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# Charakterisierung der *Phytophthora infestans* Resistenz der Kulturkartoffel (*Solanum tuberosum*) anhand des Genpools des Julius Kühn-Instituts

Dissertationen aus dem Julius Kühn-Institut

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Bundesforschungsinstitut für Kulturpflanzen

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# **Charakterisierung der *Phytophthora infestans* Resistenz der Kulturkartoffel (*Solanum tuberosum*) anhand des Genpools des Julius Kühn-Instituts**

Kumulative Dissertation

zur Erlangung des akademischen Grades Doktor der Agrarwissenschaften (doctor agriculturae) an der Agrar- und Umweltwissenschaftlichen Fakultät der Universität Rostock

vorgelegt von M. Sc. Johanna Blossei

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**Inhaltsverzeichnis**

**Abstract**

The production of potato, as an important source of food has high annual yield losses due to late blight. Despite intensive research and breeding work, there is still no approved cultivar that bears a durable resistance. In the present study it was determined which wild relatives of the cultivated potato carry resistance to late blight and how this can be made accessible for progress in potato breeding. Based on this literature search, 85 species were found to have a resistance potential and about half of them are not yet further characterised. In addition, it was explained which new methods could be used to make potato breeding faster and more efficient in the future.

Another aim of this work was to characterise the JKI potato gene pool for late blight resistance. An examination of the pre-breeding clones for various resistance genes from wild relatives revealed that individual clones carry up to four of these resistance genes. As further investigations, two genome-wide association studies were performed. In the first, five QTL were detected on chromosomes 1, 7, 10 and 11, in the second, two marker-trait associations were detected on chromosomes 9 and 11.

Finally, it was analysed whether the amount of organic nitrogen fertilisation can influence late blight infestation in cultivars and pre-breeding clones. It was shown that the influence is marginal. Overall, however, in contrast to the cultivars, the clones were hardly or not at all infected at all fertilisation levels, so that they carry great potential for resistance breeding.

The results of this work can be used in potato breeding to develop cultivars with a possibly durable late blight resistance.

**Zusammenfassung**

Die Produktion der Kartoffel, als eine wichtige Nahrungsquelle, hat vor allem durch die Kraut- und Knollenfäule jährlich hohe Ertragseinbußen. Trotz intensiver Forschungs- und Züchtungsarbeit gibt es bis heute keine zugelassene Sorte, die eine dauerhafte Resistenz trägt. In der vorliegenden Arbeit wurde herausgearbeitet, welche wilden Verwandten der Kulturkartoffel Resistenzen gegen die Krautfäule tragen und wie diese für die Züchtung zugänglich gemacht werden können. Diese Literaturrecherche ergab, dass 85 Arten ein Resistenzpotential aufwiesen und davon ca. die Hälfte noch nicht näher charakterisiert ist. Zudem wurde erläutert, mit welchen neuen Methoden die Kartoffelzüchtung in Zukunft schneller und effizienter ablaufen kann.

Ein weiteres Ziel dieser Arbeit war die Charakterisierung des JKI Kartoffelgenpools auf seine Krautfäuleresistenz. Dabei zeigte sich bei einer Untersuchung der Stämme auf verschiedene Resistenzgene aus Wildarten, dass einzelne pre-breeding Stämme bis zu vier dieser Resistenzgene tragen. Als weitere Untersuchungen wurden zwei genomweite Assoziationsstudien durchgeführt. Bei ersterer wurden fünf QTL auf den Chromosomen 1, 7, 10 und 11 detektiert, bei der zweiten waren es zwei Marker-Merkmalsassoziationen auf den Chromosomen 9 und 11.

Abschließend wurde untersucht, wie weit die Menge einer organischen Stickstoffdüngung den Befall mit Krautfäule bei Sorten und pre-breeding Stämmen beeinflussen kann. Hier ergab sich, dass dieser Einfluss vernachlässigbar ist. Allerdings waren die Stämme im Gegensatz zu den Sorten in allen Düngestufen kaum bis gar nicht befallen, sodass diese ein großes Potential für die Resistenzzüchtung darstellen.

Die Ergebnisse dieser Arbeit können in der Kartoffelzüchtung genutzt werden, um künftig Sorten mit einer möglicherweise langfristigen Krautfäuleresistenz zu züchten.

**Abkürzungsverzeichnis**

| | |
|---|---|
| *acl* | *acaule* |
| ANOVA | Analysis of variance (Varianzanalyse) |
| BC | Backcross (Rückkreuzung) |
| BLE | Federal Office of Agriculture and Food (Bundesanstalt für Landwirtschaft und Ernährung) |
| BMEL | Federal Ministry of Food and Agriculture (Bundesministerium für Ernährung und Landwirtschaft) |
| bp | Base pair (Basenpaar) |
| C | Carbon (Kohlenstoff) |
| C9/11 | Chromosome 9/11 (Chromosom 9/11) |
| cv. | Cultivar (Sorte) |
| DArT | Diversity Arrays Technology |
| DNA | Deoxyribonucleic acid (Desoxyribonukleinsäure) |
| EBN | Endosperm balance number groups |
| ETI | Effector-triggered immunity (Effektor-gesteuerte Immunität) |
| FDR | False discovery rate (Falscherkennungsrate) |
| FDR | First division restitution |
| G | Genotype (Genotyp) |
| GBS | Genotyping-by-sequencing (Genotypisierung durch Sequenzierung) |
| GLM | Generalised linear model (generalisiertes lineares Modell) |
| GMO | Genetically modified organism (genetisch veränderter Organismus) |
| GWAS | Genome-wide association study (genomweite Assoziationsstudie) |
| $h^2$ | Heritability (Heritabilität) |
| JKI | Julius Kühn Institute (Julius Kühn-Institut) |
| LD | Linkage disequilibrium ($r^2$, Kopplungsungleichgewicht) |

| | |
|---|---|
| LfL | Bavarian State Research Centre for Agriculture (Bayerische Landesanstalt für Landwirtschaft) |
| LRR | Leucine rich repeats (Leucine-reiche Widerholung) |
| LS-Means | Least Square-Means |
| Mb | Megabase |
| MAMP | Microbe-associated molecular pattern (Mikroben-assoziiertes molekulares Muster) |
| MLM | Mixed linear model (gemischtes lineares Modell) |
| MTI | MAMP-triggered immunity (MAMP-gesteuerte Immunität) |
| N | Nitrogen (level) (Stickstoff(stufe)) |
| NBS | Nucleotide-binding site (Nukleotid-Bindungsstelle) |
| PCR | Polymerase chain reaction (Polymerasekettenreaktion) |
| *P.i.* | *Phytophthora infestans* |
| PRR | Pattern-recognition receptor (Mustererkennungsrezeptor) |
| QTL | Quantitative trait locus/loci |
| $R^2$ | Phenotypic variance (phänotypische Varianz) |
| $r^2$ | Linkage disequilibrium (Kopplungsungleichgewicht) |
| rAUDPC | Relative area under the disease progress curve (relative Fläche unter der Krankheitsverlaufskurve) |
| RF | Relative Feuchte |
| R-Gen/ R gene | Resistance gene (Resistenzgen) |
| RH | relative Humidity (relative Feuchte) |
| RLK | Receptor-like kinase (rezeptorähnliche Kinase) |
| RLP | Receptor-like protein (rezeptorähnliches Protein) |
| S | Supplementary (Ergänzende Informationen) |
| SDR | Second divison restitution |
| SNP | single nucleotide polymorphism (Einzelnukleotid-Polymorphismus) |

| | |
|---|---|
| TPS | True potato seeds (echte Kartoffelsamen) |
| *tub* | *tuberosum* |
| *ver* | *vernei* |
| Y | Year (Jahr) |

# 1. Einleitung

## 1.1 Geschichte der Kulturkartoffel

Fossilien belegen, dass die Kulturkartoffel (*Solanum tuberosum* L.) der Menschheit schon seit über 10.000 Jahren als wichtige Nahrungsquelle dient (Engel 1970). Ursprünglich stammt sie dabei aus den Anden Perus in Südamerika (Spooner et al. 2005) und kam erst im 16. Jahrhundert über Spanien nach Europa (Hawkes 1990). Dabei blieb sie zunächst eher als Anschauungs- und Forschungsobjekt für die botanischen Gärten interessant (De Jong 2016). So erlangte sie beispielsweise erst Ende des 17. Jahrhundert in Irland ihre Bedeutung für die Versorgung der Bevölkerung (Burton 1989) und in Preußen ordnete Friedrich der Große Mitte des 18. Jahrhunderts sogar den Anbau und Verzehr der Kartoffel an (De Ferrière le Vayer 2017).

Der rasche Anstieg der Produktion brachte allerdings auch eine Ausbreitung der Kraut- und Knollenfäule (*Phytophthora infestans* (Mont.) de Bary) mit sich, die zu verheerenden Hungerkatastrophen wie beispielsweise 1845/46 in Irland führte (Woodham-Smith 1962). Dennoch wurde die Kartoffel von Europa aus in nahezu die ganze Welt gebracht.

Die Züchtung von Kartoffeln begann mit den ersten händisch durchgeführten Kreuzungen 1807 in England (Knight 1814). Im 20. Jahrhundert wurde dann auch Wildmaterial in den Genpool eingebracht (Bradshaw 2007). Mittlerweile gibt es weltweit über 4200 verschiedenen Sorten aus über 100 Ländern (Struik 2008).

## 1.2 Nutzung der Kulturkartoffel heute

Die tetraploide (2n=4x=48) Kulturkartoffel aus der Familie der *Solanaceae* zählt heutzutage zu den fünf am meisten produzierten Grundnahrungsmitteln weltweit (Birch et al. 2012; FAO 2021). Ihre Anbauschwerpunkte befinden sich hauptsächlich in den gemäßigten Klimazonen. Führend ist dabei China mit einer Produktionsmenge von knapp 92 Mio. Tonnen im Jahr 2019, gefolgt von Indien, Russland, der Ukraine und den USA. Deutschland lag mit 10,6 Mio. Tonnen auf Platz 6 (FAOSTAT 2022).

Kartoffeln gelten als gesund und vielseitig einsetzbar. Sie bestehen zu etwa 80 % aus Wasser, 18 % Stärke und 2 % Proteinen, abhängig von der jeweiligen Sorte (Navarre et al. 2009). Zudem enthalten sie viele Vitamine und Mineralstoffe wie Calcium, Magnesium, Eisen und Vitamin C (U.S. Department of Agriculture 2021).

