.7097	17.8005	17.9841	5.79617	4.1	
64.4	0.64	16	17.4794	16.7506	17.8898	17.8813	5.82517	3.7	
69.4	0.57	16	17.4481	16.8375	17.9532	17.7432	5.86970	2.9	
74.0	0.51	17	17.4284	16.9353	17.9914	17.6146	5.90509	2.3	GP173
79.0	0.22	20	17.4558	17.1458	17.9635	17.4408	5.96289	1.4	
84.0	0.07	20	17.5374	17.3820	17.8560	17.2310	5.99542	0.8	
85.5	0.07	20	17.5597	17.4464	17.8210	17.1705	5.99451	0.9	TG294

Linkage group (IX)									
map	lod	iter	$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$	var	%expl	locus
0.0	0.43	7	17.2360	17.5200	17.2131	17.9955	5.95112	1.6	CP44
3.4	0.78	6	17.3016	17.2429	17.1958	18.1780	5.87402	2.8	GP97
5.8	0.90	5	17.1492	17.2651	17.2435	18.2116	5.85190	3.2	CP20
10.8	1.05	8	16.7887	17.4931	17.3298	18.2459	5.78878	4.3	
15.8	1.29	6	16.6379	17.5792	17.3867	18.2677	5.74946	4.9	
18.5	1.37	5	16.6372	17.5855	17.3947	18.2770	5.75826	4.8	Sol16
19.2	1.37	4	16.6544	17.5802	17.3816	18.2848	5.76202	4.7	Sol16-1
24.2	1.56	7	16.6352	17.5575	17.2379	18.4208	5.68109	6.0	
24.3	1.56	7	16.6360	17.5632	17.2350	18.4161	5.68272	6.0	StVe1
29.3	1.76	8	16.3801	17.5700	17.3156	18.4451	5.58699	7.6	
34.3	1.90	8	16.1418	17.6077	17.4811	18.3126	5.55832	8.1	
36.8	2.00	8	16.0501	17.6513	17.5743	18.1841	5.56659	7.9	GP35
41.8	2.03	8	15.9695	17.9025	17.6917	17.8957	5.54322	8.3	
46.8	1.94	7	16.0494	17.9882	17.7784	17.6958	5.57548	7.8	
47.1	1.92	7	16.0619	17.9841	17.7816	17.6879	5.58289	7.7	GP190
51.3	1.17	7	16.3803	17.7885	17.8360	17.5815	5.75590	4.8	CP135
55.7	0.75	8	16.5957	17.7233	17.9139	17.3645	5.82802	3.6	CP67
60.7	0.48	10	16.7647	17.8539	17.8073	17.2725	5.87495	2.8	
65.7	0.30	10	17.0377	17.9224	17.6504	17.2179	5.93717	1.8	
68.5	0.26	9	17.1750	17.9355	17.5744	17.2042	5.95758	1.5	GP94

Linkage group (X-A)									
map	lod	iter	$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$	var	%expl	locus
0.0	0.45	4	17.5900	17.7703	17.5900	16.9489	5.95041	1.6	CP47-1
0.7	0.44	5	17.5879	17.7746	17.5879	16.9479	5.94952	1.6	TG303
5.7	0.89	44	16.1873	17.9917	18.9687	16.8072	4.91087	18.8	
9.3	0.68	70	16.1762	18.0095	18.9514	16.8725	4.91724	18.7	CP59
14.3	0.59	43	18.6715	17.8993	16.3668	16.9246	5.27605	12.7	
19.3	0.72	33	18.8303	17.8407	16.3062	16.9355	5.18527	14.2	
24.3	0.78	31	18.8500	17.8172	16.3624	16.9403	5.23841	13.4	
25.3	0.79	32	18.8433	17.8162	16.3793	16.9416	5.25763	13.0	GP218
30.3	0.90	27	18.9094	17.6399	16.1643	17.2428	5.10506	15.6	
35.3	1.06	33	18.9194	17.4643	16.0140	17.5808	4.92286	18.6	
40.3	1.18	33	18.8711	17.3689	15.9829	17.7932	4.82790	20.2	
44.0	1.24	32	18.8169	17.3289	16.0076	17.8903	4.81677	20.3	PSC

Linkage group (X-B)									
map	lod	iter	$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$	var	%expl	locus
0.0	0.46	4	17.2506	17.2506	17.8913	17.8913	5.95014	1.6	GP232-1
5.0	0.13	6	17.3411	17.3411	17.7178	17.7178	6.01231	0.6	
10.0	0.00	4	17.4935	17.4935	17.4857	17.4857	6.04625	0.0	
15.0	0.13	5	17.6520	17.6520	17.2860	17.2860	6.01322	0.5	
19.1	0.37	4	17.7462	17.7462	17.1874	17.1874	5.96874	1.3	TG63
21.2	0.45	4	17.7838	17.7838	17.1635	17.1635	5.95035	1.6	CP105
22.0	0.63	4	17.8417	17.8417	17.1109	17.1109	5.91294	2.2	GP87
27.0	0.68	6	17.8815	17.8815	17.0763	17.0763	5.88429	2.7	
32.0	0.69	6	17.8923	17.8923	17.0723	17.0723	5.87822	2.8	

37.0	0.64	5	17.8709	17.8709	17.1003	17.1003	5.89780	2.5	
40.7	0.59	4	17.8389	17.8389	17.1362	17.1362	5.92284	2.0	TG420
Linkage group (XI)									
map	lod	iter	$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$	var	%expl	locus
0.0	0.21	5	17.8036	17.6060	17.2591	17.5541	6.00022	0.8	TG105-1
5.0	0.25	8	17.7503	17.6203	17.1219	17.7318	5.96817	1.3	
10.0	0.25	9	17.6137	17.6404	17.0615	17.7755	5.96732	1.3	
15.0	0.22	4	17.4568	17.6631	17.1310	17.7197	5.99816	0.8	Sol01
15.6	0.26	4	17.4579	17.5735	17.1262	17.8119	5.99205	0.9	GP185
20.6	0.41	9	17.5455	17.6682	16.8582	17.8443	5.92066	2.1	
25.6	0.42	8	17.4585	17.8260	16.9098	17.7154	5.92778	2.0	
29.9	0.45	7	17.2914	17.9532	17.0620	17.5755	5.93035	1.9	GP38
34.9	0.88	8	17.3485	18.2296	17.0189	17.1843	5.81482	3.8	
36.9	1.02	6	17.3748	18.2304	17.0084	17.1584	5.81137	3.9	CP117-1
37.9	1.07	5	17.3611	18.2230	17.0144	17.1832	5.82081	3.7	GP232
42.9	0.88	7	17.3453	18.1946	17.1068	17.1294	5.83821	3.4	
46.4	0.65	5	17.3614	18.0670	17.2012	17.1664	5.90301	2.4	CP117
50.9	0.74	8	17.3674	18.1533	17.3859	16.9675	5.83507	3.5	GP198-3
55.9	0.96	11	17.2436	18.4566	17.3363	16.9636	5.73815	5.1	
60.9	0.93	7	17.2756	18.4924	17.2857	17.2080	5.82007	3.7	
60.9	0.93	7	17.2757	18.4923	17.2857	17.2081	5.82020	3.7	GP255-3
65.9	0.53	13	17.2336	18.1438	17.6848	16.9314	5.82577	3.6	
67.0	0.37	8	17.4234	17.8918	17.6673	17.0246	5.93261	1.9	CP58
72.0	0.21	7	17.4156	17.7556	17.6732	17.1558	5.98737	1.0	
74.1	0.16	7	17.4178	17.7049	17.6707	17.2034	6.00271	0.7	TG194
Linkage group (XII-A)									
map	lod	iter	$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$	var	%expl	locus
0.0	1.16	14	16.7521	17.2275	18.7102	17.4051	5.57768	7.7	GP204
5.0	0.98	12	16.9190	17.1182	18.5644	17.4483	5.68121	6.0	
10.0	0.81	10	17.1234	16.9851	18.3531	17.5360	5.78427	4.3	
15.0	0.72	9	17.3097	16.8741	18.1254	17.6438	5.84529	3.3	
20.0	0.72	7	17.4368	16.8202	17.9374	17.7301	5.87092	2.9	
20.4	0.72	7	17.4450	16.8183	17.9240	17.7355	5.87245	2.9	TG263
24.2	0.82	4	17.5290	16.8238	17.9910	17.6146	5.87370	2.9	TG68
28.7	1.13	6	17.3987	16.7628	18.1460	17.5788	5.79406	4.2	GP99
29.2	1.16	6	17.3981	16.7595	18.1643	17.5755	5.78874	4.3	CP48
31.5	1.08	4	17.4166	16.7667	18.0541	17.6540	5.82078	3.7	CP134-1
33.1	1.18	5	17.4841	16.7597	18.0901	17.6010	5.79293	4.2	TG360
Linkage group (XII-B)									
map	lod	iter	$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$	var	%expl	locus
0.0	0.03	4	17.5623	17.5623	17.4148	17.4148	6.04083	0.1	Sol22
0.8	0.07	4	17.6128	17.6128	17.3658	17.3658	6.03102	0.3	GP268
1.5	0.06	4	17.5993	17.5993	17.3760	17.3760	6.03381	0.2	TG602
6.5	0.13	6	17.6669	17.6669	17.3038	17.3038	6.01333	0.5	
11.5	0.23	6	17.7305	17.7305	17.2342	17.2342	5.98477	1.0	
16.5	0.33	6	17.7676	17.7676	17.1898	17.1898	5.96293	1.4	

