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Mapping of a novel, major late blight resistance locus in the diploid (1EBN) Mexican *Solanum pinnatisectum* Dunal on chromosome VII

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Abstract

Late blight caused by the oomycete *Phytophthora infestans* (Mont.) de Bary (*Pi*) is the most important foliar disease of potato worldwide. An intraspecific hybrid between individuals of a resistant and a susceptible *S. pinnatisectum* accession was backcrossed to the susceptible parent to generate a segregating population for late blight resistance consisting of 84 plants. In detached-leaflet assays, reaction to late blight segregated in a 1r:1s manner in BC_1 progeny indicating the presence of a single dominant resistance gene. A genetic map was constructed based on 1,583 DArT/SSR markers which were allocated to 12 linkage groups, covering 1,793.5 cM with an average marker distance of 1.1 cM. The late blight resistance locus derived from *S. pinnatisectum* was mapped on chromosome VII. In comparison with the previously reported resistance genes *Rpi1* and *Rpi2*, the new target resistance locus most likely is located on the opposite arm of chromosome VII. Results of this study will serve as a basis for future fine mapping of the late blight resistance locus and the development of locus-specific markers for marker-assisted selection.

KEYWORDS
genetic mapping, resistance to late blight, wild potato species

1 | INTRODUCTION

The cultivated potato (*Solanum tuberosum* L.) is the fourth most important food crop next to wheat, rice and maize in the world (Spooner et al., 2010). Late blight caused by the oomycete *Phytophthora infestans* (Mont.) de Bary (*Pi*) is the most widely spread foliar disease of potato worldwide. It can be assumed that the expected climate changes with higher temperatures and increasing precipitations will enhance the damage caused by *Pi*.

Breeding of resistant varieties is considered to be the most sustainable approach for the management of late blight, and it also contributes to the reduction in fungicide applications. Race-specific late blight resistance genes have already been introgressed into common potato from the wild species *S. demissum*, *S. stoloniferum* and the semi-cultivated *S. tuberosum* subsp. *andigenum* and *S. phureja* (Bradshaw, Bryan, & Ramsay, 2006). Of the eleven *S. demissum*-derived resistance genes, five have been mapped and cloned. These are *R1* on chromosome V (Ballvora et al., 2002), *R2* on chromosome IV (Li et al., 1998; Lokossou et al., 2009; Park et al., 2005), *R3a* (El-Kharbotly, Palomino-Sanchez, Salamini, Jacobsen, & Gebhardt, 1996; Huang et al., 2004) and *R3b* on chromosome XI (Huang et al., 2005; Li et al., 2011), *R4* and *R8* on chromosome IX (Jo et al., 2011), while *R5* to *R11* (except *R8*) turned out to constitute alleles of the *R3a* gene (Bradshaw, Bryan, Lees, McLean, & Solomon-Blackburn, 2006). So far, only *R1*, *R2*, *R3*, *R4* and *R10* have been widely used in potato breeding (Vleeshouwers, Raffaele, et al., 2011). Nowadays, resistance genes from the hexaploid *S. demissum* can even be found in modern potato

cultivars and it is estimated that more than 50% of the common potato cultivars harbour genetic contributions from *S. demissum* (Bradeen & Kole, 2011; Perez et al., 2001). This type of resistance will not confer durable late blight resistance as vertical resistance based on *R*-genes from *S. demissum* can be overcome after a few years in the field by newly evolved virulent *Pi* races (Saldana, 2011). Hence, it would be desirable to combine *R*-genes with high levels of field resistance (Stewart, Bradshaw, & Pande, 2003).