Derzeit nimmt die frische Kartoffel immer noch den größten Konsumanteil ein, aber die verarbeiteten Produkte sind stark auf dem Vormarsch. Dabei ist der Anteil an gefrorenen

Kartoffeln, für beispielsweise Pommes, besonders hoch (Keijbets 2008). Kartoffeln werden aber aufgrund ihres hohen Stärkeanteils auch für Zwecke außerhalb der Ernährung verwendet. Dazu zählen unter anderem die Papier-, die Klebstoff- und die Textilindustrie (Kraak 1992).

### 1.3 Die Kraut- und Knollenfäule und ihr Erreger

Die Kraut- und Knollenfäule ist die häufigste Kartoffelkrankheit überhaupt und kann zu jährlichen Ernteverlusten im Wert von Milliarden Euro weltweit führen (Haas et al. 2009; Haverkort et al. 2009; USABlight 2021). Sie wird vom Oomyceten *P. infestans* (Mont.) de Bary ausgelöst, der ursprünglich aus Mexiko stammt und in den zwei Paarungstypen A1 und A2 auftritt (Widmark et al. 2007; Goss et al. 2014). Lange Zeit konnte sich *P. infestans* außerhalb Mexikos ausschließlich vegetativ verbreiten, da nur A1 Typen außerhalb von Mexiko verbreitet waren (Spielman et al. 1991). Diese lösten beispielsweise die Hungersnot 1845/46 in Irland (Woodham-Smith 1962) oder 1916/17 in Deutschland (Mizubuti & Fry 2006) aus. Vermutlich kamen die ersten A2 Typen erst in den 1970ern und 1980ern nach Europa (Spielman et al. 1991; Fry et al. 1993). Dies führte dazu, dass nun auch dort eine sexuelle Vermehrung und die Entstehung neuer Genotypen von *P. infestans* im großen Stil möglich wurde (Drenth et al. 1994; Cooke et al. 2003).

Ab diesem Zeitpunkt stieß die bis Mitte des 20. Jh. noch recht vielversprechend aussehende Resistenzzüchtung an ihre Grenzen (Kapitel 1.5).

Die Symptome einer Infektion mit Kraut- und Knollenfäule erstrecken sich von kleinen braunen Flecken auf Blättern und Sprossachse bis hin zum Absterben der gesamten oberirdischen Biomasse. Zudem überzieht ein weißes Myzel vor allem die Unterseite der Blätter. Die Knollen weisen braune Stellen auf und werden durch zusätzliche Infektionen mit Bakterien oft weich und matschig (Arora et al. 2014).

Die Übertragung erfolgt über Wind und Regen zwischen den Pflanzen im Feld, durch die Einlagerung von infizierten Knollen (Van der Zaag 1956) aber auch dadurch, dass die Sporangien im Boden überwintern können (Drenth et al. 1995, Turkensteen et al. 2000).

### 1.4 Bekämpfung der Kraut- und Knollenfäule

Um den Befall gar nicht erst auftreten zu lassen, steht der Verzicht auf das Auspflanzen infizierter Knollen an erster Stelle. Darüber hinaus bieten sich aber auch einige präventive Maßnahmen an. Hierzu zählen Prognosesysteme wie ÖKOSIMPHYT von isip (Zellner et al. 2009), die Fruchtfolge (Van Bruggen et al. 2015) oder die Möglichkeit einer Vorkeimung des

Pflanzguts, wodurch die Pflanzen schneller auflaufen und somit einen Vorsprung vor dem Befall mit *P. infestans* aufbauen (Waschl & Hein 2010).

Ungeachtet der präventiven Möglichkeiten erfordert die Kartoffel dennoch den verglichen mit den übrigen Ackerkulturen größten Einsatz von Pflanzenschutzmitteln (Yuen 2021). Entsprechend stehen bei einem Ausbruch der Kraut- und Knollenfäule für die Bekämpfung im konventionellen Landbau eine Reihe an Fungiziden zur Verfügung (LTZ (Hrsg.) 2007). Im ökologischen Landbau dagegen ist nur Kupfer als Bekämpfungsmittel zulässig (Durchführungsverordnung (EU) 2018/1981). Aber auch der Kupfereinsatz ist umstritten. So können hohe Kupfermengen beispielsweise die Biodiversität der Bodenorganismen beeinträchtigen (Naveed et al. 2014). Deswegen wird viel daran geforscht die Kupfermenge einerseits zu reduzieren und andererseits kupferfreie Bekämpfungsmethoden wie beispielsweise mit Pflanzenextrakten, Mikroorganismen oder Chitosan zu entwickeln (La Torre et al. 2019). Für den konventionellen Anbau ist die Entwicklung alternativer Bekämpfungsmethoden ebenfalls sehr wichtig, da immer mehr Fungizide ihre Zulassung verlieren und es verhältnismäßig wenig Neuzulassungen gibt. Zudem ist im Zuge des Umweltschutzes eine Reduktion von Pflanzenschutzmitteln unabdingbar.

Damit empfiehlt sich derzeit als nachhaltigste und wichtigste Maßnahme zur Vermeidung eines Befalls, resistente Sorten einzusetzen.

### 1.5 Resistenz gegenüber der Kraut- und Knollenfäule

Eine Resistenz gegen *P. infestans* kann sowohl durch einzelne Resistenzgene (R-Gene, monogene Resistenz), als auch durch das Zusammenspiel mehrerer R-Gene (Pyramidisierung) und Quantitative Trait Loci (QTL) bedingt sein (polygene Resistenz).

Die R-Gene waren hierfür vor allem in der Mitte des 20. Jahrhunderts von großer Bedeutung. Als erste Resistenzquelle wurde die Wildart *Solanum demissum* entdeckt, deren Genpool elf R-Gene (*R1* - *R11*) umfasst. Von Black und Mastenbroek wurden in den 1950ern und 60ern Differentialsortimente erstellt, mithilfe derer das Vorhandensein von entsprechenden Pathotypen detektiert werden konnte (Black et al.1953; Malcolmson & Black 1966; Malcolmson 1969). Mittlerweile wurden diese monogenen Resistenzen aber fast alle von angepassten Pathotypen gebrochen (Bradshaw et al. 2006; Fry 2008; Hein et al. 2009). Das Auftreten der A2 Typen in den 1970ern und 80ern in Europa (Spielman et al. 1991; Fry et al. 1993) beschleunigte diese Entwicklung noch (Drenth et al. 1994; Cooke et al. 2003), sodass einzelne R-Gene heutzutage kaum noch eine Rolle in der Resistenzzüchtung spielen.

So wurden neben *S. demissum* auch andere Arten auf ihre Resistenzeigenschaften hin untersucht. Einige dieser Arten sind allerdings nur schwierig oder gar nicht mit *S. tuberosum* kreuzbar. Zudem dürfte es nur eine Frage der Zeit sein, bis *P. infestans* auch diese einzelnen Resistenzen bricht. Aus diesem Grund sollte über die Kombination mehrerer Resistenzquellen nachgedacht werden. Das Potential von wilden Verwandten der Kulturkartoffel wird ausführlich in Kapitel 2.1 behandelt.

Eine weitere Möglichkeit erschließt sich über die Pyramidisierung mehrerer R-Gene in einem Genotyp. Diese kann durch das Erstellen von cis- oder transgenen Pflanzen erfolgen (Zhu et al. 2012; Haverkort et al. 2016; Ghislain et al. 2019). Dadurch konnte sogar eine neue Sorte „Fortuna“ mit den R-Genen *Rpi-blb1* und *Rpi-blb2* entwickelt werden, für die BASF SE 2011 eine Zulassung beantragte (Storck et al. 2011). Diese Pflanzen gelten in Deutschland bzw. Europa aber als genetisch modifiziert und sind somit für den Anbau nicht zugelassen (Schouten 2022).

Die Pyramidisierung von R-Genen lässt sich aber auch durch die klassische Kreuzungsarbeit erreichen (Stefańczyk et al. 2020, Rogozina et al. 2021; Kapitel 2.2), sodass eine Zulassung für auf diesem Wege entstandene Sorten in Europa möglich ist. Ein Beispiel hierfür ist die Sorte „Sarpo Mira“, die die Gene *R3a*, *R3b*, *R4*, *Rpi-Smira1* und *Rpi-Smira2* trägt (Rietman et al. 2012).

Trotz der Pyramidisierung unterliegen die Genotypen der Gefahr, dass R-Gen basierte Resistenzen jederzeit gebrochen werden können, auch wenn dies bei mehreren Genen deutlich unwahrscheinlicher ist als bei einem Gen. Alternativen hierzu werden ebenfalls in Kapitel 2.1 erörtert.

Die polygene (quantitative) oder auch dauerhafte Resistenz durch nicht nur einzelne R-Gene, sondern durch QTL-Effekte oder die Kombination beider rückte besonders in den Vordergrund, als abzusehen war, dass monogene Resistenzen bei der Krautfäulebekämpfung keine längerfristige Abhilfe verschaffen können (Thurston 1971). Zu beachten ist dabei allerdings, dass die durch QTL bedingte Resistenz häufig mit einer unerwünscht späten Abreife gekoppelt ist (Visker et al. 2005). An polygener Resistenz wurde in den vergangenen Jahren bereits viel geforscht. Als Mittel dienten dafür vor allem QTL-Analysen und genomweite Assoziationsstudien (Kapitel 1.6). Dabei gibt es allerdings nur wenige Studien, die alle folgenden Aspekte vereinen:

- Tetraploide, sortennahe Genotypen
- Inokulation für die Bewertung der Resistenz mit einem breiten Genotypenspektrum von *P. infestans*
- Eine hohe Markeranzahl, mit der Methode von Selga et al. (2020), bei der die Markeranzahl reduziert werden kann, mindestens 5000

Diese Aspekte werden in der vorliegenden Arbeit in Kapitel 2.3 und mit neueren Daten und einer Ausweitung der Untersuchung auch auf die Knollenfäuleresistenz auch in Kapitel 2.4 bedacht. Zudem liegt in diesen Kapiteln ein wesentlicher Fokus auf der Resistenzbetrachtung des in langjähriger Züchtungsarbeit (Kapitel 1.8) entwickelten Kartoffelgenpools des Julius Kühn-Instituts (JKI).

Bei Danan et al. (2011) wurde aus 14 Publikationen, in denen QTL-Analysen zur Krautfäuleresistenz durchgeführt wurden, eine Meta-QTL-Analyse mit 2141 Markern erstellt. Als Ergebnis wurden QTL auf allen zwölf Chromosomen entdeckt. Bei diesen der Meta-Studie zugrundeliegenden Studien wurde allerdings häufig nur eine geringe Anzahl von unter 1000 Markern eingesetzt, beispielsweise bei Bormann et al. (2004) oder Oberhagemann et al. (1999).