21.5	0.40	4	17.7729	17.7729	17.1772	17.1772	5.95777	1.5	CP112
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A.2.4 Locations averaged data-set

Linkage group (I)									
map	lod	iter	$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$	var	%expl	locus
0.0	0.01	4	20.5263	20.7608	20.5263	20.7608	6.45601	0.0	CP108
3.7	0.24	4	20.4740	21.3462	20.4740	21.3462	6.40553	0.8	GP232-2
8.7	1.32	7	20.3078	22.1409	20.3078	22.1409	6.08669	5.8	
11.7	1.56	4	20.2914	21.9237	20.2914	21.9237	6.11448	5.3	CP90
16.7	0.90	7	20.3200	21.6521	20.3200	21.6521	6.21404	3.8	
19.1	0.47	4	20.3900	21.2478	20.3900	21.2478	6.35266	1.6	CP11
21.2	0.45	4	20.3826	21.1786	20.3826	21.1786	6.35837	1.6	CP51
26.2	0.59	6	20.3218	21.2406	20.3218	21.2406	6.30601	2.4	
31.2	0.61	5	20.3061	21.1667	20.3061	21.1667	6.31234	2.3	
32.7	0.60	4	20.3095	21.1277	20.3095	21.1277	6.32347	2.1	TG59-1
37.7	0.63	7	20.2570	21.1722	20.2570	21.1722	6.28007	2.8	
42.7	0.58	8	20.2340	21.1466	20.2340	21.1466	6.27336	2.9	
47.7	0.48	8	20.2499	21.0504	20.2499	21.0504	6.31096	2.3	
52.7	0.36	6	20.2937	20.9243	20.2937	20.9243	6.36444	1.5	
56.5	0.28	4	20.3317	20.8384	20.3317	20.8384	6.39697	1.0	GP167-2
61.5	0.23	6	20.3223	20.8210	20.3223	20.8210	6.39796	0.9	
66.5	0.15	6	20.3522	20.7590	20.3522	20.7590	6.41802	0.6	
71.5	0.08	4	20.4111	20.6763	20.4111	20.6763	6.44160	0.3	
71.5	0.08	4	20.4121	20.6751	20.4121	20.6751	6.44189	0.3	TG53
73.7	0.01	3	20.5782	20.5024	20.5782	20.5024	6.45773	0.0	CP13
77.5	0.01	4	20.5865	20.4954	20.5865	20.4954	6.45709	0.0	GP198-2

Linkage group (II)									
map	lod	iter	$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$	var	%expl	locus
0.0	1.81	12	20.1777	20.5138	19.9719	22.1561	5.91275	8.5	GP23
3.4	2.06	10	20.1496	20.5098	20.0444	22.3285	5.87673	9.0	Sol20
7.3	1.75	8	20.1505	20.6758	20.0606	22.2237	5.97274	7.5	GP128
12.3	1.56	7	20.0424	20.7816	20.3767	22.0685	6.05751	6.2	
14.6	1.48	6	20.0239	20.8603	20.4876	21.9242	6.10549	5.5	GP131
17.7	1.43	6	20.0986	20.8319	20.3923	22.0246	6.13246	5.1	GP33-1
22.7	0.66	6	20.3962	20.6302	20.2803	22.0973	6.28374	2.7	
24.9	0.39	4	20.5377	20.5250	20.3432	21.9809	6.37020	1.4	GP288-3
28.6	0.47	6	20.5695	20.4808	20.2381	21.7976	6.33671	1.9	GP209
33.6	0.68	7	20.6152	20.3995	20.1499	21.9905	6.25835	3.1	
38.6	0.85	8	20.6528	20.3422	20.1014	22.1022	6.19624	4.1	
43.6	0.96	8	20.6614	20.3228	20.1081	22.1510	6.17117	4.5	
44.0	0.97	8	20.6606	20.3230	20.1109	22.1523	6.17111	4.5	CP157
49.0	0.85	8	20.5212	20.4475	20.1459	22.1010	6.19841	4.0	
54.0	0.81	7	20.3891	20.5840	20.1811	21.9580	6.23665	3.4	
54.1	0.81	7	20.3864	20.5871	20.1819	21.9533	6.23770	3.4	PFC
58.1	0.71	5	20.4068	20.6134	20.1941	21.7582	6.29082	2.6	GP216
60.5	0.70	5	20.4474	20.5637	20.1834	21.7124	6.29150	2.6	GP504

Linkage group (III)									
map	lod	iter	$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$	var	%expl	locus
0.0	2.85	4	19.8940	21.4922	19.8940	21.4922	5.84385	9.5	CP15
2.3	4.12	46	20.5524	22.5159	19.0236	20.4154	4.94920	23.4	GP198-1
2.8	3.92	50	20.6122	22.5016	19.0228	20.4145	4.97982	22.9	GP167-1
7.8	3.36	51	20.5429	22.1407	19.0724	20.7004	5.30291	17.9	
12.8	2.53	20	20.6641	21.5234	19.1704	20.9248	5.71327	11.5	
15.0	2.18	15	20.7509	21.3311	19.2406	20.8800	5.84597	9.5	GP1
19.2	1.79	10	20.8852	21.0679	19.3114	20.8901	5.95416	7.8	CP61
20.3	1.76	9	20.9769	20.9342	19.3037	20.9223	5.95777	7.8	CP133
20.3	1.76	9	20.9768	20.9342	19.3038	20.9223	5.95783	7.8	CP6
25.3	1.95	9	20.8221	21.0329	19.2876	21.0759	5.90912	8.5	
30.3	1.82	7	20.6505	21.1324	19.4506	20.9654	6.01006	7.0	
32.5	1.70	4	20.5876	21.1597	19.5705	20.8351	6.08529	5.8	GP276
34.7	1.53	5	20.7700	21.0263	19.5532	20.8289	6.10820	5.4	GP226
39.7	1.33	7	20.6962	21.1730	19.5599	20.7090	6.09231	5.7	
44.7	1.20	15	20.6013	21.4336	19.6448	20.4126	6.04553	6.4	
49.7	1.22	30	20.5408	21.8843	19.8019	19.8356	5.75184	11.0	
54.7	1.34	25	20.6193	22.1012	19.9143	19.4530	5.48186	15.1	
57.5	1.37	23	20.7152	22.0847	19.9406	19.3706	5.46197	15.4	GP198-4
62.5	1.53	26	20.6459	22.1468	19.7541	19.5723	5.45653	15.5	
67.5	1.70	38	20.7638	22.1579	19.4479	19.7332	5.36819	16.9	
69.2	1.75	47	20.8657	22.1679	19.3043	19.7495	5.27225	18.4	TG28