Besides *R*-genes derived from *S. demissum*, many more genes conferring resistance to *P. infestans* are already known. Sixty-three genes have been identified from various *Solanum* species, and out of them, 27 have been cloned by now (Kim et al., 2012; Rodewald & Trognitz, 2013). Late blight resistance genes were identified and cloned from related wild potato species such as RB/*Rpiblb1*, *Rpi-blb2*, *Rpi-blb3*, *Rpi-bt1* and *Rpi-abpt* from *S. bulbocastanum* (Lokossou et al., 2009; Naess et al., 2000; Oosumi et al., 2009; Park et al., 2005; Song et al., 2003; Van der Vossen et al., 2003); *Rpi-ber1* and *Rpi-ber2* from *S. berthaultii* (Rauscher et al., 2006); *Rpi-mcd1* from *S. microdontum* (Tan et al., 2008); *Rpi-mch1* from *S. michoacanum* (Śliwka et al., 2012); *Rpi-ver1* from *S. verrucosum* (Jacobs et al., 2010); *Rpi1* and *Rpi2* from *S. pinnatisectum* (Kuhl, Hanneman, & Havey, 2001; Yang et al., 2017); *Rpi-sto1* and *Rpi-sto2* from *S. stoloniferum* (Vleeshouwers et al., 2008; Vleeshouwers, Finkers, et al., 2011; Wang et al., 2008); *Rpi-vnt1*, *Rpi-vnt1.2* and *Rpi-vnt1.3* from *S. venturii* (Foster et al., 2009; Pel et al., 2009); *Rpi-phu1* from *S. phureja* (Śliwka et al., 2006); *Rpi-dlc1* from *S. dulcamara* (Golas, van der Weerden, van den Berg, Mariani, & Allefs, 2010); and *Rpi-moc1*from *S. mochiquense* (Smilde, Brigneti, Jagger, Perkins, & Jones, 2005).

It is estimated that less than seven of approximately 220 tuber bearing wild potato species have been used in breeding of potato cultivars worldwide (Bradshaw, 2009). Extensive systematic analyses of compatibility with many of these wild relatives have been conducted and show that *S. pinnatisectum*, *S. tarnii*, *S. bulbocastanum* and *S. cardiophyllum* are not directly crossable with cultivated potato (Jackson & Jr Hanneman, 1999). To circumvent the problem of sexual incompatibility with common tetraploid potato, different approaches such as somatic hybridization *via* protoplast fusion (Thieme et al., 2009), embryo rescue and bridge crosses (Jansky, 2006) have been used. Only by producing "double-bright" hybrids using *S. acaule* and *S. phureja*, it was possible to effectively introduce *Rpi*-genes from *S. bulbocastanum* indirectly into *S. tuberosum* (Hermsen & Ramanna, 1973). Embryo rescue and double pollination were used to transfer late blight resistance from *S. pinnatisectum* into *S. tuberosum*, too (Ramon & Hanneman, 2002). Hermsen and Taylor (1979) have already reported about the successful hybridization of *S. etuberosum* with *S. pinnatisectum*.

However, *S. pinnatisectum* still constitutes a so far mostly untapped genetic resource for potato resistance breeding as numerous efforts to use pathogen resistances originating from *S. pinnatisectum* in breeding have largely been unsuccessful.

The availability of new modern marker technologies enables the determination of genome structure for potato wild species and was used to generate genomewide linkage maps (Gao, 2013; Śliwka et al., 2012). Diversity Array Technology (DArT), Software: http://www.diversityarrays.com/software.html#dartsoft is a community-based molecular marker technology that allows high-throughput and cost-effective genotyping without the necessity of prior genomic sequence information (Jaccoud, Peng, Feinstein, & Kilian, 2001; Wenzl et al., 2004). DArT markers are highly transferable across populations or even across distinct species (Traini et al., 2013). For wild *Solanum* species with potential in potato breeding, a DArT array has been developed (Iorizzo et al., 2014). Śliwka et al. (2012) constructed one of the first maps made of DArT markers from the genus *Solanum*, and by now, DArT-linkage maps have been constructed for *S. bulbocastanum* and *S. commersonii* (Bradeen et al., 2010; Iorizzo et al., 2014).

This study reports on the evaluation of late blight resistance in a segregating diploid progeny of an intraspecific *S. pinnatisectum* backcross followed by the mapping of the causative late blight resistance gene in *S. pinnatisectum*.

2 | MATERIALS AND METHODS

2.1 | Plant material

A late blight resistant genotype of the Mexican diploid (1EBN) *Solanum* species *S. pinnatisectum* Dunal (GLKS 31607, *pnt* 2G) and a susceptible genotype (GLKS 32586, *pnt* 3GA) were obtained from the Gross Lüsewitz Potato Collections (GLKS) of the Leibniz Institute of Plant Genetics and Crop Plant Research, Genebank Gatersleben, Germany, and crossed to obtain the F_1 progeny. A single resistant F_1 individual (K53, score of 8) was backcrossed as female to the susceptible *pnt* 3GA genotype (score of 3) to generate a BC_1 mapping population (code: POP 53) consisting of 84 individuals (Figure 1).