Li et al. (2011) beschrieben sechs QTL auf den Chromosomen 2, 7, 9 und 12 einer diploiden Kreuzungspopulation. Ein QTL auf Chromosom 9 wurde bei Genotypen aus tropischen Hochebenen gefunden (Lindqvist-Kreuze et al. 2014). Bei Massa et al. (2015) wurde ebenfalls auf Chromosom 9 ein QTL detektiert, allerdings wurde für die Inokulation nur der US-8 Genotyp verwendet. Eine neuere Studie 2016 beschrieb 27 QTL anhand einer Gruppe von 96 verschiedenen Genotypen aus den Kreuzungsprogrammen zweier deutscher Kartoffelzüchter (Mosquera et al. 2016). In weiteren Studien von Lindqvist-Kreuze et al. (2021) wurde ein QTL auf Chromosom 9 detektiert und Santa et al. (2018) entdeckten sechs QTL. Muktar et al. (2015) und Rojas et al. (2019) nutzten beide die gleichen Genotypen der wenig sortennahen Phureja Gruppe. In der ersten Studie wurden sieben, in der zweiten 16 QTL gefunden. Dabei nutzte die Gruppe um Rojas über 80.000 Marker. QTL auf den Chromosomen 5, 6, 11 und 12 wurden bei Kreuzungspopulationen mit *S. microdontum* und *S. pampasense* detektiert (Meade et al. 2020). Wang et al. (2020) führten keine Feldversuche durch, sondern testeten Blattmaterial und konnten auf nahezu allen Chromosomen QTL nachweisen. Insgesamt gibt es somit einige Studien, die QTL für eine *P. infestans* Resistenz detektierten. Mit der Frage zu QTL im Kartoffelgenpool des JKI setzen sich nachstehend die Kapitel 2.3 und 2.4 auseinander.

## 1.6 Hintergrund genomweite Assoziationsstudien

Genomweite Assoziationsstudien (GWAS) dienen dazu, Verbindungen zwischen einem bestimmten Merkmal und Abschnitten auf dem Genom festzustellen. Sie kommen ursprünglich aus dem medizinischen Bereich. Der große Vorteil dieser Studien ist darin begründet, dass keine, gerade in der Humanmedizin nicht realisierbare, Kartierungspopulationen notwendig sind. Es wird lediglich eine möglichst große Gruppe an wenig verwandten Individuen benötigt, die das zu betrachtende Merkmal tragen oder nicht tragen.

Seit den ersten Assoziationsstudien an Kulturpflanzen (z. B. Remington et al. 2001; Thornsberry et al. 2001) sind tausende solcher Studien durchgeführt worden. Dabei wird das gesamte Genom auf Marker untersucht, die sich mit dem Zielmerkmal in einem Kopplungsungleichgewicht (Linkage Disequilibrium, LD) befinden. Um falsch positive Assoziationen zu vermeiden, ist eine Analyse der Populationsstruktur unerlässlich (Rafalski 2010). Für die Berechnung der GWAS werden Modelle wie das generalisierte (GLM) oder das gemischte (MLM) Modell verwendet. Diese verwenden die Populationsstruktur als Cofaktor (Korte & Farlow 2013). Nachteile der GWAS liegen in einer höheren Fehleranfälligkeit aufgrund der Populationsstruktur sowie im multiplen Testen, bei dem Korrekturen wie beispielsweise mit Bonferroni oder der false discovery rate (FDR) vorgenommen werden müssen, um das Risiko von falsch positiven Assoziationen zu minimieren (Korte & Farlow 2013).

In Kapitel 2.3 wird eine GWAS für Kraufäuleresistenz mit Daten des Kartoffelgenpools des JKI berechnet und in Kapitel 2.4 wird eine zweite GWAS mit neuen Genotypen berechnet, bei der neben der Krautfäuleresistenz auch die Knollenfäuleresistenz untersucht wird.

## 1.7 Einfluss von Stickstoff auf den Befall mit *P. infestans*

Aufgrund der Düngeverordnung von 2020 ist ein primäres Ziel die Verringerung des Einsatzes von Düngemitteln, unter anderen um Nährstoffeinträge in Gewässer zu minimieren. Dennoch ist die Aufnahme von Stickstoff essentiell für das Wachstum und die Entwicklung von Pflanzen. Aber auch auf die Abwehr von Pathogenen wie *P. infestans* kann die Menge an verfügbarem Stickstoff einen Einfluss haben. Juárez et al. (2000) untersuchten zwei Sorten und drei verschiedene Stickstoffgaben. Dabei folgerten sie, dass höhere Stickstoffgaben zu einem schwereren Krankheitsverlauf führten. Auch Agu (2004) kam zu diesem Ergebnis, bezog aber noch Phosphoreffekte mit ein. Zudem untersuchte er nur eine Sorte. Gewächshausversuche mit einer Sorte und zwei Stickstoffstufen von Mittelstraß et al. (2006) ergaben bei den Pflanzen,

die in der hohen Stickstoffstufe wuchsen, ebenfalls eine höhere Anfälligkeit. Zum gleichen Ergebnis kamen auch Ros et al. (2008), die vier Sorten untersuchten und Bangemann (2010) anhand von zwei Sorten, dabei aber vier Stickstoffstufen. Jensen und Nielsen (2015) sahen eine Tendenz, dass mehr Stickstoff zu mehr Befall führen könnte. Sunita et al. (2011) dagegen kamen zu gegenteiligen Ergebnissen, Cicore et al. (2012) stellten gar keinen Unterschied zwischen den Stufen fest, es wurden allerdings auch nur zwei argentinische Sorten verwendet. Bei Jin et al. (2014) und Jha et al. (2019) wurde der geringste Befall mit *P. infestans* bei einer mittleren Stickstoffgabe nachgewiesen. In zwei Studien von Möller et al. (2006 und 2007) wurde in Bezug auf den ökologischen Landbau gänzlich angezweifelt, ob Stickstoff überhaupt einen Einfluss auf den *P. infestans* Befall hat.

Es gibt somit keine eindeutige Aussage darüber, welche Stickstoffmenge besonders geeignet ist, um einen Befall mit *P. infestans* zu minimieren. Zudem wird in keiner der oben genannten Studien die Kombination aus Feld- und Labortests an mehr als vier Sorten und Genotypen untersucht, was eine Verallgemeinerung der Ergebnisse erschwert. Auch wurde mit Ausnahme von Möller et al. (2006 und 2007) ausschließlich anorganischer Stickstoff für die Versuche verwendet. Da aktuell der ökologische Landbau stark expandiert, sollte neben einer Erweiterung der Prüfgliederanzahl auch ein stärkerer Fokus auf den Einsatz von organischem Dünger gelegt werden.

Eine weitere Besonderheit der vorliegenden Arbeit (Kapitel 2.5) ist, dass der Einfluss nicht nur bei Sorten, sondern auch auf resistente Zuchtstämme untersucht wurde. Sollten diese sich wenig von der Stickstoffmenge beeinflussen lassen, stellen sie ein großes Potential für den ökologischen Landbau dar, bei dem der Stickstoffbedarf verglichen mit dem konventionellen Landbau weniger genau eingestellt werden kann.

### 1.8 Der Kartoffelgenpool des Julius Kühn-Instituts

Am Julius Kühn-Institut wird seit über 60 Jahren in einem Langzeitprogramm an der *P. infestans* Resistenz von Kartoffeln geforscht. Anfänglich wurden Kreuzungen mit resistenten Akzessionen der Wildarten *S. andigena, S. bulbocastanum* (über Brückenkreuzungen), *S. demissum, S. okade, S. phureja, S. sparsipilum, S. stoloniferum* und *S. vernei* durchgeführt. Anschließend erfolgten bis zum heutigen Zeitpunkt eine Art Rückkreuzung mit hochwertigen Sorten und die Selektion von Stämmen, die sowohl eine hohe *P. infestans* Resistenz, als auch sortennahe, agronomische Eigenschaften mit dem Schwerpunkt der Speiseeignung vereinen. So entstand über die Jahre ein hochwertiger Genpool, der als Basis für die vorliegende Arbeit dient.

## 1.9 Zielstellung und Hypothesen dieser Arbeit

Zunächst wird in dieser Arbeit ein Überblick über die *P. infestans* Resistenz in wilden Verwandten der Kulturkartoffel gegeben. Dazu wurden knapp 80 Studien ausgewertet und neben den Arten auch die dazugehörigen QTL und R-Gene gelistet. Anschließend wurden die Möglichkeiten abgewogen, diese Resistenzquellen für die Züchtung besser zu erschließen (Kapitel 2.1).

Ziel dieser Arbeit war die Charakterisierung der *P. infestans* Resistenz des JKI Kartoffelgenpools. Da im Pool Kreuzungen mit R-Gen tragenden Wildarten vorgenommen worden waren, wurde der Genpool zunächst auf das Vorhandensein von R-Genen untersucht (Kapitel 2.2).

Anschließend erfolgte die weitere Charakterisierung auf Basis der quantitativen Resistenz. Diese ist, wie in Kapitel 1.5 beschrieben, bereits in einigen Studien untersucht worden. Es mangelt allerdings an Studien, die sich mit tetraploidem Material beschäftigen. Zudem wurde in den letzten Jahren die Möglichkeit geschaffen, mit wesentlich mehr Markerdaten arbeiten zu können. Aus diesem Grund war ein Ziel dieser Arbeit, die quantitative *P. infestans* Resistenz des JKI Genpools anhand von genomweiten Assoziationsstudien zu untersuchen (Kapitel 2.3 und 2.4).

Des Weiteren spielt die Zufuhr von Stickstoff, gerade im Hinblick auf den ökologischen Landbau, eine wichtige Rolle bei der Kartoffelproduktion. Ein weiteres Ziel dieser Arbeit war das Auffinden von Zusammenhängen zwischen der Menge einer organischen Stickstoffgabe und dem Befall von resistenten Zuchtstämmen und herkömmlichen Sorten mit *P. infestans* um somit Aussagen darüber treffen zu können, ob gerade im Hinblick auf die Vorgaben der aktuellen Düngeverordnung auch eine geringere Stickstoffgabe ohne nennenswerte Ertrags- und Qualitätseinbußen möglich ist (Kapitel 2.5).

Hypothesen:

1. Im Kartoffelgenpool des JKI kommen einige R-Gene aus Wildarten für eine *P. infestans* Resistenz vor.
2. Die genomweiten Assoziationsstudien liefern zusätzliche QTL für die *P. infestans* Resistenz des JKI Kartoffelgenpools.
3. Organischer Stickstoff erhöht in hohen Gaben den Krankheitsbefall mit *P. infestans* bei herkömmlichen Sorten, nicht aber bei resistenten Zuchtstämmen.