Linkage group (IV)									
map	lod	iter	$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$	var	%expl	locus
0.0	1.19	5	21.3258	20.5869	20.5449	19.8983	6.19469	4.1	GP180
5.0	0.95	6	21.3117	20.4785	20.5364	19.9825	6.22647	3.6	
10.0	0.64	5	21.1561	20.4099	20.5545	20.1150	6.30798	2.3	
12.2	0.51	4	21.0665	20.3953	20.5705	20.1728	6.34395	1.8	TG123
17.2	0.78	5	21.3150	20.3192	20.5918	20.1637	6.27279	2.9	
19.0	0.82	5	21.3290	20.3299	20.6333	20.1713	6.27592	2.8	CP54
24.0	1.03	7	21.4891	20.2354	20.7044	20.1152	6.19222	4.1	
27.2	1.05	8	21.4510	20.2511	20.6921	20.1154	6.20684	3.9	GP99-2
32.2	1.01	8	21.4340	20.1571	20.6644	20.1094	6.19492	4.1	
37.2	0.85	8	21.3290	20.0922	20.5610	20.2120	6.24355	3.3	GP161-2
42.2	0.81	8	21.2586	20.0293	20.7137	20.1316	6.22736	3.6	
47.2	0.69	7	21.1315	20.0282	20.7615	20.1765	6.26845	3.0	
51.4	0.52	4	20.9812	20.1146	20.7321	20.2746	6.34282	1.8	TG62
51.6	0.53	4	20.9865	20.1036	20.7381	20.2714	6.33846	1.9	Sol21
56.6	0.86	8	21.2125	19.9590	20.7257	20.1704	6.22335	3.7	
61.6	1.25	10	21.4354	19.8685	20.6125	20.1353	6.10225	5.5	
66.6	1.60	9	21.5491	19.8649	20.4651	20.1747	6.04293	6.4	
66.8	1.61	9	21.5495	19.8671	20.4604	20.1772	6.04332	6.4	GP83
71.8	2.01	8	21.6365	19.7002	20.4380	20.2340	5.92209	8.3	
76.8	2.02	7	21.5209	19.7163	20.4690	20.2437	5.98244	7.4	
77.9	1.98	7	21.4807	19.7352	20.4790	20.2372	6.00952	7.0	GP165

Linkage group (V)									
map	lod	iter	$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$	var	%expl	locus
0.0	1.00	57	22.0785	20.4004	22.9386	20.8113	4.54979	14.8	GP21A-8
5.0	0.88	47	22.0469	20.5702	22.9557	20.5993	4.55577	14.7	
10.0	0.86	40	22.0883	20.6929	22.9471	20.3509	4.50489	15.5	
10.8	0.86	39	22.0993	20.7060	22.9417	20.3163	4.49689	15.6	GP179A
15.8	0.78	38	22.1375	20.5901	22.8164	20.3437	4.55759	14.7	
20.8	0.72	37	22.1885	20.4426	22.6191	20.4028	4.66181	13.1	
25.8	0.74	35	22.2513	20.2602	22.3483	20.4678	4.77604	11.3	
30.8	0.86	33	22.3134	20.0504	22.0347	20.4996	4.85680	10.0	
35.8	1.12	30	22.3538	19.8329	21.7353	20.4746	4.89302	9.5	
38.0	1.27	28	22.3608	19.7411	21.6234	20.4446	4.90095	9.4	GP248
39.5	1.55	26	22.3952	19.5069	21.3004	20.2455	4.84406	10.2	GP34
40.9	1.42	22	22.3466	19.4723	21.5224	20.2633	4.83327	10.4	GP188
45.9	1.87	17	22.3902	18.9302	21.0706	20.2596	4.71385	12.3	
50.9	2.19	13	22.3870	18.6694	20.6892	20.1537	4.72078	12.2	
55.9	2.13	7	22.2558	18.8050	20.6720	20.0169	4.98205	8.1	
57.9	2.01	3	22.1636	18.9683	20.7885	19.9819	5.12652	5.9	CP113
59.3	1.62	5	22.1105	18.9374	20.7373	19.6216	5.17399	5.1	CP14-1
62.3	1.80	6	22.1298	18.3959	20.6397	20.1706	5.08550	6.5	Sol22-1
64.4	1.39	9	22.0391	18.4612	19.7465	20.1554	5.11355	6.1	GP284
65.8	4.14	4	21.8008	20.5923	20.8467	19.1670	5.56139	13.9	CP49
67.9	4.54	2	21.7279	20.6833	20.9736	19.0547	5.50574	14.8	TG69
71.6	5.17	5	22.0844	20.6114	20.8429	18.9880	5.30091	17.9	GP22

Linkage group (VI)									
map	lod	iter	$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$	var	%expl	locus
0.0	0.47	36	20.7121	21.7559	20.1581	19.4910	5.80899	10.1	GP164-2
5.0	0.36	41	20.7520	21.6260	20.1894	19.5140	5.87771	9.0	
10.0	0.25	45	20.8375	21.3005	20.1897	19.7709	6.11527	5.3	
12.1	0.22	36	20.8775	21.1238	20.1871	19.9313	6.22116	3.7	CP18
14.0	0.22	29	20.8993	21.0242	20.2047	20.0140	6.26985	2.9	Sol24
19.0	0.22	23	20.7908	21.0112	20.1812	20.1573	6.31716	2.2	
24.0	0.27	16	20.6870	21.0089	20.1203	20.3207	6.34003	1.8	
29.0	0.35	11	20.5934	21.0263	20.0907	20.4216	6.34188	1.8	
33.0	0.41	8	20.5329	21.0387	20.1028	20.4562	6.34353	1.8	GP89
38.0	0.49	6	20.4377	21.1412	20.1923	20.4238	6.33625	1.9	
38.4	0.48	6	20.4448	21.1340	20.2086	20.4120	6.34137	1.8	GP30
42.6	0.57	4	20.3692	21.1600	20.2352	20.4242	6.33041	2.0	GP24
46.3	0.69	6	20.3121	21.2767	20.2850	20.3419	6.29059	2.6	GP211
51.3	0.58	9	20.3444	21.2785	20.3372	20.2510	6.29018	2.6	
56.3	0.47	13	20.3888	21.2558	20.4213	20.1300	6.29057	2.6	
61.3	0.39	16	20.4464	21.2068	20.5038	20.0165	6.29064	2.6	
66.3	0.33	16	20.5273	21.1343	20.5343	19.9568	6.30106	2.4	
71.3	0.29	16	20.6356	21.0517	20.5034	19.9457	6.31782	2.2	
72.0	0.28	18	20.6536	21.0405	20.4939	19.9464	6.31958	2.2	GP76