2.2 | Resistance assay

Three plants of each parental *pnt* line (*pnt* 2G, *pnt* 3GA, K53) and the 84 BC_1 progeny were propagated *in vitro* and transferred to the greenhouse in spring. Fully expanded leaves from 6-week-old plants were assessed for resistance to foliage blight using the detached-leaflet assay according to Thieme et al. (2008). Each genotype was

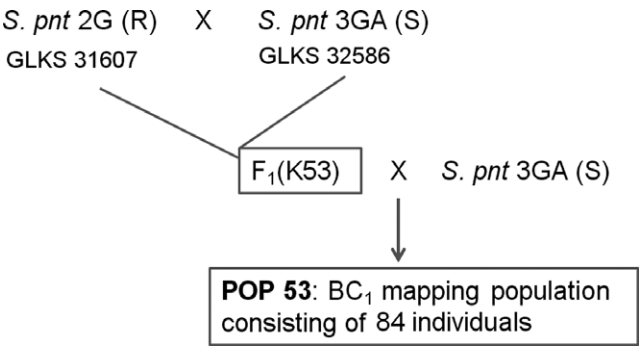

FIGURE 1 Crossing scheme to generate the BC_1 mapping population POP 53

represented by three replicates: five leaflets from different compound leaves of each of the three different plants; that is, 15 leaflets per genotype were collected from the middle part of plants and inoculated on the abaxial side with a single *Pi* suspension droplet of about 10 μl (50,000 zoospores per ml) at 15°C in light, 16-hr photoperiod and 95% relative humidity. The inoculum consisted of a common *Pi* isolate (Pi-GL-07) with a complex virulence spectrum, which is able to overcome all known *R*-genes. According to the Euroblight a potato late blight network for Europe (http://euroblight.net/protocols/), the virulence expression of the used isolate was evaluated in relation to late blight single *R*-gene differentials carrying *r0* and *R1-R11* based on different disease response patterns every year. The evaluation of foliage blight was conducted 5–6 days after inoculation by scoring the affected leaf area and the intensity of *Pi* sporulation on a 1–9 scale, where score 9 means no attack visible (most resistant) and 1 indicating that the leaf is completely necrotic and covered with mycelium (most susceptible). A genotype was considered as resistant when its score was ≥6 (Śliwka et al., 2012). The cultivar 'Delikat' (*S. tuberosum* L. subsp. *tuberosum*) was used as a susceptible control. The mean value of the disease attack was determined from the individual leave scores. Goodness-of-fit to expected segregation ratio of the BC_1 progeny was estimated by chi- squared test.

2.3 | DNA isolation and genotyping

Genomic DNA was prepared from *in vitro* potato plants according to the modified CTAB protocol (Saghai-Maroof, Soliman, Jorgensen, & Allard, 1984). About 50 mg of fresh leaf material was vigorously homogenized in a mixer-mill 300 disruptor (Retsch Inc., Hannover, Germany). The concentration and quality of DNA was measured using a NanoDrop 8000 spectrophotometer (Thermo Scientific, Germany). All samples were adjusted to a final concentration of 25 ng/μl and stored at −20°C in 0.1 × TE buffer.

The DArTseq analysis, which represents a combination of a DArT complexity reduction methods and next-generation sequencing platforms (Cruz, Kilian, & Dierig, 2013; Kilian et al., 2012), was performed by Diversity Arrays Technology Pty Ltd, Canberra, Australia. The identification and marker classification was performed by DArTsoft14 calling algorithms, and binary (0: allele absent; 1: allele present) scores were used for map construction (http://www.diversityarrays.com/software.html#dartsoft).