## 2. Forschungsartikel

## 2.1 Late blight resistance in wild potato species - Resources for future potato (*Solanum tuberosum*) breeding

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REVIEW ARTICLE

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# Late blight resistance in wild potato species—Resources for future potato (*Solanum tuberosum*) breeding

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## Abstract

Late blight remains the most devastating disease in potato cultivation. The best protection against this disease could be achieved by durably resistant cultivars, but these do not exist at present. To advance resistance breeding, the search for resistant wild potato species and the characterization of their resistance is important. There have recently been a number of new developments in this area. For this reason, all wild potato species known to the authors in which resistance has been found to date are listed in this article with their respective genes and QTL. Lastly, an overview is given, how these new resistance sources can be used for future resistance breeding.

**KEYWORDS**
late blight, plant breeding, potato, resistance, Solanum crop, wild species

## 1 | INTRODUCTION

With a global production of about 360 million tonnes per year, potato (*Solanum tuberosum* L.) is the fifth most important crop after sugar cane, maize, rice and wheat (FAO, 2020). Potato is vegetatively propagated, which makes it especially susceptible to several pathogens. Infected seed tubers can cause early onset of diseases and promote fast spreading in fields. One of the most severe and best studied diseases is late blight, caused by the oomycete *Pythophthora infestans* (Mont.) de Bary. Ever since the first reported outbreaks in 1843 (Andrivon, 1996) leading to the devastating Irish potato famine from 1845 to 1849 (Woodham-Smith, 1962), potato cultivation has suffered from high yield losses caused by this disease. Today, late blight causes annual yield losses with an estimated cost of 6.7 billion dollars worldwide (Haas et al., 2009; USABlight, 2021). At present, potato production relies on fungicides to control the disease. However, registrations for many of these are gradually expiring and few novel fungicides are coming onto the market. Therefore, new more environmentally friendly alternative control strategies are needed. Even organic farming heavily relies on copper-based fungicides (Nechwatal & Zellner, 2015), which can also have adverse effects on soil microorganisms (Rehman et al., 2019). For both conventional and organic farming, breeding of resistant cultivars is of outstanding importance in order to reduce overall fungicide applications. However, more than 160 years of resistance breeding have not yet resulted in cultivars that can keep their resistance in the long term (Nowicki et al., 2012). Wild relatives of cultivated potatoes have been regarded as a valuable source of resistance for decades. In the middle of the 20th century, the species *S. demissum* bearing 11 major resistance genes became the focus of attention. However, the resistance of these individually incorporated race-specific resistance genes (R genes) were overcome quickly by highly adaptable *P. infestans* strains (Collins et al., 1999; Fry, 2008; Hein et al., 2009). Thus, to date, a primary goal in potato breeding is to establish quantitative resistance against a wide spectrum of races by many quantitative trait loci (QTL) and/or stacking of different R genes to avoid breaking the resistance of only one R gene (Haverkort et al., 2016; Stefańczyk

Short informative: This review compiles the wild potato species in which resistance to Late blight has been found. It also provides ideas for future potato breeding.

et al., 2020; Zhu et al., 2012). All of these approaches rely on the discovery of new resistances in wild tuber bearing species (section *Petota*) or *S. tuberosum* landraces. A second important aspect is whether the resistance of the wild species is caused by one or more resistance genes or if it is based on QTL effects. In this regard, some new insights have been gained since the last reviews by Tiwari et al. (2013) and Rodewald and Trognitz (2013). Therefore, this review summarizes all currently known *P. infestans* resistance sources in wild potato species and the known loci of respective resistance genes in the genome, in order to inform breeders and researchers on the diversity of possible resistance sources. Only a few *P. infestans* resistant species have been used in the development of commercial cultivars such as *S. bulbocastanum*, *demissum*, *microdontum*, *phureja*, *sparsipilum*, *stoloniferum*, *venturii* and *verrucosum* (Bethke et al., 2017; Bradshaw, 2021; Hawkes, 1994). What further species may have been used in the past remains elusive, because the transition of material from academic breeding research to commercial breeding is rarely documented. Nonetheless, this highlights that there is still a wealth of new resistance sources that can be made accessible for potato cultivar improvement.

## 2 | LATE BLIGHT RESISTANT WILD RELATIVES OF POTATO

The genus *Solanum* in the family Solanaceae includes about 1500 species (Weese & Bohs, 2007), many of which are tuber bearing (section *Petota*) and are sufficiently closely related to *S. tuberosum* to form hybrids. Thus, their resistance can be introgressed into potato cultivars. Taxonomy is of course always a work in progress and in a large group such as *Petota* the status of many species has been revised and re-revised over the decades. Today, potato scientists rely on two taxonomic systems, one of which was established by Hawkes in 1990 and recognizes 232 species within *Petota*, while the other was published by Spooner et al. (2014) and merges the taxonomy of Hawkes into 107 species using additional molecular data on top of morphological characterization (Spooner et al., 2014, 2018). The system by Hawkes is still used by many scientists and especially by institutions conserving and distributing potato genetic resources, because it is easier to reconcile with their information on the material they collected and catalogued in the past. For listing and comparing the wealth of publications in which resistances against *P. infestans* had been identified in the past, the system by Hawkes may still give the most comprehensive overview and was adapted for this review. Whenever studies used synonyms, the author's original species description is indicated after the accepted name. To ensure comparability to the new taxonomy of Spooner et al. (2014), the new name is included, whenever a species was reclassified. Independent of the applied taxonomy the section *Petota* obviously is large and comprises a wealth of species with potential to provide genetic resources for improving late blight resistance in potato. In the known literature, resistance to *P. infestans* is described in accessions of 85 wild potato species compiled from 74 studies (Table 1) published over the last four decades. Thus, 33 new species have been discovered in the years since Tiwari's last review in 2013. In most of the papers, resistance was identified by field tests, whole plant testing or detached leaf assays and in some cases by additional tuber slice tests. In about two thirds of the studies, the detached leaf assay was used and in some cases supplemented with greenhouse tests. Accordingly, far fewer field tests were carried out. Vleeshouwers et al. (1999) were able to show that leaf tests are a good alternative to field tests due to a high correlation. An exception is the work of Bachmann-Pfabe et al. (2019), where testing was restricted to small, cut tubers. As it is not yet clear whether foliage and tuber resistance are genetically linked, the results of tuber and tuber slice tests can be compared only to a limited extent to those of studies using the detached leaf assay or field tests (Douches et al., 2002; Mayton et al., 2010; Platt & Tai, 1998). For example Park, Vleeshouwers, Kim, et al. (2005) studied foliage and tuber blight resistance in three populations. In one of them, tuber blight resistance occurred independently of foliage blight resistance. In the second population, tuber and foliage blight resistance were correlated and the third population proved to be completely susceptible, so that no conclusion could be drawn so far (Park, Vleeshouwers, Kim, et al., 2005). Species such as *S. demissum*, *S. bulbocastanum* or *S. microdontum*, whose resistance potential has been known for a long time, are now joined by 25 species, which have only been investigated in recent studies such as those of Khiutti et al. (2015) or Bachmann-Pfabe et al. (2019). For most of these 25 species, there is a lack of studies addressing the genomic localisation of their resistance, as well as for 30 other wild species that have long been known to have resistant accessions. Among the newly discovered resistance sources *S. pampasense* is the exception, two QTL for late blight resistance were discovered on chromosome 5 and 6, respectively. In addition, newly discovered resistances could also turn out to be homologues of already characterized R genes. For instance, among the already known R genes, *Rpi-sto1* and *Rpi-abpt* are homologues of *Rpi-blb1* (Wang et al., 2008) and *R2* (Lokossou et al., 2009). Thus, there is a need for further clarification for the other genes.

## 3 | RESISTANCE MECHANISMS AGAINST *P. infestans*

*Phytophthora infestans* evolved in central Mexico, which is also a diversity centre of wild potato species (Grünwald & Flier, 2005). The antagonistic interaction of host species and the pathogen led to the evolution of multiple resistance genes and diverse virulence genes promoting infection and counteracting host resistance (Grünwald & Flier, 2005). The vast majority of hitherto described resistances follows the gene for gene interaction model. In line with the classical R gene and Avr gene nomenclature, R genes are labelled with their respective species abbreviation, for example, *Rpi-sto1* is the first *P. infestans* resistance gene identified in *Solanum stoloniferum*. The corresponding (a)virulence gene, by which the resistant host detects the pathogen, is then called *Avr-sto1*.