Linkage group (VII)									
map	lod	iter	$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$	var	%expl	locus
0.0	1.82	5	19.9480	21.5042	20.0739	20.4088	6.05277	6.3	CP52
0.8	1.73	4	19.9520	21.4529	20.0729	20.4189	6.07835	5.9	CP43
4.1	2.21	6	19.7452	21.5955	20.2048	20.3891	5.95499	7.8	GP121
8.1	2.28	7	19.6305	21.6123	20.2712	20.3927	5.90539	8.6	GP179A1
11.9	2.00	9	19.6130	21.5394	20.3382	20.4264	5.95234	7.8	GP193
16.9	1.49	8	19.6130	21.2828	20.2241	20.8035	6.05394	6.3	
21.4	1.21	7	19.7167	21.0360	20.0995	21.0494	6.11712	5.3	GP27
26.4	0.93	7	19.8893	20.9038	20.0352	21.0320	6.20534	3.9	
31.4	0.69	6	20.1245	20.7308	20.0138	20.9862	6.29933	2.5	
31.9	0.67	6	20.1472	20.7146	20.0136	20.9806	6.30656	2.4	CP56
36.9	0.70	6	20.2547	20.6370	19.9910	21.1120	6.28234	2.7	
41.3	0.81	6	20.4067	20.5512	19.9893	21.2181	6.26332	3.0	CP51-2
46.3	0.81	8	20.4348	20.4893	19.9607	21.3483	6.20247	4.0	
51.3	0.55	6	20.4886	20.4413	20.1531	21.1548	6.31915	2.2	
51.7	0.53	5	20.4903	20.4378	20.1724	21.1349	6.32903	2.0	GP219-2
52.6	0.49	4	20.5039	20.4227	20.2072	21.1004	6.34569	1.8	TG20
57.6	0.35	7	20.6581	20.2717	20.2939	21.0393	6.36011	1.5	
58.1	0.34	7	20.6731	20.2561	20.3056	21.0295	6.36124	1.5	GP219-1

Linkage group (VIII)									
map	lod	iter	$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$	var	%expl	locus
0.0	1.33	13	20.3093	19.7277	20.5088	21.8598	5.88743	8.9	GP128-2
5.0	1.27	12	20.4304	19.6965	20.5453	21.7209	5.93518	8.1	
5.8	1.25	12	20.4396	19.7040	20.5695	21.6742	5.95912	7.7	CP112-1
10.8	0.89	10	20.4414	19.7924	20.9178	21.2213	6.16384	4.6	
14.2	0.96	7	20.4526	19.8461	21.1493	20.8161	6.20245	4.0	GP189
15.9	1.03	7	20.5339	19.8064	21.1104	20.8485	6.19709	4.1	CT92
20.8	0.87	5	20.4534	19.9116	20.9781	20.9693	6.25958	3.1	GP74
25.8	0.97	6	20.4328	19.9817	21.3093	20.4695	6.22290	3.7	
27.0	1.07	6	20.4289	20.0157	21.3755	20.3696	6.20307	4.0	GP171
31.1	1.53	7	20.3143	20.0722	21.6090	20.2209	6.08350	5.8	TG349
36.1	1.53	8	20.4089	20.0359	21.6497	20.2054	6.06390	6.1	
41.1	1.32	6	20.6391	20.0127	21.4981	20.2607	6.14669	4.8	
41.8	1.29	6	20.6719	20.0151	21.4655	20.2723	6.16225	4.6	GP92
44.4	0.88	4	20.6268	20.0779	21.2714	20.3232	6.26244	3.0	TG302
49.4	0.84	7	20.6463	20.0531	21.3272	20.2741	6.23120	3.5	
54.4	0.78	9	20.6979	20.0375	21.3557	20.2083	6.20405	3.9	
59.4	0.72	11	20.7878	20.0313	21.3527	20.1240	6.17819	4.3	
64.4	0.67	13	20.9033	20.0295	21.3329	20.0273	6.14349	4.9	
69.4	0.64	17	21.0206	20.0209	21.3196	19.9317	6.09230	5.7	
74.0	0.63	20	21.1173	19.9988	21.3228	19.8546	6.03235	6.6	GP173
79.0	0.69	23	21.0732	20.2018	21.4146	19.6100	5.95374	7.8	
84.0	0.79	27	21.0525	20.3080	21.4532	19.4605	5.89418	8.7	
85.5	0.81	29	21.0596	20.3043	21.4560	19.4435	5.88637	8.9	TG294

Linkage group (IX)									
map	lod	iter	$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$	var	%expl	locus
0.0	0.36	5	20.0387	20.5484	20.5140	20.9373	6.37747	1.3	CP44
3.4	0.61	7	20.0200	20.4036	20.4964	21.1202	6.30955	2.3	GP97
5.8	0.73	6	19.9692	20.4701	20.4451	21.1524	6.28399	2.7	CP20
10.8	0.87	8	19.6859	20.7779	20.4647	21.1035	6.20517	3.9	
15.8	0.89	6	19.7103	20.8784	20.4408	21.0239	6.22830	3.6	
18.5	0.83	4	19.8016	20.8767	20.4114	20.9836	6.27103	2.9	Sol16
19.2	0.80	4	19.8314	20.8781	20.3905	20.9811	6.27891	2.8	Sol16-1
24.2	0.85	6	19.7454	20.8896	20.3394	21.0463	6.23609	3.5	
24.3	0.85	6	19.7443	20.8906	20.3386	21.0459	6.23568	3.5	StVe1
29.3	0.81	8	19.7136	20.8289	20.3500	21.0885	6.22816	3.6	
34.3	0.74	8	19.6873	20.7830	20.4424	21.0137	6.25759	3.1	
36.8	0.72	7	19.6703	20.7762	20.5051	20.9397	6.27536	2.8	GP35
41.8	0.51	7	19.7272	20.8242	20.6234	20.7317	6.31176	2.3	
46.8	0.34	6	19.9249	20.7530	20.7299	20.5370	6.36901	1.4	
47.1	0.33	6	19.9406	20.7438	20.7347	20.5281	6.37264	1.3	GP190
51.3	0.31	6	20.0497	20.6278	20.8618	20.3943	6.37316	1.3	CP135
55.7	0.49	7	20.2347	20.4731	21.0398	20.1805	6.32616	2.1	CP67
60.7	0.51	9	20.2184	20.5129	21.0896	20.1013	6.29231	2.6	
65.7	0.50	10	20.2750	20.5198	21.1058	20.0444	6.27943	2.8	
68.5	0.48	10	20.3281	20.5086	21.1046	20.0232	6.27919	2.8	GP94

Linkage group (X-A)									
map	lod	iter	$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$	var	%expl	locus
0.0	0.15	4	20.6070	20.7035	20.6070	20.2085	6.42361	0.6	CP47-1
0.7	0.15	4	20.6064	20.7069	20.6064	20.2056	6.42282	0.6	TG303
5.7	0.29	41	19.9576	20.9221	21.1210	20.1355	6.21372	3.8	
9.3	0.32	35	20.0316	20.9401	21.0624	20.1278	6.24365	3.3	CP59
14.3	0.15	39	20.4055	20.9085	20.6589	20.1619	6.37961	1.2	
19.3	0.12	36	20.9905	20.7935	20.1009	20.2411	6.32619	2.1	
24.3	0.17	26	21.1839	20.7077	19.9262	20.3267	6.26219	3.0	
25.3	0.18	25	21.1998	20.6920	19.9109	20.3456	6.25834	3.1	GP218
30.3	0.32	33	21.4354	20.4792	19.5631	20.6772	6.02529	6.7	
35.3	0.54	37	21.5984	20.2894	19.3171	20.9779	5.70659	11.7	
40.3	0.71	36	21.6412	20.2080	19.2497	21.1117	5.54467	14.2	
44.0	0.79	34	21.6340	20.1838	19.2554	21.1597	5.50183	14.8	PSC

Linkage group (X-B)									
map	lod	iter	$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$	var	%expl	locus
0.0	0.06	4	20.4534	20.4534	20.6865	20.6865	6.44645	0.2	GP232-1
5.0	0.00	4	20.5335	20.5335	20.5514	20.5514	6.45909	0.0	
10.0	0.05	6	20.6427	20.6427	20.4000	20.4000	6.44481	0.2	
15.0	0.20	5	20.7440	20.7440	20.2844	20.2844	6.40706	0.8	
19.1	0.36	4	20.8012	20.8012	20.2322	20.2322	6.37878	1.2	TG63
21.2	0.42	4	20.8314	20.8314	20.2169	20.2169	6.36505	1.5	CP105
22.0	0.60	4	20.8949	20.8949	20.1582	20.1582	6.32369	2.1	GP87
27.0	0.77	6	20.9793	20.9793	20.0736	20.0736	6.25429	3.2	
32.0	0.87	7	21.0179	21.0179	20.0405	20.0405	6.22048	3.7	