Single sequence repeat (SSR) analyses were carried out with a set of EST-derived StI markers (Feingold, Lloyd, Norero, Bonierbale, & Lorenzen, 2005). The PCR was performed in a 10 μl reaction volume containing the universal fluorescent-labelled M13-primer (0.07 μM) in combination with an M13-tailed forward primer (0.1 μM) and the common reverse primer (0.17 μM) described by Schuelke (2000) in a PeqSTAR 96 HPL Thermocycler (PeqLab, Erlangen, Germany). Moreover, a touchdown profile with decreasing the annealing temperature by 0.5°C/cycle in the course of 12 cycles from 60 to 54°C was used. PCR products were separated and detected on a GeXP platform (AB Sciex Germany GmbH).

2.4 | Linkage analyses and map construction

The data generated by different marker systems were recorded in a binary manner. Only markers with less than 10% missing data which are known to be located to single chromosomes were integrated into the mapping file. As the population type code was selected "BC_1," the genetic maps for all single chromosomes were calculated separately using JoinMap 4.0 (http://www.joinmap.nl/, Van Ooijen, 2006) applying the regression mapping algorithm and based on phenotypic data, and the resistance to late blight was integrated. Only polymorphic markers with LOD > 5 were integrated into the map. Recombination rates were converted into map distances using the Kosambi transformation (Kosambi, 1943).

3 | RESULTS

3.1 | Late blight resistance

Resistance assessment was carried out using a *Phytophthora infestans* (*Pi*) isolate with a complex virulence spectrum collected from the field. The crossing between the resistant (GLKS 31607, *pnt* 2G) and susceptible (GLKS 32586, *pnt* 3GA) *S. pinnatisectum* produced resistant and susceptible F_1 progeny in the same proportion (29:31). Therefore, it can be assumed that the resistant parent is heterozygous and the *R*-gene is inherited in a dominant mode. Because not enough plants were available for mapping, a highly resistant F_1 individual (K53; score of 8) was backcrossed as female to the susceptible parent *pnt* 3GA whose score of 3 was generally comparable with the susceptible control cv. 'Delikat' (Figure 2).

Late blight resistance of all individuals was scored after infection in groups from 1 to 9 and classified into two classes, that is resistant (score ≥6) and susceptible ones (score <6). It turned out that in the detached-leaflet assay, the BC_1 progeny segregated into 45 resistant and 39 susceptible genotypes. This ratio is not significantly different from a 1:1 ratio ($\chi^2 = 3.84$; $\alpha = 0.05$; $P = .0102$, df = 1) and confirms that a single dominant locus controlled the *Pi* resistance in *S. pinnatisectum* (Figure 3).

3.2 | Genetic mapping

Based on the DArT and SSR analyses, twelve linkage groups that correspond to the twelve potato chromosomes were constructed. The map consists of 1,583 markers covering 1,793.5 cM. The lengths of the chromosomes ranged from 88.4 cM for chromosome (X) to 198.8 cM for chromosome (III). The marker distance on the map ranged from 1 marker per 0.6 cM (VI) to 1 marker per 2.4 cM (V) with an average marker distance of 1.1 cM (Tab. 1). The least marker distance was found on chromosome VI (0.6 cM), followed by chromosomes IX (0.7 cM), VII and II (0.9 cM), respectively (Table 1).

The late blight resistance locus derived from *S. pinnatisectum* was mapped on chromosome VII in an interval of 5.3 cM, that is 2.3 cM distal from the DArT marker 100028495|F|0 and 3.0 cM proximal from the marker 100000417|F|0 (Figure 4).

FIGURE 2 Assessment of foliage blight by detached-leaflet assay of the resistant accession *pnt* 2G, the susceptible *pnt* 3GA and the susceptible control cv. 'Delikat' (from top to bottom)

Inclusion of SSR anchor markers within the mapping procedure enabled the comparison of the constructed map with previously published ones of chromosome VII displaying the position of the known *Rpi1* gene. In the map constructed by Kuhl et al. (2001), the *Rpi1* is located between markers TG438 and CP56 on chromosome VII (Figure 5). These two markers are also included in the potato meta-consensus map of chromosome VII and are located in a distance of approximately 25 cM from anchor marker StI033 (Figure 5). StI033 is also included in the newly constructed map of chromosome VII (Figure 4) and located in a distance of approximately 77 cM from the target *Rpi* locus. In view of this large distance, the comparison of the different linkage maps indicates that the *Rpi* locus is different from the known *Rpi1* gene and located most likely on the opposite arm of chromosome VII.