**TABLE 1** Wild *Solanum* species with resistance against *P. infestans* according to Hawkes, 1990

| Species | Accepted by Spooner | Ploidy | EBN | Reference |
|---|---|---|---|---|
| *S. acaule* Bitt. | | 4 | 2 | Bachmann-Pfabe et al. (2019); Budin (2002); Khiutti et al. (2015) |
| *S. agrimonifolium* Rybd. | | 4 | 2 | Karki et al. (2021); Khiutti et al. (2015) |
| *S. ajanhuiri* Juz. & Buk. | | 2 | 2 | Gabriel et al. (2007) |
| *S. alandiae* Cárd. | *S. brevicaule* Bitt. | 2 | | Bhardwaj et al. (2018); Muratova et al. (2020); Ramsay et al. (1999) |
| *S. albicans* (Ochoa) C. Ochoa | | 6 | 4 | Bhardwaj et al. (2018); Khiutti et al. (2015) |
| *S. albornozii* Corr. | | 2 | 2 | Karki et al. (2021); Khiutti et al. (2015) |
| *S. ambosinum* Ochoa | *S. candolleanum* Berth. | 2 | 2 | Zoteyeva et al. (2012) |
| *S. andreanum* Baker | | 2 | | Budin (2002); Khiutti et al. (2015) |
| *S. arnezii* Cárd. | *S. chacoense* Bitt. | 2 | | Bhardwaj et al. (2018) |
| *S. astleyi* Hawkes & Hjert. | *S. boliviense* Dun. | 2 | 2 | Ruiz De Galarreta et al. (1998) |
| *S. avilesii* Hawkes & Hjert. | *S. brevicaule* Bitt. | 2 | 2 | Bhardwaj et al. (2018); Ruiz De Galarreta et al. (1998); Spooner et al. (2001); Verzaux et al. (2011) |
| *S. berthaultii* Hawkes | | 2,3 | 2 | Bhardwaj et al. (2018); Budin (2002); Colon and Budding (1988); Ewing et al. (2000); Khiutti et al. (2015); Manrique-Carpintero et al. (2020); Mayton et al. (2011); Park, Foster, et al. (2009); Ramsay et al. (1999); Rauscher et al. (2006, 2010); Tiwari et al. (2015); Zoteyeva et al. (2012) |
| *S. brevicaule* Bitt. | | 2 | 2 | Bhardwaj et al. (2018); Khiutti et al. (2015) |
| *S. boliviense* Dun. | | 2 | 2 | Budin (2002); Khiutti et al. (2015); Ruiz De Galarreta et al. (1998) |
| *S. brachistotrichum* Rydb. | *S. stenophyllidium* Rydb. | 2 | 1 | Bachmann-Pfabe et al. (2019); Hein et al. (2009); Ruiz De Galarreta et al. (1998) |
| *S. brachycarpum* Corr. | *S. iopetalum* Hawkes | 6 | 4 | Bachmann-Pfabe et al. (2019); Budin (2002); Ruiz De Galarreta et al. (1998) |
| *S. bulbocastanum* Dun. | | 2,3 | 1 | Bachmann-Pfabe et al. (2019); Budin (2002); Champouret (2010); Helgeson et al. (1998); Khiutti et al. (2015); Lokossou et al. (2009); Naess et al. (2000); Oosumi et al. (2009); Park, Gros, Sikkema, et al. (2005); Song et al. (2003); van der Vossen et al. (2003, 2005); |
| *S. candolleanum* Berth. | | 2,3 | 2 | Khiutti et al. (2015) |
| *S. capsicibaccatum* Cárd. | *S. stipuloideum* Rusby | 2 | 2 | Jacobs et al. (2010) |
| *S. cardiophyllum* Lindl. (Including ssp. *S. ehrenbergii* Bitt.) | | 2,3,4 | 1 | Bachmann-Pfabe et al. (2019); Bhardwaj et al. (2018); Budin (2002); Karki et al. (2021); Khiutti et al. (2015); Ramsay et al. (1999); Thieme et al. (2010); Tiwari et al. (2015); Zlesak and Thill (2004); Zoteyeva et al. (2012) |
| *S. chacoense* Bitt. | | 2,3 | 2 | Bachmann-Pfabe et al. (2019); Bhardwaj et al. (2018); Budin (2002); Chakrabarti et al. (2014); Khiutti et al. (2015); Monino-Lopez et al. (2021); Ramsay et al. (1999); Tiwari et al. (2015); Vossen et al. (2017); Zoteyeva et al. (2012) |
| *S. chomatophilum* Bitt. | | 2 | 2 | Karki et al. (2021); Khiutti et al. (2015) |
| *S. circaeifolium* Bitt. (Including *S. stipuloideum* Rusby) | *S. stipuloideum* Rusby | 2 | 1 | Bachmann-Pfabe et al. (2019); Karki et al. (2021) |
| *S. circaeifolium* spp. *quimense* Hawkes & Hjert. | *S. stipuloideum* Rusby | 2 | 1 | Ruiz De Galarreta et al. (1998); Verzaux (2010) |
| *S. commersonii* Dun. | | 2,3 | 1 | Bachmann-Pfabe et al. (2019); Budin (2002); Ramsay et al. (1999); Ruiz De Galarreta et al. (1998) |

(Continues)

**TABLE 1** (Continued)

| Species | Accepted by Spooner | Ploidy | EBN | Reference |
|---|---|---|---|---|
| *S. curtilobum* Juz. & Buk. | | 5 | | Bachmann-Pfabe et al. (2019) |
| *S. demissum* Lindl. | | 6 | 4 | Bachmann-Pfabe et al. (2019); Bhardwaj et al. (2018); Bormann et al. (2004); Bradshaw, Bryan, Lees, et al. (2006); Budin (2002); Champouret (2010); El-Kharbotly et al. (1994, 1996); Hein et al. (2007, 2009); Huang (2005); Huang et al. (2004, 2005); Jo et al. (2011); Khiutti et al. (2015); Leonards-Schippers et al. (1992); Li et al. (2011); Li et al. (1998); Lokossou et al. (2009); Meksem et al. (1995); Park, Vleeshouwers, Huigen, et al. (2005); van Poppel (2009); Ramsay et al. (1999); Ruiz De Galarreta et al. (1998); Zoteyeva et al. (2012) |
| *S. x edinense* Berth. | | 5 | 4 | Lokossou et al. (2009); Champouret (2010); Park, Vleeshouwers, Huigen, et al. (2005); Verzaux (2010) |
| | | 2 | 1 | Karki et al. (2021); Khiutti et al. (2015) |
| *S. fendleri* A. Grey | *S. stoloniferum* Schltdl. | 4 | 2 | Bachmann-Pfabe et al. (2019); Ramsay et al. (1999) |
| *S. gandarillasii* Cárd. | | 2 | 2 | Bhardwaj et al. (201); Ruiz De Galarreta et al. (1998) |
| *S. gourlayi* Hawkes | *S. brevicaule* Bitt. | 2,4 | 2,4 | Bachmann-Pfabe et al. (2019); Bhardwaj et al. (2018) |
| *S. guerreroense* Corr. | | 6 | 4 | Zoteyeva et al. (2012) |
| *S. hjertingii* Hawkes | | 4 | 2 | Champouret (2010) |
| *S. hondelmannii* Hawkes & Hjert. | *S. brevicaule* Bitt. | 2 | Na | Bachmann-Pfabe et al. (2019) |
| *S. hougasii* Corr. | | 6 | 4 | Bachmann-Pfabe et al. (2019); Haynes and Qu (2016); Ramsay et al. (1999); Tiwari et al. (2015) |
| *S. huancabambense* Ochoa | | 2 | 2 | Bhardwaj et al. (2018); Tiwari et al. (2015) |
| *S. hypacrarthrum* Bitt. | | 2 | 1 | Karki et al. (2021) |
| *S. immite* Dun. | | 2 | Na | Khiutti et al. (2015) |
| *S. incamayoense* Okada & Clausen | *S. brevicaule* Bitt. | 2 | Na | Bachmann-Pfabe et al. (2019) |
| *S. infundibuliforme* Phil. | | 2 | 2 | Khiutti et al. (2015) |
| *S. iopetalum* Hawkes | | 6 | 4 | Karki et al. (2021); Khiutti et al. (2015); Ramsay et al. (1999); Tiwari et al. (2015) |
| *S. jamesii* Torr. | | 2 | 1 | Bachmann-Pfabe et al. (2019); Khiutti et al. (2015); Tiwari et al. (2015) |
| *S. juzepczukii* Buk. | | 3 | 2 | Gabriel et al. (2007) |
| *S. kurtzianum* Bitt. & Wittm. | *S. boliviense* Dun. | 2 | 2 | Khiutti et al. (2015) |
| *S. leptophyes* Bitt. | *S. brevicaule* Bitt. | 2 | 2 | Bachmann-Pfabe et al. (2019); Budin (2002) |
| *S. lesteri* Hawkes & Hjert. | | 2 | Na | Khiutti et al. (2015); Tiwari et al. (2015) |
| *S. megistacrolobum* Bitt. | *S. boliviense* Dun. | 2 | 2 | Bachmann-Pfabe et al. (2019); Budin (2002) |
| *S. x michoacanum* Rydb. | | 2 | 1 | Jakuczun and Wasilewicz-Flis (2004); Śliwka et al. (2012b); Szczerbakowa et al. (2010) |
| *S. microdontum* Bitt. (Including ssp. *gigantophyllum* or *simplicifolium*) | | 2 | 2 | Bachmann-Pfabe et al. (2019); Bhardwaj et al. (2018); Budin (2002); Colon and Budding (1988); Khiutti et al. (2015); Lin et al. (2020); Meade et al. (2020); Ramsay et al. (1999); Sandbrink et al. (2000); Tan et al. (2008); Tiwari et al. (2015); Zoteyeva et al. (2012) |
| *S. mochiquense* Ochoa | | 2 | 1 | Jones et al. (2009); Smilde et al. (2005) |
| *S. morelliforme* Bitt. & Muench. | *S. boliviense* Dun. | 2 | 1 | Karki et al. (2021) |
| *S. multidissectum* Hawkes | *S. brevicaule* Bitt. | 2 | 2 | Bachmann-Pfabe et al. (2019) |