37.0	0.89	6	21.0058	21.0058	20.0619	20.0619	6.23646	3.4	
40.7	0.85	4	20.9740	20.9740	20.1005	20.1005	6.26840	3.0	TG420
Linkage group (XI)									
map	lod	iter	$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$	var	%expl	locus
0.0	0.66	6	20.9870	20.8402	20.1014	20.7377	6.31008	2.3	TG105-1
5.0	0.75	9	21.0681	20.8851	19.9100	20.6446	6.21913	3.7	
10.0	0.68	10	20.9562	20.9364	19.8869	20.4477	6.24676	3.3	
15.0	0.55	4	20.7525	20.9770	20.0936	20.2414	6.33592	1.9	Sol01
15.6	0.42	4	20.7522	20.8792	20.1036	20.3090	6.36351	1.5	GP185
20.6	1.01	9	21.1078	20.8963	19.6290	20.2928	6.12945	5.1	
25.6	1.42	9	21.2465	20.8743	19.5334	20.2691	6.04038	6.5	
29.9	1.44	7	21.1809	20.8586	19.6713	20.2710	6.13049	5.1	GP38
34.9	2.31	7	21.1982	21.2481	19.5386	19.8371	5.87024	9.1	
36.9	2.56	6	21.1838	21.2938	19.5326	19.7938	5.84249	9.5	CP117-1
37.9	2.63	6	21.1613	21.3069	19.5215	19.8123	5.84904	9.4	GP232
42.9	2.29	7	21.0489	21.3064	19.5060	19.8658	5.90925	8.5	
46.4	1.89	6	20.9644	21.1957	19.5539	19.9774	6.03962	6.5	CP117
50.9	2.03	7	20.9476	21.3671	19.6780	19.7687	5.92955	8.2	GP198-3
55.9	2.37	9	20.8605	21.7130	19.5001	19.9082	5.77093	10.7	
60.9	2.54	9	20.8928	21.8782	19.5604	20.0484	5.77043	10.7	
60.9	2.54	9	20.8929	21.8782	19.5605	20.0485	5.77052	10.7	GP255-3
65.9	1.95	10	20.8351	21.5549	20.0816	19.5872	5.88243	8.9	
67.0	1.83	8	20.9625	21.3744	20.1529	19.6035	5.94245	8.0	CP58
72.0	1.49	7	20.9109	21.2424	20.2576	19.7200	6.08433	5.8	
74.1	1.34	7	20.8886	21.1676	20.2964	19.7865	6.15063	4.8	TG194
Linkage group (XII-A)									
map	lod	iter	$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$	var	%expl	locus
0.0	1.44	20	19.3119	20.0867	21.8478	20.9406	5.63717	12.7	GP204
5.0	1.27	16	19.4607	20.1305	21.5992	20.9441	5.84972	9.4	
10.0	1.14	11	19.6316	20.1281	21.3213	20.9937	6.02735	6.7	
15.0	1.07	8	19.7822	20.1061	21.0859	21.0551	6.13439	5.0	
20.0	1.07	7	19.8997	20.0929	20.9189	21.0933	6.19405	4.1	
20.4	1.07	6	19.9086	20.0928	20.9072	21.0949	6.19817	4.0	TG263
24.2	1.15	4	19.9344	20.1021	21.0400	21.0092	6.20421	3.9	TG68
28.7	1.16	6	19.8068	20.1054	21.0400	21.0160	6.16988	4.5	GP99
29.2	1.23	6	19.8050	20.1231	21.2296	20.8176	6.15582	4.7	CP48
31.5	1.04	4	19.8829	20.1668	21.1434	20.7660	6.22668	3.6	CP134-1
33.1	1.05	5	19.9897	20.0531	21.1865	20.7164	6.21186	3.8	TG360
Linkage group (XII-B)									
map	lod	iter	$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$	var	%expl	locus
0.0	0.01	4	20.4935	20.4935	20.5899	20.5899	6.45685	0.0	Sol22
0.8	0.00	3	20.5273	20.5273	20.5540	20.5540	6.45899	0.0	GP268
1.5	0.00	3	20.5559	20.5559	20.5246	20.5246	6.45892	0.0	TG602
6.5	0.07	6	20.6807	20.6807	20.3924	20.3924	6.43841	0.3	
11.5	0.28	7	20.8238	20.8238	20.2381	20.2381	6.37352	1.3	
16.5	0.58	6	20.9251	20.9251	20.1238	20.1238	6.29890	2.5	

21.5 0.87 5 20.9674 20.9674 20.0679 20.0679 6.25745 3.1 CP112

A.2.5 Locations averaged with 19 clones removal data-set

map	lod	iter	Linkage group (I)				var	%expl	locus
			$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$			
0.0	0.02	4	20.5210	20.8401	20.5210	20.8401	6.96628	0.1	CP108
3.7	0.27	4	20.4601	21.4730	20.4601	21.4730	6.89699	1.1	GP232-2
8.7	1.72	6	20.2574	22.5383	20.2574	22.5383	6.40619	8.1	
11.7	2.24	4	20.2242	22.4598	20.2242	22.4598	6.36471	8.7	CP90
16.7	1.92	7	20.2034	22.3446	20.2034	22.3446	6.36360	8.7	
19.1	1.40	4	20.2609	21.9253	20.2609	21.9253	6.58470	5.6	CP11
21.2	1.36	4	20.2477	21.8248	20.2477	21.8248	6.59584	5.4	CP51
26.2	1.56	6	20.1598	21.8675	20.1598	21.8675	6.46682	7.2	
31.2	1.43	6	20.1593	21.6546	20.1593	21.6546	6.54732	6.1	
32.7	1.35	4	20.1740	21.5554	20.1740	21.5554	6.60007	5.3	TG59-1
37.7	1.33	8	20.0988	21.6069	20.0988	21.6069	6.50101	6.8	
42.7	1.15	9	20.0772	21.5292	20.0772	21.5292	6.51401	6.6	
47.7	0.86	8	20.1158	21.3325	20.1158	21.3325	6.63570	4.8	
52.7	0.58	6	20.1950	21.0985	20.1950	21.0985	6.77935	2.8	
56.5	0.41	4	20.2585	20.9519	20.2585	20.9519	6.85615	1.7	GP167-2
61.5	0.35	6	20.2404	20.9381	20.2404	20.9381	6.85288	1.7	
66.5	0.25	6	20.2758	20.8594	20.2758	20.8594	6.88776	1.2	
71.5	0.13	4	20.3550	20.7440	20.3550	20.7440	6.93444	0.5	
71.5	0.13	4	20.3563	20.7422	20.3563	20.7422	6.93504	0.5	TG53
73.7	0.00	3	20.5444	20.5369	20.5444	20.5369	6.97218	0.0	CP13
77.5	0.00	3	20.5594	20.5224	20.5594	20.5224	6.97186	0.0	GP198-2

map	lod	iter	Linkage group (II)				var	%expl	locus
			$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$			
0.0	2.05	13	20.1623	20.6948	19.5278	22.2862	6.17450	11.4	GP23
3.4	2.16	11	20.1358	20.6874	19.6064	22.3619	6.18755	11.3	Sol20
7.3	1.94	9	20.1441	20.8651	19.6387	22.2493	6.28947	9.8	GP128
12.3	1.66	7	20.0465	20.9827	19.9359	22.0734	6.43692	7.7	
14.6	1.56	6	20.0095	21.0588	20.1001	21.9327	6.50091	6.8	GP131
17.7	1.66	6	20.1411	21.0058	19.8781	22.0632	6.50945	6.6	GP33-1
22.7	0.88	7	20.4977	20.7055	19.8376	22.1761	6.67241	4.3	
24.9	0.53	4	20.6294	20.5729	20.0426	21.9809	6.82105	2.2	GP288-3
28.6	0.67	5	20.6374	20.5179	19.9693	21.9318	6.77104	2.9	GP209
33.6	0.75	7	20.6730	20.4980	19.8594	21.9882	6.71154	3.7	
38.6	0.78	8	20.6917	20.5003	19.8085	22.0170	6.68021	4.2	
43.6	0.76	8	20.6775	20.5253	19.8423	22.0191	6.69218	4.0	
44.0	0.75	8	20.6750	20.5279	19.8480	22.0179	6.69479	4.0	CP157
49.0	0.66	8	20.5669	20.6264	19.9173	22.0337	6.71909	3.6	
54.0	0.59	7	20.4621	20.7285	20.0027	21.8941	6.76747	2.9	
54.1	0.59	7	20.4598	20.7308	20.0048	21.8884	6.76886	2.9	PFC
58.1	0.49	5	20.4660	20.7687	20.0292	21.6224	6.82452	2.1	GP216
60.5	0.48	5	20.5115	20.7322	20.0151	21.5407	6.82974	2.0	GP504