4 | DISCUSSION

Common potato in Europe has a narrow genetic base because it originates from the limited germplasm dated back to the time when it was introduced to Europe as a crop (Xu et al., 2011). To increase the genetic diversity of potato germplasm, wild *Solanum* species which offer a broad spectrum of resistances to pathogens and pests are being utilized and a number of valuable resistance genes have already been isolated in these genetic resources (Jo et al., 2011). The occurrence of genetically highly variable pathogens with new virulences which overcome existing disease resistances as well as the more strongly restricted availability of ingredients for pesticides from year to year requires more effective strategies to protect potato plants against pathogens. One way includes the introgression

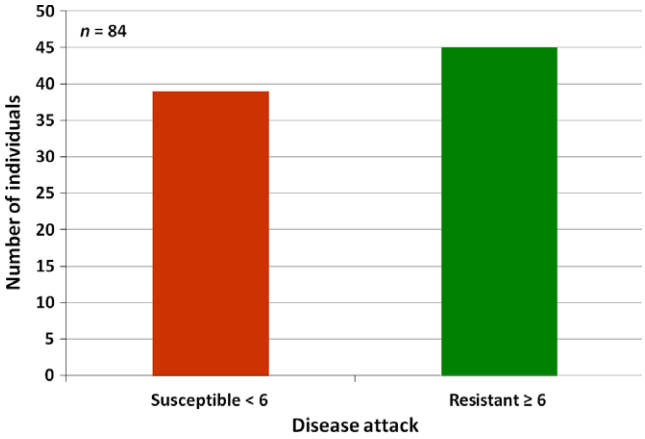

FIGURE 3 Distribution of late blight attack in the BC_1 mapping population POP 53 of *S. pinnatisectum*. The resistance was assessed using a 1–9 scale, where 9 means most resistant. Values ≥6 are defined as resistance [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 The distribution and distances of mapped markers across the 12 potato chromosomes

Chromosome	No. of markers	Length (cM)	Mean marker distance (cM)
I	131	134.8	1.0
II	147	132.8	0.9
III	144	198.8	1.4
IV	91	122.3	1.3
V	55	130.6	2.4
VI	259	158.7	0.6
VII	200	182.2	0.9
VIII	118	162.0	1.4
IX	191	133.5	0.7
X	69	88.4	1.3
XI	91	170.8	1.9
XII	87	178.6	2.1
Total	1,583	1,793.5 cM	Ø 1.1 cM

of multiple resistance genes into cultivars (Hajianfar et al., 2014; Zhu, Li, Vossen, Visser, & Jacobsen, 2012).

Based on the evaluation of GenBank accessions of Mexican wild potato species, *Solanum pinnatisectum* Dunal ($2n = 2x = 24$, 1 EBN) genotypes were selected expressing high levels of resistance to late blight (Douches, Inglis, Helgeson, & Brown, 2001; Ramon & Hanneman, 2002), potato virus Y (Thieme et al., 2009), Colorado potato beetle (Chen, Kawchuk, Lynch, Goettel, & Fujimoto, 2003; Thieme, Rakosy-Tican, Molnar, & Thieme, 2014) and tolerance to abiotic stresses, like heat and drought (Hawkes, 1990). Therefore, this species is a promising source for improving resistance, but because of the sexual incompatibility of *pnt* to *S. tuberosum*, direct crosses with potato were not successful (Jackson & Jr Hanneman, 1999). Many efforts were conducted to transfer genetic material from *pnt* into cultivated potato using bridging crosses, embryo rescue (Chen, Lynch, et al., 2004; Dinu, Hayes, Kynast, Phillips, & Thill, 2005) or somatic hybridization (Polzerová, Patzak, & Greplová, 2011; Sarkar et al., 2011; Szczerbakowa, Boltowicz, Lebecka, Radomski, & Wielgat, 2005; Thieme, Darsow, Gavrilenko, Dorokhov, & Tiemann, 1997). A number of these somatic hybrids obtained by protoplast fusion between *S. pinnatisectum* (+) and cultivated potato turned out to be resistant to late blight (Luthra, et al., 2016; Tiwari et al., 2013), and PVY (Thieme et al., 2009). Using different cultivars of potato as males, backcross progeny were produced showing increased yield, starch content, tuber quality and high fertility (Thieme et al., 2009, Thieme, unpublished). These promising properties, particularly in combination with resistance to late blight, render these progeny a valuable genetic resource for practical potato breeding and pyramiding of *R*-genes which may be an effective strategy to create durable resistance to late blight.

