Identification and characterization of resistance quantitative trait loci against bacterial wilt caused by the *Ralstonia solanacearum* species complex in potato

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**Abstract** Bacterial wilt (BW) caused by the *Ralstonia solanacearum* species complex (RSSC) represents one of the most serious diseases affecting potato cultivation. The development of BW-resistant cultivars represents the most efficient strategy to control this disease. The resistance-related quantitative trait loci (QTLs) in plants against different RSSC strains have not been studied extensively. Therefore, we performed QTL analysis for evaluating BW resistance using a diploid population derived from *Solanum phureja*, *S. chacoense*, and *S. tuberosum*. Plants cultivated in vitro were inoculated with different strains (phylotype I/biovar 3, phylotype I/biovar 4, and phylotype IV/biovar 2A) and incubated at 24 °C or 28 °C under controlled conditions. Composite interval mapping was performed for the disease indexes using a resistant parent-derived map and a susceptible parent-derived map consisting of single-nucleotide polymorphism markers. We identified five major and five minor resistance QTLs on potato chromosomes 1, 3, 5, 6, 7, 10, and 11. The major QTLs *PBWR-3* and *PBWR-7* conferred stable resistance against *Ralstonia pseudosolanacearum* (phylotype I) and *Ralstonia syzygii* (phylotype IV), whereas *PBWR-6b* was a strain-specific major resistance QTL against phylotype I/biovar 3 and was more effective at a lower temperature. Therefore, we suggest that broad-spectrum QTLs and strain-specific QTLs can be combined to develop the most effective BW-resistant cultivars for specific areas.

**Keywords** Bacterial wilt · *Ralstonia solanacearum* species complex · Phylotype · Potato · Quantitative trait loci

**Introduction**

*Solanum tuberosum* L. (potato) is cultivated worldwide and is the most important *Solanaceae* crop (Liu et al. 2016); over 354 million metric tons was produced in 2019 (Food and Agriculture Organization of the United Nations 2021). However, its cultivation is frequently limited by pests and diseases, including bacterial wilt (BW), which represents one of the most serious and widespread bacterial diseases in the tropics, subtropics, and warm temperate regions (Hayward 1985).

BW is caused by the *Ralstonia solanacearum* species complex (RSSC), which mainly enters plants via roots and then colonizes the xylem vessels and spreads through...
the vascular system. RSSC infection causes characteristic wilting symptoms, leading to rapid death of the host plant. RSSC has been reported to infect over 250 plant species including many cash crops and major food crops, such as banana, potato, tomato, and eggplant (Peeters et al. 2013). Recently, it has been ranked second in the list of the most scientifically/economically important bacterial pathogens (Mansfield et al. 2012).

RSSC is divided into five races based on host range, six biovars based on metabolic ability (Buddenhagen and Kelman 1964; Denny 2006), and four phylotypes based on molecular analysis (Gillings and Fahy 1994). The latter division also reflects probable geographical origin, with phylotypes I, II, III, and IV considered to originate from Asia, the Americas, Africa, and Indonesia and Australia, respectively (Fegan and Prior 2005; Wicker et al. 2012). More recently, RSSC has been suggested to comprise three species: R. solanacearum (including phylotype II), R. pseudosolanacearum (including phylotypes I and III), and R. syzygii (including R. solanacearum phylotype IV and the closely related pathogen R. syzygii) (Safni et al. 2014).

Strategies to control BW (such as crop rotation, elimination of weeds that represent alternative hosts, and biological control) are insufficient, and the disease continues to cause major profit loss (Huet 2014). In addition, chemical-based control using chloropicrin has an adverse impact on the environment and its use is undesirable. The development of BW-resistant cultivars is cost-effective and environmentally friendly; however, only a few factors that confer BW resistance have been identified (Laferriere et al. 1999). BW resistance has been found in cultivated diploid species and closely related wild species (Andino et al. 2022; Carputo et al. 2009; Chen et al. 2013; Fock et al. 2000; Kim-Lee et al. 2005; Laferriere et al. 1999). The cultivated diploid species Solanum phureja is often used as a source of BW resistance factors (Fock et al. 2000; French et al. 1998; French and De Lindo 1982; Lopes et al. 2021; Sequeira and Rowe 1969; Thurston and Lozano 1968; Watanabe et al. 1992). The S. phureja-derived breeding clone Saikai 35 has a high level of BW resistance (Mori et al. 2012), from which a BW-resistant cultivar Nagasaki Kogane has been derived (Sakamoto et al. 2017).