Linkage group (III)									
map	lod	iter	$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$	var	%expl	locus
0.0	2.42	4	19.8579	21.4997	19.8579	21.4997	6.31738	9.4	CP15
2.3	3.51	51	20.5226	22.5862	18.9944	20.3553	5.33331	23.5	GP198-1
2.8	3.32	56	20.6005	22.5800	18.9903	20.3455	5.35906	23.1	GP167-1
7.8	3.01	49	20.4871	22.4263	19.0413	20.4862	5.55206	20.4	
12.8	2.35	31	20.5506	21.9192	19.1652	20.6736	6.03400	13.5	
15.0	2.03	20	20.6378	21.6591	19.2440	20.6958	6.24123	10.5	GP1
19.2	1.52	11	20.8217	21.2166	19.3161	20.8017	6.44481	7.6	CP61
20.3	1.46	9	20.9051	21.0846	19.3152	20.8388	6.46622	7.3	CP133
20.3	1.46	9	20.9050	21.0845	19.3153	20.8389	6.46628	7.3	CP6
25.3	1.60	9	20.7814	21.1303	19.2992	21.0144	6.41334	8.0	
30.3	1.47	7	20.6457	21.1910	19.4720	20.9020	6.52064	6.5	
32.5	1.36	4	20.5970	21.2042	19.5928	20.7778	6.59629	5.4	GP276
34.7	1.22	5	20.7632	21.0767	19.5759	20.7679	6.61976	5.1	GP226
39.7	1.12	8	20.6728	21.2460	19.5713	20.6470	6.58605	5.5	
44.7	1.08	16	20.5651	21.5385	19.6297	20.3643	6.49537	6.8	
49.7	1.12	31	20.5170	21.9998	19.7374	19.8413	6.15818	11.7	
54.7	1.19	26	20.6404	22.1970	19.8012	19.5141	5.91150	15.2	
57.5	1.18	24	20.7634	22.1744	19.8070	19.4408	5.89791	15.4	GP198-4
62.5	1.36	29	20.7306	22.2545	19.5750	19.6257	5.83864	16.3	
67.5	1.53	57	21.0046	22.3215	19.1057	19.7017	5.51060	21.0	
69.2	1.60	106	21.2688	22.4320	18.7634	19.6199	5.04546	27.6	TG28

Linkage group (IV)									
map	lod	iter	$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$	var	%expl	locus
0.0	1.24	5	21.2969	20.5667	20.7072	19.7463	6.62882	4.9	GP180
5.0	1.15	6	21.3255	20.4697	20.7200	19.7570	6.62524	5.0	
10.0	0.94	5	21.2221	20.4132	20.7402	19.8414	6.69485	4.0	
12.2	0.84	4	21.1514	20.3984	20.7459	19.8959	6.73719	3.4	TG123
17.2	0.96	5	21.3427	20.3518	20.7689	19.9377	6.68950	4.1	
19.0	0.94	5	21.3411	20.3723	20.7838	19.9791	6.71017	3.8	CP54
24.0	1.24	7	21.5310	20.2099	20.8869	19.9330	6.58764	5.5	
27.2	1.30	7	21.5169	20.1755	20.8631	19.9597	6.59887	5.4	GP99-2
32.2	1.11	8	21.4842	20.0723	20.7695	20.0153	6.62327	5.0	
37.2	0.86	8	21.3997	19.9910	20.5643	20.2068	6.70135	3.9	GP161-2
42.2	0.86	9	21.3613	19.8947	20.7261	20.1421	6.66790	4.4	
47.2	0.74	8	21.2354	19.8964	20.7933	20.1776	6.71224	3.7	
51.4	0.56	4	21.0519	20.0262	20.7839	20.2593	6.81362	2.3	TG62
51.6	0.57	4	21.0582	20.0153	20.7891	20.2570	6.80859	2.3	Sol21
56.6	0.83	8	21.3291	19.9278	20.7218	20.1591	6.68584	4.1	
61.6	1.13	10	21.6108	19.9092	20.5408	20.1148	6.54900	6.1	
66.6	1.40	10	21.7401	19.9667	20.3541	20.1355	6.48493	7.0	
66.8	1.41	10	21.7396	19.9706	20.3487	20.1372	6.48590	7.0	GP83
71.8	1.73	8	21.7868	19.8157	20.3463	20.1520	6.38018	8.5	
76.8	1.70	6	21.6057	19.8313	20.4051	20.1254	6.47452	7.1	
77.9	1.66	6	21.5536	19.8487	20.4190	20.1151	6.50662	6.7	GP165

Linkage group (V)									
map	lod	iter	$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$	var	%expl	locus
0.0	0.77	65	21.9677	20.5591	22.9592	20.8385	5.11792	12.6	GP21A-8
5.0	0.68	49	21.9630	20.7202	23.0012	20.6244	5.08547	13.0	
10.0	0.65	40	22.0461	20.8223	23.0060	20.3903	5.01195	14.1	
10.8	0.65	39	22.0631	20.8332	23.0013	20.3588	5.00280	14.2	GP179A
15.8	0.56	37	22.1154	20.7361	22.8599	20.3785	5.08379	13.1	
20.8	0.49	36	22.1806	20.6200	22.6374	20.4420	5.21813	11.1	
25.8	0.48	35	22.2553	20.4803	22.3333	20.5304	5.36598	9.0	
30.8	0.56	34	22.3236	20.3226	21.9774	20.6111	5.47529	7.4	
35.8	0.75	34	22.3626	20.1625	21.6247	20.6585	5.52680	6.7	
38.0	0.86	32	22.3669	20.0946	21.4900	20.6624	5.53551	6.6	GP248
39.5	1.12	30	22.3938	19.8731	21.1262	20.4754	5.47022	7.5	GP34
40.9	0.94	22	22.3459	19.8222	21.4554	20.4554	5.46403	7.6	GP188
45.9	1.27	17	22.3745	19.2753	20.8895	20.4002	5.33233	9.5	
50.9	1.59	16	22.3515	18.8718	20.2504	20.1934	5.25891	10.5	
55.9	1.63	9	22.2106	18.8863	19.9332	19.9509	5.47506	7.4	
57.9	1.57	3	22.1197	19.0076	19.9485	19.9116	5.62024	5.4	CP113
59.3	1.21	4	22.0948	19.1446	20.4984	19.9102	5.68137	4.5	CP14-1
62.3	1.57	5	22.1353	18.3915	19.9620	20.2521	5.53022	6.7	Sol22-1
64.4	1.16	8	21.9680	18.6281	19.3932	20.2922	5.59412	5.7	GP284
65.8	3.29	4	21.7873	20.6193	20.8461	19.2221	6.07344	12.9	CP49
67.9	3.71	2	21.7530	20.7259	20.9902	19.0958	5.99409	14.0	TG69
71.6	4.20	5	22.0688	20.6513	20.8254	19.0281	5.79693	16.9	GP22