**TABLE 1** (Continued)

| Species | Accepted by Spooner | Ploidy | EBN | Reference |
|---|---|---|---|---|
| *S. nayaritense* Rydb. | *S. stenophyllidum* Rydb. | 2 | 1 | Lokossou et al. (2010) |
| *S. neocardenasii* Hawkes & Hjert. | | 2 | 2 | Karki et al., 2021 |
| *S. neorossii* Hawkes & Hjert. | | 2 | 2 | Bachmann-Pfabe et al. (2019); Jones et al. (2009) |
| *S. okadae* Hawkes & Hjert. | | 2 | 2 | Jones et al. (2009); Muratova et al. (2020) |
| *S. palustre* Poepp. | | 2 | 1 | Karki et al. (2021) |
| *S. pampasense* Hawkes | | 2 | 2 | Meade et al. (2020) |
| *S. papita* Rydb. | | 4 | 2 | Bachmann-Pfabe et al. (2019); Ramsay et al. (1999); Ruiz De Galarreta et al. (1998); Vleeshouwers et al. (2008); Wang et al. (2008); Zoteyeva et al. (2012) |
| *S. paucissectum* Ochoa | | 2 | 2 | Villamon et al. (2005) |
| *S. phureja* Juz. & Buk. | *S. boliviense* Dun. | 2 | 2 | Costanzo et al. (2005); Ghislain et al. (2001); Śliwka et al. (2006); Trognitz et al. (2002) |
| *S. pinnatisectum* Dun. | | 2 | 1 | Bachmann-Pfabe et al. (2019); Bhardwaj et al. (2018); Budin (2002); Khiutti et al. (2015); Kuhl et al. (2001); Nachtigall et al. (2018); Ruiz De Galarreta et al. (1998); Tiwari et al. (2015); Yang et al. (2017); Zoteyeva et al. (2012) |
| *S. piurae* Bitt. | *S. brevicaule* Bitt. | 2 | 2 | Karki et al. (2021); Rietman (2011) |
| *S. polyadenium* Greenm. | | 2 | 2 | Bachmann-Pfabe et al. (2019); Budin (2002); Khiutti et al. (2015); Tiwari et al. (2015) |
| *S. polytrichon* Rydb. | | 4 | 2 | Bachmann-Pfabe et al. (2019); Ramsay et al. (1999); Ruiz De Galarreta et al. (1998); Tiwari et al. (2015); Wang et al. (2008); Zoteyeva et al. (2012) |
| *S. raphanifolium* Cárd. & Hawkes | *S. boliviense* Dun. | 2 | 2 | Bachmann-Pfabe et al. (2019); Khiutti et al. (2015); Ruiz De Galarreta et al. (1998) |
| *S. sanctae-rosae* Hawkes | | 2 | 2 | Budin (2002) |
| *S. schenckii* Bitt. | *S. brevicaule* Bitt. | 6 | 4 | Champouret (2010); Jacobs et al. (2010) |
| *S.* x *semidemissum* Juz. (Hawkes, 1990) | *S. demissum* Lindl. | 6 | 4 | Ramsay et al. (1999) |
| *S. sparsipilum* Juz. & Buk. (Including *S. ruiz-ceballosii* Cárd.) | *S. brevicaule* Bitt. | 2 | 2 | Bachmann-Pfabe et al. (2019); Bhardwaj et al. (2018); Budin (2002); Danan et al. (2009); Śliwka et al. (2012a); Zoteyeva et al. (2012) |
| *S. spegazzini* Bitt. | | 2 | 2 | Bachmann-Pfabe et al. (2019); Bhardwaj et al. (2018); Budin (2002); Danan et al. (2009) |
| *S. stenophyllidum* Rydb. | | 2 | Na | Bachmann-Pfabe et al. (2019); Khiutti et al. (2015) |
| *S. stenotomum* Juz. & Buk. | *S. tuberosum* Andigenum group | 2 | 2 | Bachmann-Pfabe et al. (2019); Costanzo et al. (2005); Gabriel et al. (2007); Simko et al. (2006) |
| *S. stoloniferum* Schltdl. & Bouché (Including *S. antipovichii* Buk. and *S. neoantipovichii* Buk.) | *S. boliviense* Dun. | 4 | 2 | Bachmann-Pfabe et al. (2019); Budin (2002);, Champouret (2010); Khiutti et al. (2015); Ramsay et al. (1999); Ruiz De Galarreta et al. (1998); Tiwari et al. (2015); Vleeshouwers et al. (2008); Wang et al. (2008); Zoteyeva et al. (2012) |
| *S. x sucrense* Hawkes | | 4 | 4 | Bachmann-Pfabe et al. (2019); Colon and Budding (1988) |
| *S. tarijense* Hawkes | *S. berthaultii* Hawkes | 2 | 2 | Bachmann-Pfabe et al. (2019); Budin (2002); Vossen et al. (2017); Zoteyeva et al. (2012) |
| *S. tarnii* Hawkes | | 2 | 1 | Bachmann-Pfabe et al. (2019); Thieme et al. (2008) |
| *S. toralapanum* Cárd. & Hawkes | *S. boliviense* Dun. | 2 | 2 | Budin (2002) |
| *S. trifidum* Corr. | | 2 | 1 | Bachmann-Pfabe et al. (2019); Budin (2002); Karki et al. (2021); Ruiz De Galarreta et al. (1998); Tiwari et al. (2015) |

(Continues)

**TABLE 1** (Continued)

| Species | Accepted by Spooner | Ploidy | EBN | Reference |
|---|---|---|---|---|
| *S. tuberosum subsp. Andigena* Hawkes | | 4 | 4 | Bachmann-Pfabe et al. (2019); Bhardwaj et al. (2018); Budin (2002); Gabriel et al. (2007) |
| *S. tuberosum subsp. tuberosum* L. | | 4 | 4 | Bachmann-Pfabe et al. (2019); Bradshaw, Hackett, Lowe, et al. (2006) |
| *S. tuquerrense* Hawkes | *S. brevicaule* Bitt. | 4 | 2 | Bachmann-Pfabe et al. (2019) |
| *S. venturii* Hawkes & Hjert. | | 2 | 2 | Bachmann-Pfabe et al. (2019); Colon and Budding (1988); Foster et al. (2009); Pel (2010); Pel et al. (2009); Rietman (2011) |
| *S. vernei* Bitt. & Wittm. | *S. boliviense* Dun. | 2 | 2 | Bachmann-Pfabe et al. (2019); Bhardwaj et al. (2018); Budin (2002); Sørensen et al. (2006); Zoteyeva et al. (2012) |
| *S. verrucosum* Schltdl | | 2 | 2 | Bachmann-Pfabe et al. (2019); Budin (2002); Chen et al. (2018); Colon and Budding (1988); Jacobs et al. (2010); Khiutti et al. (2015); Ramsay et al. (1999); Tiwari et al. (2015); Zoteyeva et al. (2012) |
| *S. virgultorum* Cárd. & Hawkes | *S. boliviense* Dun. | 2 | | Ruiz De Galarreta et al. (1998) |
| *S. violaceimarmoratum* Bitt. | | 2 | 2 | Khiutti et al. (2015) |

Most resistance genes from the various *Solanum* species are classical NLR genes, which encode proteins with a nucleotide-binding site and leucine rich repeats (also NB-LRR or NBS-LRR genes) (Witek et al., 2016). They express receptors, which detect pathogen specific effector proteins, thus starting a signal transduction cascade, leading to induced cell death by hypersensitive response (Rodewald & Trognitz, 2013). The current research indicates that all *P. infestans* effectors detectable by host NLRs belong to the RXLR class (Du et al., 2018; Haas et al., 2009; Luo et al., 2021), which are involved in the suppression of plant defence (Whisson et al., 2016; Yin et al., 2017). These effectors show remarkable diversity, with more than 560 RXLR effector genes predicted in the *P. infestans* genome (Haas et al., 2009).

Various host pathogen interaction models have been proposed to explain resistance and susceptibility in more detail than the simplistic gene-for gene-interaction model. Perhaps the most adapted one is the zigzag model, which explains the interaction as a process with multiple phases in which the pathogen can counteract multiple layers of plant defence (Jones & Dangl, 2006). A detailed description and comparison of the different models was given by Cook et al. (2015), for the scope of this review it may suffice to point out that NBS-mediated detection of RXLR effectors falls in the category of effector-triggered immunity (ETI), which takes place in the cytosol (Schellenberger et al., 2019). ETI represents the host's second line of defence, after the pathogen successfully entered the cell. Recent publications have shown that another resistance mechanism may also be available for *P. infestans* resistance breeding, which enables pathogen detection at an earlier stage. This mechanism detects apoplastic effectors through receptor-like proteins (RLPs) and receptor-like kinases (RLKs), which were found in two accessions of *S. microdontum*, localized on chromosome 9 and 12 (Lin et al., 2020). In the zigzag model context the reaction is classified as the first line of defence MAMP-triggered immunity (MTI), where microbe-associated molecular patterns (MAMPs) are detected at the cell surface by pattern-recognition receptors (PRRs). Applicability of PRR genes for *P. infestans* resistance breeding in potato remains, though, to be demonstrated.

## 4 | R GENES AND QTL FOR *P. infestans* RESISTANCE IN WILD POTATO SPECIES

In 32 of the 85 wild species compiled in Table 1, the genetic basis of the resistance has already been described (Table 2). A total of 61 R genes were described in 27 species and 37 QTL in 11 species. In the majority of cases, several genes or QTL were described for one species, in 12 species only one gene or QTL was detected. While the QTL are distributed quite evenly across all chromosomes (Danan et al., 2011), with a slightly higher incidence on chromosomes 10 and 11, the R genes are mainly concentrated on chromosomes 4 (12 R genes), 9 (14 R genes) and 11 (16 R genes). In contrast, there were no R genes at all reported on chromosomes 1–3. In addition to the fact that many genes have homologues, this concentrations on specific genome regions reflects the arrangement of R genes in clusters (Hulbert et al., 2001; Michelmore & Meyers, 1998). According to Park, Vleeshouwers, et al. (2009), there are 12 R gene clusters on 10 chromosomes for late blight resistance. Verzaux (2010) describes three of these as main clusters: One is the *R2* cluster on chromosome 4, which mainly contains *R2* and corresponding *R2* homologues such as *Rpi-abpt* or *Rpi-edn1.1* and *Rpi-blb3*. The second is the *R3* cluster on chromosome 11, which contains—among others—the R genes *R3*, *R5-R7* and *R9-R11 from S. demissum*. The last cluster is the N cluster on the northern arm of chromosome 11, which contains, for example, *Rpi-edn3*, *Rpi-avl1* and *Rpi-cap1*. Combining new genes from multiple clusters could be a way to develop more durable resistance in new cultivars, as soon as they have been made accessible for breeding (Zhu, 2014). Detailed information on the identity and position of

**TABLE 2** R genes against *P. infestans* of wild potato relatives

| Species | R gene/QTL | Chromosome/ position | Phenotypic variance explained (%) | Reference |
|---|---|---|---|---|
| *S. avilesii* Hawkes & Hjert. | *Rpi-avl1* | 11/1.8 Mb | | Verzaux et al. (2011) |
| *S. berthaultii* Hawkes | *Rpi-ber* | 10 | 56–66 | Ewing et al. (2000); Rauscher et al. (2006) |
| | *QTL* | 1, 3, 7, 8, 11 | | |
| | *Rpi-ber* | 10 | 12–37 | Mayton et al. (2011) |
| | | | 23–42 | Rauscher et al. (2010) |
| | *Rpi-ber1* | 10/54.0 Mb[a] | | Park, Foster, et al. (2009) |
| | *Rpi-ber2* | 10/53.1–53.2 Mb[a] | | |
| | *QTL* | 5, 10 | 18; 26.8–71.7 | Manrique-Carpintero et al. (2020) |
| *S. brachistotrichum* Rydb. | *Rpi-bst1* | 4 | | Hein et al. (2009) |
| *S. bulbocastanum* Dun. | *RB/Rpi-blb1* | 8/50.3 Mb[a] | 62 | Naess et al. (2000); Song et al. (2003); van der Vossen et al. (2003) |
| | *Rpi-blb2* | 6/16.8 Mb | | van der Vossen et al. (2005) |
| | *Rpi-blb3* | 4/6.5 Mb | | Champouret (2010); Lokossou et al. (2009); Park, Gros, Sikkema, et al. (2005) |
| | *Rpi-bt1* | 8/50.0 Mb | | Oosumi et al. (2009) |
| *S. capsicibaccatum* Cárd. | *Rpi-cap1* | 11 | | Jacobs et al. (2010) |
| *S. chacoense* Bitt. | *Rpi-chc1* | 10/54.05 Mb | | Monino-Lopez et al. (2021); Vossen et al. (2017) |
| | *Rpi-chc2* | 10 | | Monino-Lopez et al. (2021) |
| | *QTL* | 9, 10 | 14.7; 3.4 | Chakrabarti et al. (2014) |
| *S. circaeifolium* spp. *quimense* Hawkes & Hjert. | *Rpi-qum1* | 11 | | Verzaux (2010) |
| *S. demissum* Lindl. | *R1* | 5/5.0 Mb | 4.1–17.4 | Bormann et al. (2004); El-Kharbotly et al. (1994); Leonards-Schippers et al. (1992); Meksem et al. (1995) |
| | *R2* | 4/6.7 Mb | | Champouret (2010); Li et al. (1998); Lokossou et al. (2009); Park, Vleeshouwers, Huigen, et al. (2005) |
| | *R3 (a,b)* | 11 | | El-Kharbotly et al. (1994); Huang et al. (2004); Huang et al. (2005); Li et al. (2011) |
| | *R4* | 12 | | Van van Poppel (2009) |
| | *R5* | 11 | | Huang (2005) |
| | *R6* | 11 | | Huang (2005); El-Kharbotly et al. (1996) |
| | *R7* | 11 | | Huang (2005); El-Kharbotly et al. (1996) |
| | *R8* | 9 | | Jo et al. (2011) |
| | *R9* | 11 | | Huang (2005) |
| | *R10* | 11 | 47.6-56.9 | Bradshaw, Bryan, Lees, et al. (2006); Huang (2005) |
| | *R11* | 11 | 51.6-63.6 | Bradshaw, Bryan, Lees, et al. (2006); Huang (2005) |
| | *Rpi-dmsf1* | 4 | | Hein et al. (2007, 2009) |
| *S. edinense* Berth. | *Rpi-edn1.1* | 4 | | Champouret (2010) |
| | *Rpi-edn2* | 9 | | Verzaux (2010) |
| | *Rpi-edn3* | 11 | | Verzaux (2010) |
| *S. hjertingii* Hawkes | *Rpi-hjt1.1* *Rpi-hjt1.2* *Rpi-hjt1.3* | 4 | | Champouret (2010) |
| *S. michoacanum* Rydb. | *Rpi-mch1* | 7 | 82.7 | Śliwka et al. (2012b) |