BW resistance is controlled by multiple genes (Elphinstone 1994; Rowe and Sequeira 1970; Sequeira 1979). Two major quantitative trait loci (QTLs), Bwr-12 and Bwr-6, and several minor QTLs have been identified in the tomato cultivar Solanum lycopersicum Hawaii 7996. The Bwr-12 confers partial resistance to the phylotype I strain, and Bwr-6 confers partial resistance to both phylotype I and II strains or broad-spectrum resistance (Carmeille et al. 2006; Thoquet et al. 1996a, 1996b; Wang et al. 2000, 2013). In potatoes, BW resistance against race I/biovar 3 strains has been found in somatic hybrids of S. tuberosum + Solanum chacoense, and the resistance QTLs have been identified in chromosomes 2 and 9 (Chen et al. 2013). However, resistance QTLs against different strains have not been studied extensively.

We previously identified resistance QTLs against the phylotype I/biovar 4 strain on chromosomes 1, 3, 7, 10, and 11 using a diploid mapping population consisting of S. tuberosum, S. chacoense, and S. phureja (Habe et al. 2019). In this study, we assayed the same diploid population but used different RSSC strains (phylotypes I and IV or biovars 3, 4, and 2A) and different incubation temperatures (24 °C and 28 °C) after inoculation before performing QTL analysis.

**Materials and methods**

**Plant materials**

Saikai 35 is a tetraploid potato breeding clone highly resistant to BW (Mori et al. 2012). A resistant haploid clone (10–03-30) was obtained via parthenogenesis by crossing Saikai 35 with the pollen of a haploid inducer, S. phureja 460 (= IvP 35). This resistant parent (RP) was crossed as the female parent with a susceptible diploid clone F1-1 (SP) as the male parent, generating 94 F1 plants grown in vitro using Murashige and Skoog (MS) medium (Murashige and Skoog 1962). The F1 population (Habe et al. 2019) was previously characterized for BW resistance to the strain MAFF327001 (phytotype I/biovar 4).

**Inoculation and disease resistance analysis**

In vitro inoculation tests (Habe 2018) were performed to evaluate resistance in the F1 plants. The in vitro screening medium, containing 30 mL vermiculite and 20 mL MS liquid medium, was placed in a glass tube (40 mm × 130 mm) and was sterilized via autoclaving. The plants cultivated in vitro were
cut at nodes below the third or fourth leaf from the apex. The cut stems were transplanted into the screening medium and incubated in a growth chamber for 2 weeks to promote rooting. The light–dark cycle was 16 h light at 3000–4000 lx and 8 h dark; incubation temperature was 18 °C.

The RSSC strains MAFF327001 (phytoltype I/biovar 4), MAFF327095 (phytoltype IV/biovar 2A), and MAFF327142 (phytoltype I/biovar 3) isolated from potato (Horita et al. 2010) were used in this study for our inoculation tests (Table 1). The strains were cultured at 30 °C in 2,3,5-triphenyltetrazolium chloride solid medium (Kelman 1954). White fluid–containing colonies were transferred to casamino acid-peptone-glucose medium (Hendrick and Sequeira 1984). The inoculum cell concentration was determined by measuring the optical density at 600 nm and adjusted to $10^8$ colony-forming units/mL in sterile water. The bacterial suspension (1 mL) was poured into each screening medium. Nine or ten plantlets per genotype represented one replicate, and three replicates were tested for BW resistance. After inoculation, one set was incubated at 24 °C and the other set was incubated at 28 °C.

Resistance level was expressed as a disease index (DI), measured 20 days after inoculation using a 0–4 scale based on the extent of stem wilting: 0 (no symptoms), 1 (up to 25% stem wilting), 2 (26–50%), 3 (51–75%), and 4 (76–100%) (Supplementary Fig. S1) (Habe 2018).