Linkage group (VI)									
map	lod	iter	$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$	var	%expl	locus
0.0	0.47	35	20.7234	22.0469	20.2340	19.0696	5.99295	14.0	GP164-2
5.0	0.38	42	20.7709	21.9763	20.2797	18.9669	5.95958	14.5	
10.0	0.21	68	20.8479	21.7093	20.2664	19.1836	6.21737	10.8	
12.1	0.15	87	20.8674	21.3153	20.2663	19.6419	6.60724	5.2	CP18
14.0	0.13	41	20.8839	20.9842	20.2942	19.9832	6.80755	2.4	Sol24
19.0	0.13	30	20.7635	21.0110	20.2787	20.1183	6.84780	1.8	
24.0	0.17	20	20.6438	21.0408	20.2171	20.2975	6.86922	1.5	
29.0	0.25	13	20.5368	21.0906	20.1738	20.4178	6.86239	1.6	
33.0	0.33	9	20.4685	21.1250	20.1721	20.4651	6.85449	1.7	GP89
38.0	0.43	6	20.3741	21.2909	20.3351	20.3536	6.83255	2.0	
38.4	0.43	6	20.3850	21.2783	20.3488	20.3427	6.83901	1.9	GP30
42.6	0.54	4	20.3165	21.3065	20.3009	20.4340	6.81976	2.2	GP24
46.3	0.66	6	20.2551	21.4196	20.3615	20.3334	6.77158	2.9	GP211
51.3	0.53	9	20.2789	21.3872	20.4462	20.2063	6.77393	2.8	
56.3	0.42	14	20.3065	21.3310	20.5759	20.0499	6.76680	2.9	
61.3	0.35	17	20.3410	21.2460	20.6998	19.9282	6.75867	3.1	
66.3	0.30	19	20.3945	21.1359	20.7624	19.8891	6.77557	2.8	
71.3	0.26	20	20.4719	21.0174	20.7601	19.9122	6.81429	2.3	
72.0	0.25	20	20.4845	21.0013	20.7554	19.9181	6.82025	2.2	GP76

Linkage group (VII)									
map	lod	iter	$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$	var	%expl	locus
0.0	2.09	5	20.0071	21.5947	19.6293	20.4585	6.39667	8.3	CP52
0.8	1.99	4	20.0097	21.5376	19.6325	20.4685	6.42878	7.8	CP43
4.1	2.07	6	19.8745	21.6010	19.7643	20.4489	6.39135	8.3	GP121
8.1	2.05	7	19.7385	21.6021	19.8417	20.4602	6.36675	8.7	GP179A1
11.9	1.74	9	19.7145	21.5096	19.9176	20.5117	6.44314	7.6	GP193
16.9	1.48	7	19.7097	21.2467	19.6946	20.9613	6.47725	7.1	
21.4	1.41	8	19.7903	21.0326	19.5219	21.2059	6.46493	7.3	GP27
26.4	1.23	7	19.9673	20.9458	19.4659	21.1379	6.55113	6.0	
31.4	1.01	6	20.1996	20.8121	19.5161	21.0336	6.68051	4.2	
31.9	0.99	6	20.2226	20.7987	19.5240	21.0233	6.69187	4.0	CP56
36.9	1.00	6	20.3412	20.7332	19.5785	21.1503	6.66627	4.4	
41.3	1.09	6	20.5259	20.6463	19.6379	21.2440	6.65716	4.5	CP51-2
46.3	1.10	8	20.5742	20.5934	19.5990	21.4465	6.53965	6.2	
51.3	0.71	6	20.6160	20.5537	19.8928	21.2016	6.74480	3.3	
51.7	0.68	5	20.6147	20.5505	19.9236	21.1739	6.76395	3.0	GP219-2
52.6	0.62	5	20.6318	20.5370	19.9738	21.1217	6.79613	2.5	TG20
57.6	0.38	6	20.7044	20.4695	20.0781	21.0331	6.84566	1.8	
58.1	0.36	7	20.7111	20.4625	20.0936	21.0182	6.85249	1.7	GP219-1

Linkage group (VIII)									
map	lod	iter	$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$	var	%expl	locus
0.0	1.31	13	20.2629	19.5745	20.5726	21.9699	6.26237	10.2	GP128-2
5.0	1.30	12	20.4597	19.5183	20.6059	21.8008	6.30478	9.6	
5.8	1.28	12	20.4793	19.5260	20.6320	21.7473	6.33151	9.2	CP112-1
10.8	1.00	11	20.4819	19.6210	21.0381	21.2122	6.57297	5.7	
14.2	1.14	8	20.4966	19.6786	21.2719	20.7713	6.60096	5.3	GP189
15.9	1.23	7	20.5771	19.6125	21.2318	20.8138	6.58723	5.5	CT92
20.8	1.02	5	20.4825	19.7259	21.1228	20.9006	6.67734	4.2	GP74
25.8	1.30	6	20.4487	19.7748	21.5044	20.3777	6.57351	5.7	
27.0	1.43	6	20.4279	19.8231	21.5768	20.2783	6.54511	6.1	GP171
31.1	1.95	7	20.2278	19.9528	21.8538	20.1271	6.37782	8.5	TG349
36.1	1.97	8	20.3422	19.9134	21.9480	20.1223	6.33640	9.1	
41.1	1.71	7	20.6445	19.8942	21.7979	20.1962	6.46766	7.2	
41.8	1.66	6	20.6889	19.8995	21.7591	20.2110	6.49455	6.9	GP92
44.4	1.16	4	20.6718	19.9716	21.5002	20.2621	6.65118	4.6	TG302
49.4	1.06	7	20.7402	19.9392	21.5239	20.1998	6.61511	5.1	
54.4	0.96	9	20.8643	19.9121	21.5068	20.1187	6.58146	5.6	
59.4	0.88	13	21.0434	19.8909	21.4546	20.0165	6.53531	6.3	
64.4	0.84	16	21.2376	19.8781	21.4003	19.8991	6.46077	7.3	
69.4	0.83	19	21.4035	19.8665	21.3768	19.7814	6.35918	8.8	
74.0	0.85	23	21.5247	19.8425	21.3874	19.6845	6.24942	10.4	GP173
79.0	0.95	27	21.5416	20.0588	21.4495	19.4062	6.12095	12.2	
84.0	1.08	34	21.5890	20.1178	21.4664	19.2445	6.00702	13.8	
85.5	1.11	36	21.6188	20.0881	21.4690	19.2236	5.97386	14.3	TG294

Linkage group (IX)									
map	lod	iter	$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$	var	%expl	locus
0.0	0.64	6	19.7085	20.6429	20.4563	21.0492	6.79045	2.6	CP44
3.4	0.75	7	19.9230	20.3904	20.3833	21.2525	6.74754	3.2	GP97
5.8	0.85	7	19.9249	20.4526	20.2830	21.3039	6.71621	3.7	CP20
10.8	0.94	9	19.5906	20.7224	20.3050	21.2984	6.62648	5.0	
15.8	0.89	6	19.6179	20.8008	20.3238	21.2047	6.68054	4.2	
18.5	0.80	5	19.7219	20.8022	20.3303	21.1289	6.74571	3.2	Sol16
19.2	0.78	4	19.7554	20.8073	20.3121	21.1223	6.75406	3.1	Sol16-1
24.2	0.78	6	19.7548	20.7797	20.2462	21.1961	6.71980	3.6	
24.3	0.78	6	19.7556	20.7819	20.2454	21.1936	6.72029	3.6	StVe1
29.3	0.73	7	19.7239	20.7139	20.2923	21.2033	6.71848	3.6	
34.3	0.67	7	19.6089	20.7140	20.4471	21.0686	6.74682	3.2	
36.8	0.69	7	19.5239	20.7433	20.5439	20.9619	6.75161	3.2	GP35
41.8	0.66	7	19.4237	20.8630	20.7112	20.7118	6.73533	3.4	
46.8	0.66	7	19.4973	20.8345	20.8473	20.4963	6.75324	3.1	
47.1	0.65	7	19.5087	20.8249	20.8530	20.4871	6.75694	3.1	GP190
51.3	0.48	6	19.7613	20.6174	20.9455	20.3788	6.80951	2.3	CP135
55.7	0.54	7	20.1165	20.4069	21.1012	20.1582	6.79026	2.6	CP67
60.7	0.47	9	20.2234	20.4342	21.1047	20.0921	6.78946	2.6	
65.7	0.40	9	20.3994	20.4176	21.0782	20.0500	6.80313	2.4	
68.5	0.36	9	20.5029	20.3921	21.0612	20.0347	6.80779	2.4	GP94