(Continues)

**TABLE 2** (Continued)

| Species | R gene/QTL | Chromosome/ position | Phenotypic variance explained (%) | Reference |
|---|---|---|---|---|
| *S. microdontum* Bitt. | *Rpi-mcd1* | 4 | 50 | Tan et al. (2008) |
| | *QTL* | 4, 5, 10 | 30 (QTL on chromosome 4) | Sandbrink et al. (2000) |
| | *QTL* | 5, 6, 10 | 21.1–47.4; 20.7–30.8; 20.3 | Meade et al. (2020) |
| | | 9, 12 | | Lin et al. (2020) |
| *S. mochiquense* Ochoa | *Rpi-moc1* | 9 | | Smilde et al. (2005) |
| | *Rpi-mcq1* | 9 | | Jones et al. (2009) |
| *S. neorossii* Hawkes & Hjert. | *Rpi-nrs1* | 9 | | Jones et al. (2009) |
| *S. okadae* Hawkes & Hjert. | *Rpi-oka1* *Rpi-oka2* *Rpi-oka3* | 9 | | Jones et al. (2009) |
| *S. pampasense* Hawkes | *QTL* | 11, 12 | 19–22.6; 16.9–20.8 | Meade et al. (2020) |
| *S. papita* Rydb. | *Rpi-pta1* | 8/50.36 Mb | | Vleeshouwers et al. (2008); Wang et al. (2008) |
| | *Rpi-pta2* | 8 | | Vleeshouwers et al. (2008); Wang et al. (2008) |
| *S. paucissectum* Ochoa | *QTL-pcs10* | 10 | | Villamon et al. (2005) |
| | *QTL-pcs11* | 11 | 25 | Villamon et al. (2005) |
| | *QTL-pcs12* | 12 | 7–10 | Villamon et al. (2005) |
| *S. phureja* Juz. & Buk | *Rpi-phu1* | 9 | 65–68 | Śliwka et al. (2006) |
| | *QTL* | 7, 11, 12 | 9.1; 8.0–10.9; 10.3–15.6 | Ghislain et al. (2001) |
| | *QTL* | 3, 12 | | Trognitz et al. (2002) |
| | *QTL* | 3, 5, 11 | 23.4; 17.9; 9.4 | Costanzo et al. (2005) |
| *S. pinnatisectum* Dun. | *Rpi1* | 7 | | Kuhl et al. (2001) |
| | *Rpi2* | 7 | | Yang et al. (2017) |
| | | 7 | | Nachtigall et al. (2018) |
| *S. piurae* Bitt. | *Rpi-pur1* | 11 | | Karki et al. (2021); Rietman (2011) |
| *S. polytrichon* Rydb. | *Rpi-plt1* | 8 | | Wang et al. (2008) |
| *S. schenckii* Bitt. | *Rpi-snk1* | 4/6.5 Mb | | Champouret (2010); Jacobs et al. (2010) |
| | *Rpi-snk2* | 4 | | Champouret (2010) |
| *S. sparsipilum* Juz. & Buk. (Including *S. ruiz-ceballosii* Cárd.) | *QTL* | 10 | 29 | Danan et al. (2009) |
| | *Rpi-rzc1* | 10 | 87.1 | Śliwka et al. (2012a) |
| *S. spegazzini* Bitt. | *QTL* | 10 | 29 | Danan et al. (2009) |
| *S. stenotomum* Juz. & Buk. | *QTL* | 3, 5, 11 | 23.4; 17.9; 9.4 | Costanzo et al. (2005) |
| | *QTL* | 8, 10 | 63 (QTL on chromosome 10) | Simko et al. (2006) |
| *S. stoloniferum* Schltdl. & Bouché | *Rpi-sto1* | 8/50.03 Mb | | Vleeshouwers et al. (2008); Wang et al. (2008) |
| | *Rpi-sto2* | 11 | | Champouret (2010) |
| *S. tarijense* Hawkes | *Rpi-tar1* | 10/54.05 Mb | | Vossen et al. (2017) |
| *S. tuberosum subsp. tuberosum* L. | *QTL* | 4 | 51–78 | Bradshaw, Hackett, Lowe, et al. (2006) |
| *S. tuberosum* L. *cv. Sarpo mira* | *Rpi-Smira1* *Rpi-Smira2* | 11 | | Rietman et al. (2012) |
| *S. venturii* Hawkes & Hjert. | *Rpi-vnt1.1* | 9/65.6 Mb | | Foster et al. (2009); Pel et al. (2009) |
| | *Rpi-vnt1.2* | 9 | | Foster et al. (2009); Pel et al. (2009) |
| | *Rpi-vnt1.3* | 9 | | Foster et al. (2009); Pel et al. (2009) |
| | *Rpi-vnt2* | 11 | | Rietman (2011); Pel (2010) |

**TABLE 2** (Continued)

| Species | R gene/QTL | Chromosome/ position | Phenotypic variance explained (%) | Reference |
|---|---|---|---|---|
| *S. vernei* Bitt. & Wittm. | *QTL* | 6, 8, 9 | 15.4; 10.9; 15.7 | Sørensen et al. (2006) |
| *S. verrucosum* Schltdl. | *Rpi-ver1* | 6 | | Jacobs et al. (2010) |
| | *Rpi-ver1* | 9/52.6–56.98 Mb | | Chen et al. (2018) |
| | *Rpi-abpt* | 4/6.7 Mb | | Champouret (2010); Lokossou et al. (2009); Park, Vleeshouwers, Hutten, et al. (2005) |

[a]BLAST information.

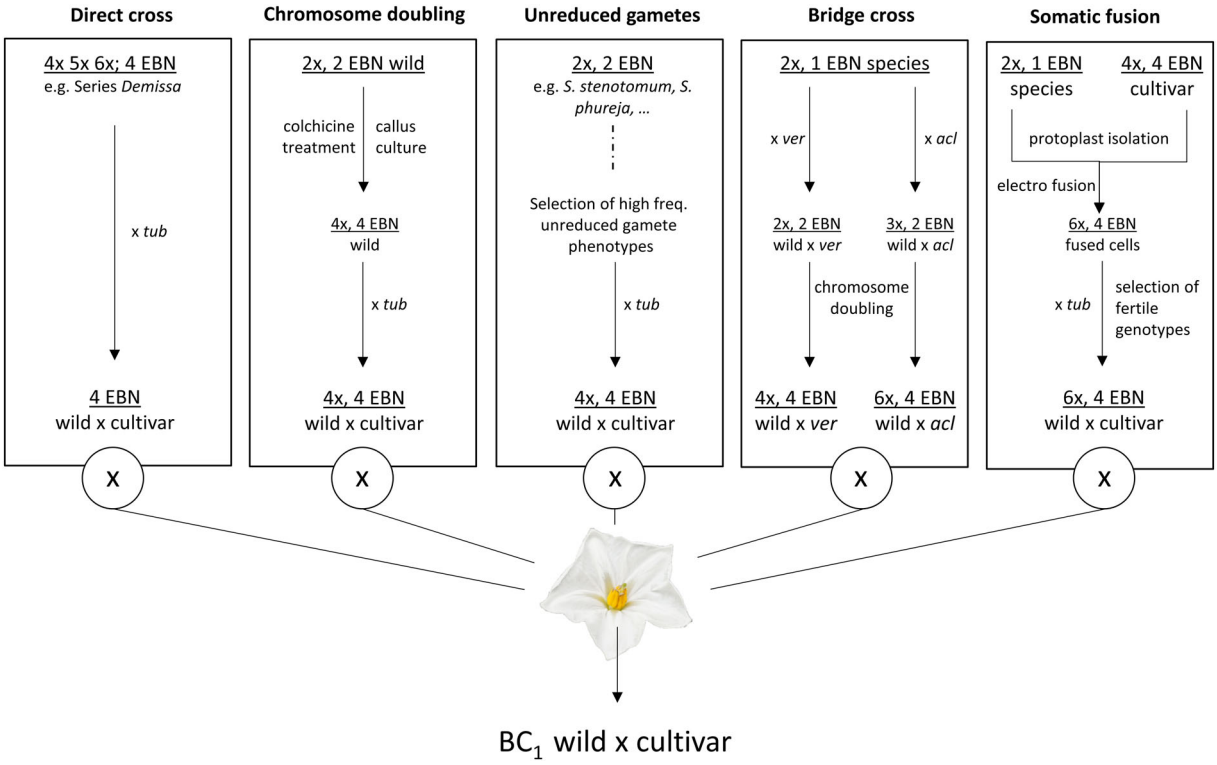


**FIGURE 1** Interspecific hybridisation for potato pre-breeding through direct cross, chromosome doubling, unreduced gametes, bridge cross and somatic fusion. EBN = endosperm balance number, *acl* = *acaule*, *tub* = *tuberosum*, *ver* = *vernei*

known *P. infestans* R genes can be derived from RenSeq analysis, which is a NLR gene-targeted enrichment sequencing technology (Jupe et al., 2013). This technology has been proven to be specific enough to discern between functional and nonfunctional alleles of homologous R genes (Van Weymers et al., 2016), hence such analysis can also elucidate if R genes from different species are alleles of the same gene. Although target specific, RenSeq was also successful in identifying new R genes from the NB-LRR gene family (Van Weymers et al., 2016; Duan et al., 2020).