### QTL analysis

A genetic map was previously constructed using single-nucleotide polymorphism (SNP) markers (Habe et al. 2019). Since both diploid parents were highly heterozygous, the segregating population was considered a two-way pseudo-testcross population (Grattapaglia and Sederoff 1994) and the parental maps were constructed. For RP, 1476 heterozygous SNP loci were mapped, while for SP, 2663 heterozygous SNP loci were mapped on 12 chromosomes (Supplementary Table S1). QTL Cartographer version 2.5 (Wang et al. 2005) was used to perform composite interval mapping (CIM; Zeng 1994), which was specifically designed to reduce background noise that can affect QTL detection; CIM was performed using a backcross design by regarding the F1 population as a backcross population. Parameters of the analysis were set for model 6 with a window size of 2 cM. A LOD threshold for QTL detection was obtained via permutation tests using 1000 repetitions to control for a genome-wide error rate of 1%. Since the DIs showed a skewed distribution following resistance tests using MAFF327142, the error rate was set to a more stringent 1% for CIM, and nonparametric QTL mapping was also performed. Nonparametric QTL mapping was performed on all

| BW strain          | Temperature | QTL | Detected map | Chr | Position (cM) | Position of maximum LOD (cM) | Maximum LOD score | Explained variance (%) |
|--------------------|-------------|-----|--------------|-----|---------------|------------------------------|--------------------|------------------------|
| **MAFF327142**     | 24 °C       | PBWR-6b | R map       | 6   | 10.8–23.7     | 21.7                         | 14.17              | 40.5                   |
|                    |             | PBWR-10b | S map       | 10  | 53.2–56.6     | 55.6                         | 4.32               | 14.5                   |
|                    | 28 °C       | PBWR-6b | R map       | 6   | 13.8–23.7     | 21.7                         | 5.51               | 17.6                   |
|                    |             | PBWR-6a | S map       | 6   | 0.0           | 0.0                          | 3.93               | 13.6                   |
| **MAFF327001**     | 24 °C       | PBWR-7  | R map       | 7   | 12.2–27.2     | 25.3                         | 6.86               | 20.5                   |
|                    |             | PBWR-1b | S map       | 1   | 79.0–79.1     | 79.1                         | 3.83               | 11.4                   |
|                    |             | PBWR-3  | S map       | 3   | 13.8–17.0     | 15.0                         | 4.30               | 13.0                   |
|                    |             | PBWR-5  | S map       | 5   | 54.7–55.7     | 54.7                         | 3.76               | 11.2                   |
|                    | 28 °C       | PBWR-7  | R map       | 7   | 15.2–27.2     | 25.3                         | 6.64               | 21.9                   |
|                    |             | PBWR-10a| S map       | 10  | 6.6–10.9      | 8.8                          | 4.93               | 15.1                   |
| **MAFF327095**     | 28 °C       | PBWR-1a | S map       | 1   | 74.6–75.7     | 74.7                         | 4.91               | 15.1                   |
|                    |             | PBWR-7  | R map       | 7   | 25.2–26.3     | 25.3                         | 4.39               | 15.3                   |
|                    |             | PBWR-11 | S map       | 11  | 32.6–33.6     | 32.6                         | 3.94               | 12.4                   |

1 Detected by a permutation test (1000 repetitions) at a 0.01 level
data using an R/qtl package (Broman et al. 2003) of R software (R Core Team 2017). The function “scanone” with model = “np” and step = 1 cM was used for nonparametric interval mapping, which is an extension of the Kruskal–Wallis test (Krusklyak and Lander 1995; Kruskal and Wallis 1952). At an adjusted error rate of 5%, the LOD score was determined using a permutation test (1000 repetitions). The interval estimate of genetic factor location was calculated using the “lodint” function, which computes the interval position corresponding to 1.0-LOD support intervals; the “expandtomarkers” argument determines the nearest flanking markers of the interval’s higher limits. QTL analyses were performed separately for each of the two parental linkage maps. Linkage maps and QTL positions were drawn using MapChart 2.30 (Voorrips 2002). Detected QTLs were named PBWR-‘linkage group number’ (PBWR being an acronym for Potato Bacterial Wilt Resistance).