The novel late blight resistance locus derived from the wild potato accession *pnt* 2G is located on chromosome VII. Previously, known resistance genes to potato late blight originating from *S. pinnatisectum* (*Rpi1*, *Rpi2*) and S. *michoacanum* (*Rpi-mch1*), a natural hybrid of *S. bulbocastanum* × *S. pinnatisectum*, were also mapped on chromosome VII (Kuhl et al., 2001; Śliwka et al., 2012; Yang et al., 2017). Therefore, it cannot be excluded that these genes and our target resistance gene are identical. Chen, Sun, et al. (2004) used a map-based cloning strategy to isolate the gene that confers resistance to late blight from the wild diploid species *S. pinnatisectum*. But so far, the resistance gene has not been isolated, the sequence of this gene has not been published, and diagnostic markers which are closely linked to the resistance locus are not available. Characterization of the *Pi* isolates used for disease evaluations revealed that the avirulence gene corresponds to the *R9* resistance locus, indicating that *Rpi1* could possibly match the *R9* locus. Norby and Havey (2005) demonstrated the independent inheritance of *R9* and *Rpi1* and proved that *Rpi1* is a unique resistance locus. Recently, a single dominant late blight resistance gene was identified in *S. pinnatisectum* by Yang et al. (2017) and mapped to an interval of 2.4 cM on the long arm of chromosome VII. This resistance locus is different from the previously reported *Rpi1* on the same chromosome and was called *Rpi2*. Both resistance genes were derived from the same wild species but from different *pnt* accessions.

The chromosome VII is not considered being a hot spot for *Pi* resistance genes, and it is still poor in polymorphic and segregating markers (Śliwka et al., 2012). With the Diversity Arrays Technology (DArT), Software: http://www.diversityarrays.com/software.html#dartsoft a solid-state open platform method for DNA polymorphism analysis is available that offers a low-cost and high-throughput genotyping. The advantage of this method consists in providing comprehensive genome coverage even in organism without any DNA sequence information (Jaccoud et al., 2001). Using this approach, the first linkage map of *S. pinnatisectum* was generated which is densely covered with genetic markers and enabled mapping of a new late blight resistance locus on chromosome VII. Based on DArT and SSR markers, the mapping resulted in twelve