Linkage group (X-A)									
map	lod	iter	$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$	var	%expl	locus
0.0	0.27	4	20.6616	20.7493	20.6616	20.0443	6.89414	1.1	CP47-1
0.7	0.27	4	20.6606	20.7544	20.6606	20.0407	6.89262	1.1	TG303
5.7	0.42	39	19.9287	21.0349	21.2060	19.9441	6.62012	5.0	
9.3	0.45	32	20.0507	21.0754	21.0815	19.9335	6.67831	4.2	CP59
14.3	0.26	36	20.3950	21.0691	20.6952	19.9532	6.80648	2.4	
19.3	0.20	32	20.9517	20.9766	20.1501	20.0193	6.77628	2.8	
24.3	0.21	26	21.1762	20.9111	19.9352	20.0919	6.70353	3.9	
25.3	0.21	26	21.1967	20.8999	19.9139	20.1078	6.69815	3.9	GP218
30.3	0.27	29	21.3619	20.6976	19.6385	20.4415	6.58359	5.6	
35.3	0.42	37	21.5085	20.4245	19.3892	20.8846	6.30999	9.5	
40.3	0.56	35	21.5565	20.2841	19.3134	21.1111	6.12486	12.2	
44.0	0.63	33	21.5557	20.2270	19.3178	21.2015	6.06498	13.0	PSC

Linkage group (X-B)									
map	lod	iter	$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$	var	%expl	locus
0.0	0.08	4	20.4258	20.4258	20.7350	20.7350	6.94987	0.3	GP232-1
5.0	0.00	5	20.5138	20.5138	20.5823	20.5823	6.97108	0.0	
10.0	0.03	6	20.6336	20.6336	20.4103	20.4103	6.96008	0.2	
15.0	0.17	5	20.7476	20.7476	20.2734	20.2734	6.91690	0.8	
19.1	0.33	4	20.8162	20.8162	20.2059	20.2059	6.87995	1.3	TG63
21.2	0.39	4	20.8514	20.8514	20.1891	20.1891	6.86295	1.6	CP105
22.0	0.57	4	20.9249	20.9249	20.1210	20.1210	6.81095	2.3	GP87
27.0	0.69	6	20.9978	20.9978	20.0340	20.0340	6.74056	3.3	
32.0	0.74	7	21.0190	21.0190	20.0049	20.0049	6.71590	3.7	

37.0	0.72	6	20.9894	20.9894	20.0349	20.0349	6.74527	3.3	
40.7	0.67	4	20.9471	20.9471	20.0807	20.0807	6.78524	2.7	TG420

Linkage group (XI)									
map	lod	iter	$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$	var	%expl	locus
0.0	0.74	7	21.2404	20.8019	20.0373	20.5997	6.75556	3.1	TG105-1
5.0	0.78	10	21.2920	20.8511	19.8530	20.4550	6.64970	4.6	
10.0	0.63	10	21.0809	20.9079	19.9299	20.2047	6.73095	3.5	
15.0	0.52	4	20.8141	20.9497	20.2203	20.0302	6.82713	2.1	Sol01
15.6	0.38	4	20.8136	20.8424	20.2298	20.1085	6.86406	1.6	GP185
20.6	0.89	10	21.2309	20.8525	19.7073	20.0687	6.60330	5.3	
25.6	1.30	10	21.4178	20.8173	19.6036	20.0487	6.48593	7.0	
29.9	1.33	7	21.3616	20.7978	19.7543	20.0785	6.58876	5.5	GP38
34.9	2.08	7	21.3710	21.1948	19.6144	19.7122	6.32213	9.3	
36.9	2.25	6	21.3518	21.2385	19.5908	19.7189	6.30631	9.6	CP117-1
37.9	2.30	6	21.3361	21.2437	19.5758	19.7507	6.31757	9.4	GP232
42.9	2.12	6	21.2142	21.2904	19.4907	19.8279	6.35243	8.9	
46.4	1.88	6	21.1267	21.2236	19.4392	19.9612	6.45086	7.5	CP117
50.9	1.99	7	21.0590	21.4446	19.5235	19.7595	6.32707	9.3	GP198-3
55.9	2.35	9	20.9031	21.8695	19.3500	19.9094	6.11501	12.3	
60.9	2.59	9	20.8845	22.1061	19.4489	20.0561	6.10432	12.4	
60.9	2.59	9	20.8846	22.1061	19.4491	20.0562	6.10446	12.4	GP255-3
65.9	1.80	10	20.8210	21.6585	20.0345	19.5434	6.30056	9.6	
67.0	1.66	8	20.9836	21.4272	20.1315	19.5503	6.38528	8.4	CP58
72.0	1.32	7	20.9134	21.2661	20.2652	19.6633	6.55665	6.0	
74.1	1.17	7	20.8852	21.1808	20.3145	19.7291	6.63301	4.9	TG194

Linkage group (XII-A)									
map	lod	iter	$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$	var	%expl	locus
0.0	0.82	17	19.6215	20.1510	21.7267	20.7082	6.42009	7.9	GP204
5.0	0.67	13	19.7814	20.1374	21.4753	20.7632	6.58858	5.5	
10.0	0.56	10	19.9440	20.0986	21.2100	20.8572	6.71059	3.8	
15.0	0.52	8	20.0763	20.0635	20.9803	20.9560	6.77131	2.9	
20.0	0.54	6	20.1669	20.0560	20.8146	21.0223	6.79685	2.5	
20.4	0.55	6	20.1731	20.0568	20.8030	21.0261	6.79850	2.5	TG263
24.2	0.81	4	20.0325	20.0779	21.0926	20.9193	6.74571	3.2	TG68
28.7	0.86	6	19.9007	20.0418	21.0783	20.9467	6.70224	3.9	GP99
29.2	0.99	6	19.8975	20.0548	21.2952	20.7201	6.66665	4.4	CP48
31.5	0.83	4	19.9920	20.0714	21.1712	20.7011	6.74011	3.3	CP134-1
33.1	0.91	5	20.0295	20.0231	21.2429	20.6166	6.70561	3.8	TG360

Linkage group (XII-B)									
map	lod	iter	$\mu_{ac}\{00\}$	$\mu_{ad}\{00\}$	$\mu_{bc}\{00\}$	$\mu_{bd}\{00\}$	var	%expl	locus
0.0	0.02	4	20.6099	20.6099	20.4728	20.4728	6.96750	0.1	Sol22
0.8	0.04	4	20.6526	20.6526	20.4347	20.4347	6.96033	0.2	GP268
1.5	0.04	4	20.6526	20.6526	20.4347	20.4347	6.96033	0.2	TG602
6.5	0.20	6	20.8119	20.8119	20.2761	20.2761	6.90045	1.0	
11.5	0.50	7	20.9735	20.9735	20.1063	20.1063	6.78423	2.7	

16.5	0.85	7	21.0697	21.0697	19.9912	19.9912	6.68153	4.2	
21.5	1.16	5	21.0956	21.0956	19.9399	19.9399	6.63881	4.8	CP112

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Vita

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