Statistical analysis

All statistical analyses, excluding QTL analysis, were performed using Rcmdr package (Fox 2005) and EZR package (Kanda 2013) of R version 3.3.3. (R Core Team 2017). Phenotypic correlations between variables were estimated using Spearman’s rank coefficient for each trial. The Mann–Whitney U test was performed to analyze the mean DIs of the F1 population on the allele differences of the markers at the nearest locus of each QTL.

Results

Evaluation of BW resistance

The 94 plants in the F1 population were evaluated under six treatments: three strains (phytotype I/biovar 3, phytotype I/biovar 4, and phytotype IV/biovar 2A) at two incubation temperatures (24 °C or 28 °C). The DIs of RP 10–03-30 varied from 0.00 to 0.73, while those of SP F1-1 ranged from 2.00 to 3.47, indicating a clear difference between the parents in all treatments (Fig. 1, Supplementary Fig. S2). The DIs of F1 plants varied consistently between susceptible and resistant plants in all treatments, with the mean DIs ranging from 1.21 to 2.88 (Fig. 1), and were all positively correlated between treatments ($r = 0.25–0.61$, $p < 0.05$) (Supplementary Table S2). Incubation at 28 °C was associated with relatively higher DIs for all strains, and phenotypes with higher and lower DIs than those of SP and RP, respectively (transgressive segregation), were observed in all treatments. Particularly, the DIs against the strain MAFF327142 (phytotype I/biovar 3) changed drastically between temperatures: the distribution was skewed toward relatively lower DIs at 24 °C, whereas it was skewed toward relatively higher DIs at 28 °C. Thus, the resistance in the F1 population against MAFF327142 varied greatly depending on incubation temperature.

QTL detection

Since the F1 population exhibited both normal and skewed distributions under different treatments, both CIM and nonparametric interval mapping were performed for the DIs. CIM identified ten QTLs on seven chromosomes (PBWR-1a, PBWR-1b, PBWR-3, PBWR-5, PBWR-6a, PBWR-6b, PBWR-7, PBWR-10a, PBWR-10b, and PBWR-11) (Table 1). Nonparametric interval mapping revealed four QTLs on three chromosomes: PBWR-3, PBWR-6a, PBWR-6b, and PBWR-7. The latter three QTLs were detected in the same treatments via both CIM and nonparametric interval mapping. In contrast, PBWR-3 was detected against MAFF327001 (phytotype I/biovar 4) at 28 °C via CIM analysis and against MAFF327095 (phytotype IV/biovar 2A) at 28 °C via nonparametric interval mapping analysis (Table 2). Notably, PBWR-7 was detected in a span between 12.2 and 27.2 cM or between 10.9 and 39.2 Mb and comprised 23 SNP loci at the peak position (25.3 cM). The locations of all QTLs are schematically shown in Fig. 2.

Resistance conferred by detected QTLs

We compared the mean DIs for two genotypes (AA or AB, since the population was treated as a pseudo-testcross population) in the SNP locus nearest to each QTL (Table 3). All QTLs showed significant resistance effects against at least one bacterial strain, although to varying degrees. The PBWR-6b locus contributed highly significant resistance to MAFF327142 (phytotype I/biovar 3) strain only, at both 24 °C and 28 °C (explaining 40.5% and 17.6% of the variances, respectively). PBWR-6a and PBWR-10b contributed to the resistance
Fig. 1  The DIs in the F1 population inoculated with *Ralstonia solanacearum* species complex strains MAFF327142 (phylo-
type I/biovar 3) (a, b), MAFF327001 (phyloptype I/biovar 4) (c, d), or MAFF327095 (phyloptype IV/biovar 2A) (e, f) and incu-
bated at 24 °C (a, c, e) or 28 °C (b, d, f). DI, disease index