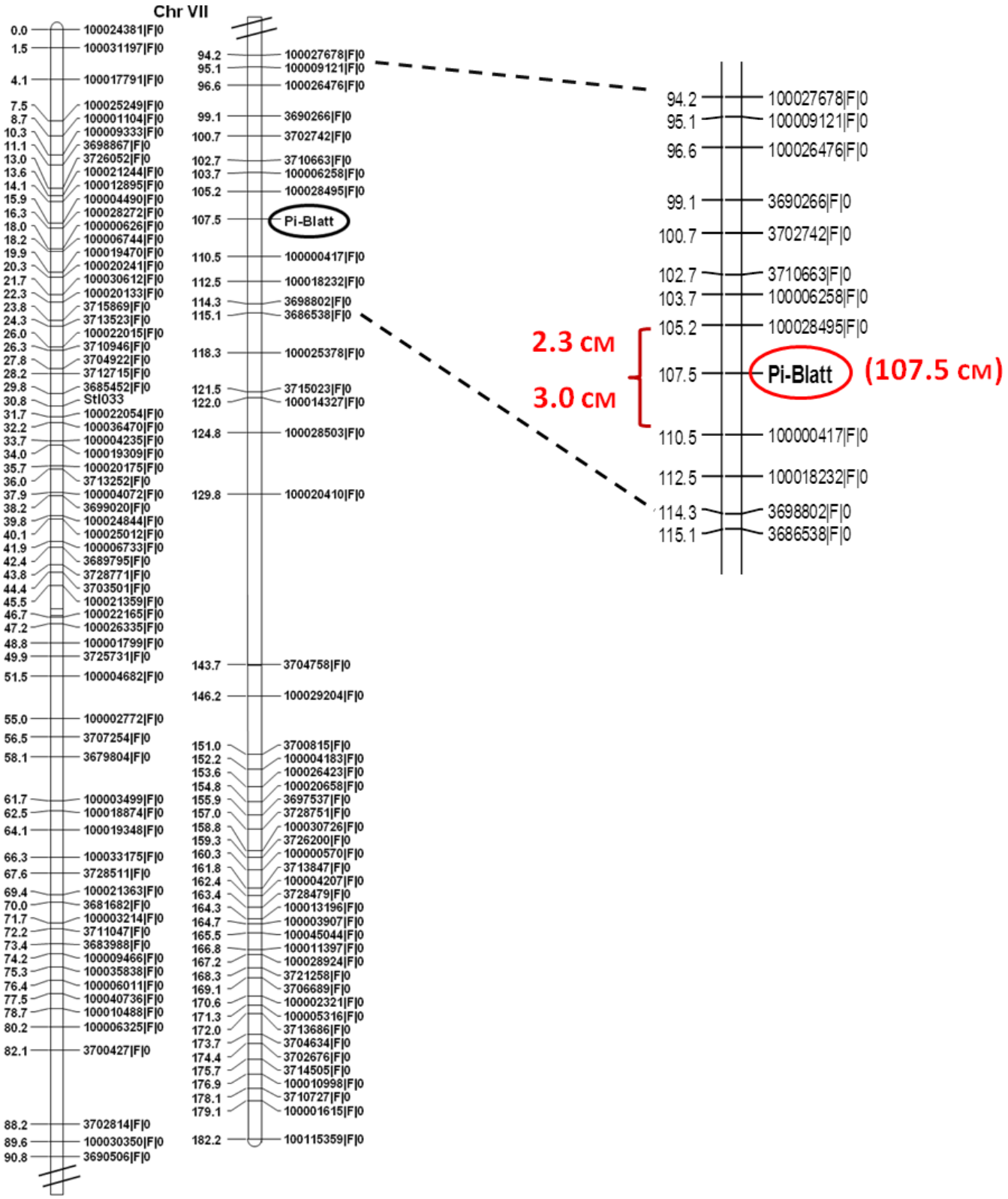

FIGURE 4 Genetic map on chromosome VII of POP 53 (*S. pinnatisectum*). Marker labels are shown to the right and distances of markers (cM) to the left [Colour figure can be viewed at wileyonlinelibrary.com]

linkage groups that correspond to the twelve potato chromosomes consisting of 1,583 markers with a total map length of 1,793.5 cM. This is twice as much as described for the *S. michoacanum* map by Śliwka et al. (2012) with 846 markers and 1,047 cM. To develop closer linked markers and to optimize the marker saturation, the resolution of our mapping population has to be increased to about

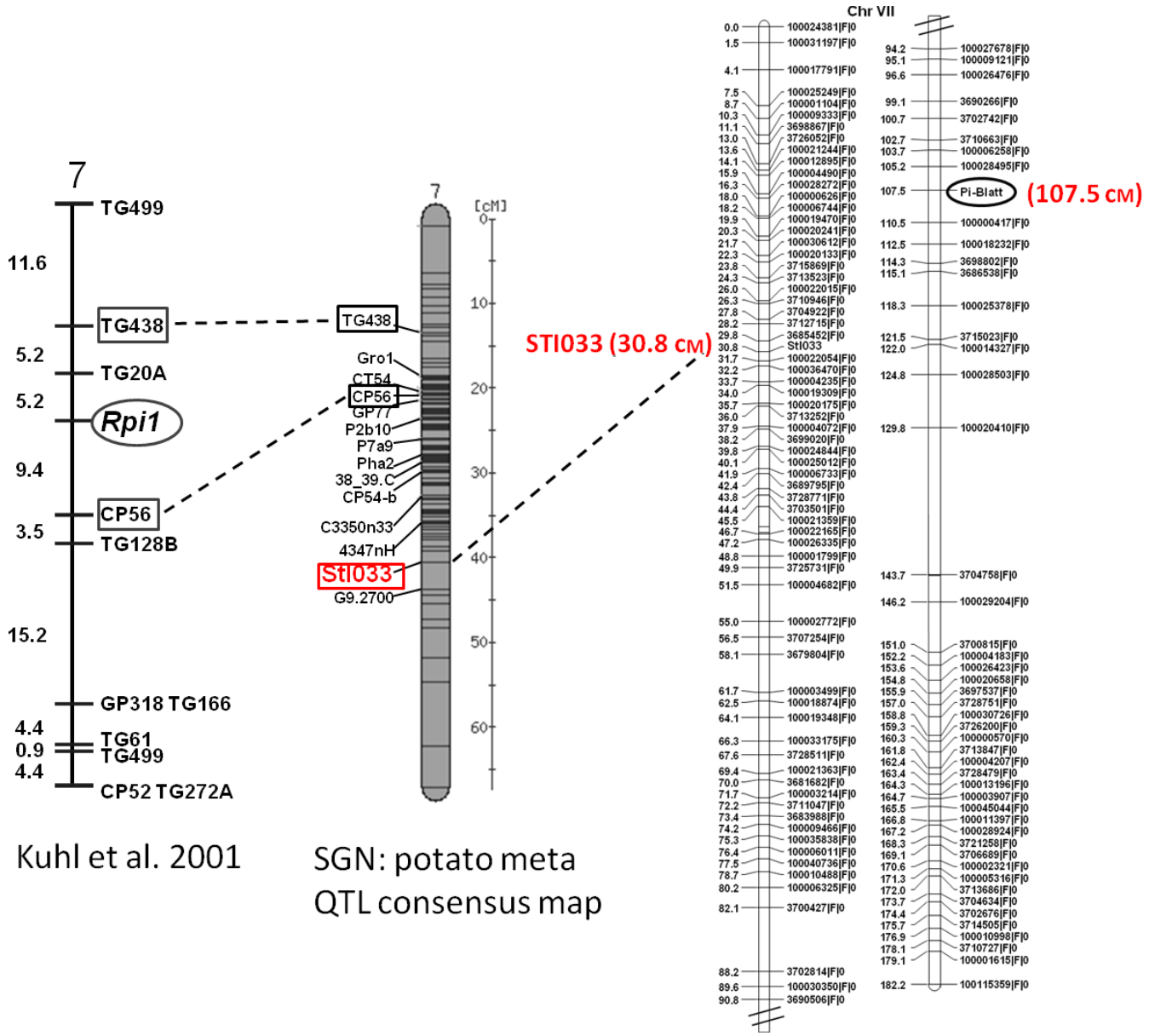

FIGURE 5 Comparison of different genetic maps of chromosome VII [Colour figure can be viewed at wileyonlinelibrary.com]

200 individuals and new markers to construct a shorter interval to the resistance loci have to be developed. However, for mapping single genes population sizes of less than 100 genotypes proved to be efficient in several cases (Manrique-Carpintero et al., 2015; Szajko, Strzelczyk-Zyta, & Marczewski, 2014 and Verzaux et al., 2011). The new late blight resistance locus from *S. pinnatisectum* was mapped on chromosome VII within an interval of 5.3 cM (2.3 cM distal from the DArT marker 100028495|F|0 and 3.0 cM proximal from the marker 100000417|F|0). However, comparison with the mapped *Rpi1* gene (Kuhl et al., 2001) by comparing existing genetic maps of chromosome VII revealed that our target *Rpi* is located far away from *Rpi1* and *Rpi2*, probably on the opposite chromosome arm. It is therefore most likely that a new resistance locus in *S. pinnatisectum* has been mapped. Only a future test for allelism will provide the final proof.

The pyramiding of effective new late blight resistance genes within modern cultivars represents an effective strategy to create durable resistance to late blight. Closely linked DNA markers will save costs and time by enabling efficient and precise introgression breeding ("Smart Breeding"). Isolation of the causative gene and development of locus-specific markers for marker-assisted selection of the *Pi* resistance in *S. pinnatisectum* will be the next steps based on the current studies.

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