| BW strain                  | Temperature | QTL\(^1\) | Detected map | Chr | Position (cM)\(^2\) | Position of maximum LOD (cM) | Maximum LOD score |
|----------------------------|-------------|------------|--------------|-----|---------------------|-----------------------------|------------------|
| MAFF327142 (phyloptype I/biovar 3) | 24 °C       | *PBWR-6b* | R map        | 6   | 10.8–33.6           | 28.0                        | 8.66             |
|                            | 28 °C       | *PBWR-6b* | R map        | 6   | 10.8–42.0           | 21.7                        | 3.42             |
| MAFF327001 (phyloptype I/biovar 4) | 24 °C       | *PBWR-6a* | S map        | 6   | 0.0–26.4            | 2.0                         | 2.59             |
|                            | 28 °C       | *PBWR-7*  | R map        | 7   | 12.2–31.1           | 27.8                        | 4.82             |
| MAFF327095 (phyloptype IV/biovar 2A) | 28 °C       | *PBWR-3*  | S map        | 3   | 5.4–36.4            | 18.8                        | 2.91             |

\(^1\)Detected by a permutation test (1000 repetitions) at a 0.05 level.

\(^2\)Positions were indicated by the 1.0-LOD interval.
1 against the same strain at 28 °C and 24 °C, respectively. *PBWR-3* located at 15.0 cM in chromosome 3 considerably contributed to resistance against MAFF327142 at 24 °C, while *PBWR-7* contributed to resistance against this strain at 28 °C. Furthermore, *PBWR-3* and *PBWR-7* conferred resistance...
against MAFF327001 (phyloctype I/biovar 4) and MAFF327095 (phyloctype IV/biovar 2A) at both temperatures. The other five QTLs (PBWR-1a, PBWR-1b, PBWR-5, PBWR-10a, and PBWR-11) conferred resistance to a minor extent and were more effective at 28 °C than at 24 °C (Table 3).

**Discussion**

Polygenic segregation of BW resistance in the hybrid population

BW resistance is controlled by multiple genes in potato plants (Elphinstone 1994; Rowe and Sequeira 1970; Sequeira 1979) and is greatly influenced by environmental conditions such as temperature and soil moisture (Tung et al. 1990a, 1990b). Different strains show resistance to different extents (French and De Lindo 1982; Katayama and Kimura 1984; Suga et al. 2013; Tung et al. 1990a). Thus, the resistance was evaluated against three strains using an in vitro assay method (Habe 2018) under controlled environmental conditions at 24 °C and 28 °C. The RP and SP plants showed stable resistance and susceptibility against all the strains used, including phylotype I/biovar 3, phylotype I/biovar 4, and phylotype IV/biovar 2A. The resistance levels in the hybrid population varied consistently, confirming that the resistance was polygenically controlled. Resistance was also positively correlated among all six treatments, indicating that the pathogenicity was similar between phylotypes I and IV in potato plants. This was in agreement with previous findings that indicated no difference in virulence between phylotypes I and IV and between phylotypes II and III in potato cultivars (Habe 2016, 2022; Sharma et al. 2021). Although Suga et al. (2013) reported that phylotype IV is more virulent than phylotype I, the classification of phylotypes may not correlate with the degree of virulence as suggested for tomato, eggplant, and pepper plants (Lebeau et al. 2011).

Segregation of multiple resistance QTLs in the hybrid population

CIM and nonparametric QTL mapping were performed to evaluate BW resistance using a hybrid population and identified ten QTLs. All of them accounted for more than 10% of the observed phenotypic variance. Those QTLs responsible for a statistically significant difference of $p < 0.001$ between genotypes were considered major QTLs in this study. Based on this definition, we identified five major QTLs (PBWR-3, PBWR-6a, PBWR-6b, PBWR-7, and PBWR-10b) and five minor QTLs (PBWR-1a, PBWR-1b, PBWR-5, PBWR-10a, and PBWR-11). Only QTLs conferring heterozygous resistance in either one of the parents could be segregated and mapped in the population. Thus, the ten QTLs we identified were likely the minimum number that could be detected using this study population. The combined segregation resulted in transgressive segregation, in other words, we cultivated hybrid plants with higher levels of resistance than that the RP and lower levels of susceptibility than the SP. Resistance-related QTL alleles were derived from both parents.

Resistance specificity to strains and temperatures

We found strain-specific and temperature-dependent QTLs (PBWR-6a, PBWR-6b, and PBWR-10b) and strain-non-specific and broad-spectrum resistance QTLs (PBWR-3 and PBWR-7). The temperature-dependent QTLs contributed considerably to the resistance to MAFF327142 (phyloctype I/biovar 3), with PBWR-6b and PBWR-10b being more effective at 24 °C. The distributions of the DIs in the F1 population were skewed toward relatively lower DIs at 24 °C and toward higher DIs at 28 °C, which was likely due to the effect of PBWR-6b (Fig. 1a and b). PBWR-6b was considered to be derived from RP 10–03-30, a haploid clone of Saikai 35 (Habe et al. 2019), which was originally derived from *S. phureja* (Mori et al. 2012). *S. phureja* is a well-known source of BW-resistant factors, and the resistance is strain-specific and sensitive to high temperatures (Ciampi and Sequeira 1980; French and De Lindo 1982; Sequeira 1979; Sequeira and Rowe 1969). The strain-specific resistance of *S. phureja* appeared to be simply inherited in few cases (Elphinstone 1994). Therefore, we suggest that PBWR-6b was derived from *S. phureja* and functions as a simply inherited, major QTL at lower temperatures. PBWR-3 and PBWR-7 showed stable resistance to all strains at low and high temperatures, irrespective of different phylotypes and biovars. These QTLs may be effective under
diverse environmental conditions and highly desired in breeding BW-resistant cultivars. In tomatoes and eggplants, there are some lines that lose resistance under high-temperature environments (Kunwar et al. 2020; Namisy et al. 2019). Research suggested that, in tomatoes, the QTLs Rbw-3 and Rbw-6 are stable at high temperatures (Carmeille et al. 2006; Kunwar et al. 2020), whereas Rbw-12 is suggested to deteriorate at higher temperatures (Kunwar et al. 2020). Indeed, temperature is the primary factor influencing host–pathogen interactions and survival in the soil for plants resistant to BW (Muthoni et al. 2012, 2020). Since few BW-resistant QTLs are known to be temperature responsive, future studies need to focus on testing QTLs under fluctuating temperatures, as was done in this study.

Reliability of the BW-resistant QTLs

Chen et al. (2013) identified S. chacoense-derived BW-resistant QTLs against the race I/biovar 3 strain on chromosomes 2 and 9. The SP used in our study was F1-1, an interspecific hybrid between S. chacoense and S. phureja (Hosaka and Hanneman 1998). However, we did not identify any QTLs on chromosomes 2 and 9, suggesting that different species or even the same species (S. chacoense) may have different QTL. In our previous study using the same F1 population and the same inoculum (MAFF327001, phylotype I/biovar 4) at 28 °C, five QTLs were identified on chromosomes 1, 3, 7, 10, and 11 (Habe et al. 2019). When their locations were compared, the previously identified QTLs qBWR-1, qBWR-2, qBWR-3, qBWR-4, and qBWR-5 correspond to the QTLs identified in the present study: PBWR-1b, PBWR-3, PBWR-7, PBWR-10a, and PBWR-11, respectively (Fig. 2). The QTL PBWR-5 on chromosome 5 which showed a minor contribution to resistance was newly found, and PBWR-11 effect was not significant in this study (Table 1). Repeated resistance assays may increase or decrease certain genetic variances, affecting significance levels of the QTLs. Here, difficulty in evaluating BW resistance was featured again, and the importance of the major QTLs is emphasized.

Universal resistance QTLs

BW-resistant QTLs have been identified in chromosomes 3, 4, 6, 8, 10, 11, and 12 in tomato plants (Carmeille et al. 2006; Mangin et al. 1999; Thoquet et al. 1996a, 1996b; Wang et al. 2000, 2013) and in chromosomes 1, 2, 3, 4, 5, 6, 7, 8, and 9 in eggplants (Lebeau et al. 2013; Mimura et al. 2012; Salgon et al. 2017, 2018). Comparison of the physical location in each chromosome indicates that the strain-specific resistance QTL PBWR-6b is likely to be colocalized with tomato QTL (Bwr-6) and eggplant QTL (ERPR6) on chromosome 6 (Fig. 3a). However, both Bwr-6 and ERPR6 confer resistance against phytophylotypes I and II (Carmeille et al. 2006; Salgon et al. 2018; Shin et al. 2020), whereas the resistance of PBWR-6b is limited to phyotype I/biovar 3. The mapping position of Bwr-6 slightly varies depending on different inoculums and field conditions (Wang et al. 2013), which was similarly observed for ERPR6 (Salgon et al. 2018). These findings indicate that strain-specific single-locus resistance genes are clustered on the same chromosome (Andolfo et al. 2013; Meyers et al. 1998), which superficially made Bwr-6 and ERPR6 broad-spectrum resistance genes (Salgon et al. 2018). For Bwr-6 in tomato, 18 candidate genes have been proposed (Abebe et al. 2020; Kim et al. 2018; Shin et al. 2020).

A tomato-derived QTL (Bwr-3) and two eggplant-derived QTLs (ERPR3a and ERPR3b) have been reported on chromosome 3 (Carmeille et al. 2006; Salgon et al. 2018; Thoquet et al. 1996b; Wang et al. 2013). Bwr-3 and ERPR3b are colocalized and may include the same locus (Salgon et al. 2018), while the potato-derived QTL PBWR-3 is likely colocalized with ERPR3a (Fig. 3b). Like PBWR-3, ERPR3a is a strain-non-specific, broad-spectrum QTL (Salgon et al. 2018). The nearest SNP locus to PBWR-3 (solcap_snpc2_50637) is located in the receptor-like kinase gene (PGSC0003DMG400016685). This gene may represent one of candidate genes for BW resistance because a leucine-rich repeat receptor-like kinase gene (ERECTA) is involved in BW resistance in Arabidopsis thaliana (Godiard et al. 2003).

The broad-spectrum resistance QTL PBWR-7 was detected in a span between 10.9 and 39.2 Mb near the centromere, where recombination is less likely to occur. There is a large body of evidence suggesting that resistance loci are clustered rather than distributed randomly across chromosomes (Yang et al. 2017). Indeed, the long arm of chromosome 7 in potato plants harbors a resistance gene hotspot containing Rpi1 and Rpi2 against
**Phytophthora infestans** and *Gro1-4* against *Globodera rostochiensis* (Ballvora et al. 1995; Kuhl et al. 2001; Paal et al. 2004; Ruggieri et al. 2014; Yang et al. 2017). Although this hot spot slightly shifted in location (50–53 Mb; Yang et al. 2017) from that of *PBWR-7*, our results encourage investigation into more resistance genes in the regions surrounding both loci. Since the effect of resistance afforded by *PBWR-7* is slightly higher than that of *PBWR-3*, it would be advantageous for the development of BW-resistant potato cultivars to conduct fine mapping and develop molecular markers to determine the accurate location of this QTL.

**Conclusion**

RSSC strains have spread worldwide and show a wide host range (Hayward 1985; Peeters et al. 2013). Potatoes are infected by all four phylotypes of this species complex. Therefore, BW-resistant varieties are sought after that show resistance to these four phylotypes. The phylotype-specific resistance has been reported in *S. phureja* (Suga et al. 2013), which emphasizes the need for phylotype-specific breeding (Horita et al. 2014). However, in tomato and eggplant, both phylotype-specific and non-specific, broad-spectrum resistance QTLs have been identified. We identified five major and five minor resistance QTLs in potato, which included both strain-specific and broad-spectrum resistance QTLs. The major QTLs *PBWR-3* and *PBWR-7* showed stable resistance against *R. pseudosolanacearum* (phytotype I) and *R. syzygii* (phytotype IV), which are major phylotypes in Asia (Fegan and Prior 2005; Wicker et al. 2012). *PBWR-6b* is a strain-specific major resistance QTL against phylotype I/biovar 3 and can be effectively used in relatively cool area because the resistance conferred was more effective at a relatively lower temperature. Therefore, we suggest that broad-spectrum QTLs and strain-specific QTLs can be combined to develop the most efficient BW-resistant cultivars in specific areas.
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Declarations

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Competing interests The authors declare no competing interests.

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