## 5 | INTERSPECIFIC HYBRIDISATION WITH WILD POTATO SPECIES

The wealth of possible resistance donor species comes in different ploidies, most of them being diploid, some tetraploid and a few are hexaploid. Additionally, there are some species with multiple ploidies, such as *S. cardiophyllum* (2n = 2x; 3x; 4x) as well as natural hybrid species, which can also be triploid (*S. x rechei*, 2n = 3x) or pentaploid (*S. x edinense*, 2n = 5x). Crossing compatibilities between species of similar and diverging ploidies have been studied in great detail in the past decades (Jackson & Hanneman, 1999), which resulted in the classification into distinct ploidy and endosperm balance number groups (EBN) (Johnston et al., 1980). Incompatibility between species is most often attributed to insufficient endosperm development, causing the death of the embryo within the seed. According to the EBN theory endosperm development depends on a specific 2:1 ratio of yet undefined maternal:paternal factors (Bethke et al., 2017; Johnston et al., 1980). Almost all potato cultivars fall into the 4x, 4 EBN category, but most tetraploid wild species are 4x, 2 EBN. Diploid species can be 2x, 1 EBN; or 2x, 2 EBN and all hexaploid species are 6x, 4 EBN. Generally, species with similar EBN numbers are compatible, even in some interploidy crosses (Figure 1). That is unless no other factors besides EBN prevent hybridisation, such as male sterility, or insufficient pollen

tube penetration (Jansky, 2006). Even before EBN categories were established, scientists realized that ploidy manipulation can enable hybridisation with otherwise incompatible species (Hanneman & Peloquin, 1968; Swaminathan, 1951). This works either by doubling chromosome numbers and EBN through classical colchicine treatment (Johnstone, 1939), or spontaneous duplication in callus culture (Jacobsen, 1981). A common application for chromosome doubling is to raise diploid (2x, 2 EBN) species to the tetraploid chromosome complement (4x, 4 EBN) to become compatible with tetraploid potato cultivars (Swaminathan, 1951) (Figure 1). Similar to somatic chromosome doubling, diploid species can also produce elevated frequencies of unreduced gametes, through first of second division restitution (FDR, SDR) which are naturally compatible with 4x, 4 EBN species (Mendiburu & Peloquin, 1977). In these cases, 4x-2x cross combinations can be successful. This method is especially relevant for hybridisation with diploid *S. stenotomum* and *S. phureja*. Past research has shown that *P. infestans* resistance can be fixed in *stenotomum x phureja* hybrids (Haynes et al., 2014), if the material can be crossed to potato cultivars via unreduced gametes. This may represent another important source of *P. infestans* resistance, especially since such hybrids occasionally show potential for yield increase through heterosis (Graebner et al., 2022). Chromosome number can also be reduced, either by prickle pollination (Hougas & Peloquin, 1958; Marks, 1966), or anther culture (Irikura & Sakaguchi, 1972). This makes it possible to cross dihaploid lines extracted from tetraploid potato cultivars, with 2x, 2 EBN wild species, which is a promising approach to develop diploid cultivars with similar quality to common potato varieties (Jansky & Peloquin, 2006). Another way to achieve hybridisation with tetraploid potato cultivars is through bridge crossing (Figure 1). This is most commonly used to produce hybrids with diploid 1 EBN species (Bethke et al., 2017). Especially *S. verrucosum* (2x, 2 EBN) is known to produce viable seeds when crossed to 2x, 1 EBN species. The resulting offspring can be used afterwards for further crossing to diploid *S. tuberosum* lines, which upon chromosome doubling can be integrated into the gene pool of tetraploid potato cultivars (Jansky & Hamernik, 2009; Yermishin et al., 2014). To a lesser extent, *S. acaule* was used for bridge crosses in a similar way (Dionne, 1963; Hermsen & Ramanna, 1973). Probably the most common method to make 2x, 1 EBN species accessible for potato breeding is the development of somatic hybrids through protoplast fusion (Millam et al., 1995; Pandey et al., 2010).

Eighty-five species of the section *Petota* across all ploidy and EBN groups show resistance against *P. infestans*. Looking at the available gene pool for resistance breeding against *P. infestans*, only a few resistant or partial resistant cultivars and landraces from *S. tuberosum* subsp. *tuberosum* and *andigena* are available in the primary gene pool. The secondary gene pool contains 68 species, but only 11 (4 EBN) show no strong hybridisation barriers and can be directly crossed to potato cultivars with some success. One is *S. demissum* (6x, 4 EBN) which was the first wild species used for resistance introgression on a larger scale since the 1950ies (Bradshaw, Bryan, & Ramsay, 2006). The widely used but broken resistance genes R1 to R11 came from this species. Another 57 species are 2 EBN; these need ploidy manipulation to be made accessible for resistance breeding. The remaining 22 species are diploid 1 EBN, or are of unknown EBN (*S. lesteri*), they form the tertiary gene pool. In summary, only 13% of the species with some degree of *P. infestans* resistance can be used for resistance breeding in tetraploid potato cultivars, without ploidy manipulation or other ways to circumvent hybridisation barriers.

## 6 | OPPORTUNITIES OF DIPLOID BREEDING

Potential benefits to breed diploid potato cultivars have been recognized at least since the 1950ies (Hougas & Peloquin, 1958). In general, Mendelian segregation of traits at the diploid level would make it much more feasible to select for recessive alleles (Jansky et al., 2016) and develop superior combinations of the upwards of 40 other important traits for high quality potato cultivars (McCauley, 2021). In the context of *P. infestans* resistance breeding, the fact that 40 of the 85 potential late blight resistance donor species are 2x, 2 EBN (Table 1) and can directly be crossed to diploid potato cultivars makes it even more interesting to attempt potato breeding at the diploid level.

Public and private breeding operations aiming to develop diploid potato cultivars are mostly focusing on the development of high quality inbred lines for hybrid breeding (Birhman & Hosaka, 2000; Hosaka & Sanetomo, 2020; Lieshout et al., 2020), which may express heterosis effects that may match the performance of tetraploid cultivars (Lindhout et al., 2011, 2016). Inbred lines would also enable propagation of uniform potato cultivars from true potato seeds (TPS) (Lindhout et al., 2016), which bears potential to greatly reduce propagation costs of potato cultivars, since true seeds are mostly free of disease which are problematic in seed tuber production (Jansky et al., 2016; Lindhout et al., 2016).

Ultimately, high quality inbred lines could become the ideal vehicle to transfer new resistance genes from diploid wild species into cultivars (Su et al., 2020). This could not only benefit the development of diploid cultivars, because they can easily hybridized with conventional potato cultivars after chromosome doubling. The classical approach for resistance introgression is to double the chromosome number in the wild resistance donor and hybridize directly with potato cultivars. This method, however, has the great disadvantage, that undesirable "wild" traits such as exclusive tuberization under short day conditions, long stolons, irregular tuber shape and bad taste are co-transferred to the generated hybrid (Bethke et al., 2017). Once these traits are present at the tetraploid level, it is very difficult and time consuming to select against these adverse traits, due to linkage drag and the long breeding cycles in conventional potato breeding (Bethke et al., 2017). By the use of elite inbred lines, the "wild" traits however can easily be purged by backcrossing and selfing in a much more controlled manner before crossing with tetraploid cultivars (Su et al., 2020).

However, there are two major obstacles which have hampered advances in the development of diploid cultivars in the past. These are the natural self-incompatibility of the diploid potato species

(Hosaka & Hanneman, 1998) and inbreeding depression, which is especially problematic in diploid lines extracted from tetraploid potato cultivars (De Jong & Rowe, 1971). The inbreeding depression in potato is predominantly caused by unfavourable recessive lethal and sublethal alleles (Bachem et al., 2019; Zhang et al., 2019). These can have negative influences on gamete development, prezygotic and postzygotic embryo development, flower development and plant vigour (Zhang et al., 2019; Zhou et al., 2020). In conventional potato breeding, there is no effective method to select against such alleles, because tetraploid cultivars are propagated vegetatively and breeding commences exclusively by selection among heterozygous $F_1$ crosses (Jansky et al., 2016; Lian et al., 2019; Lindhout et al., 2011). Even in the diploid wild species, inbreeding depression is observed (De Jong & Rowe, 1971; Lian et al., 2019; Phumichai et al., 2005). Similar to tetraploid cultivars, inbreeding depression is caused by deleterious alleles, which are shared by diploid and tetraploid potatoes and may be ancestral (Zhang et al., 2019). In contrast to tetraploid cultivars, deleterious alleles in diploids tend to persist through strong self-incompatibility rather than through the breeding methodology itself.

Self-incompatibility, which is predominant in diploid species, can be overcome since a self-compatibility inducer has been discovered in accessions of *S. chacoense* (Cappadocia & Cheng, 1986). The self-compatibility induction is linked to the single gene *Sli* (Eggers et al., 2021) which interacts with the self-incompatibility inducing S-locus (Hosaka & Hanneman, 1998). Interestingly, the gene is also relatively common in tetraploid potato cultivars (Clot et al., 2020). Through the use of publically available self-compatibility inducers such as the line M6 (Jansky et al., 2014; Leisner et al., 2018), it became possible to develop the first homozygous diploid potato inbred lines (Hosaka & Sanetomo, 2020; Lieshout et al., 2020). The M6 is self-compatible due to the S-locus inhibitor gene *Sli*, which is inherited dominantly (Hosaka & Hanneman, 1998), so that hybrids with M6 become self-compatible as well. In the future, careful selection and recombination of inbred lines from wild and cultivated diploid species may lead to the development of diploid elite lines. Reciprocal recurrent selection (Ortiz, 2020), in parallel to elite inbred line development, potentially enables selection for allele combinations of significant heterotic potential for the development of diploid $F_1$ hybrid potatoes (Lindhout et al., 2016). There are also many potential benefits of diploid potato breeding for scientific investigation. M6 derived segregating populations have already been used to locate genes for resistance against Colorado potato beetles (Kaiser et al., 2020), resistance against bacterial rot (Chung et al., 2017) and for investigating the genetic basis of physiological traits such as skin colour, tuber shape and the occurrence of undesirable characteristics like eye tubers and jelly ends (Endelman & Jansky, 2016).

## 7 | LATE BLIGHT RESISTANCE THROUGH GENETIC ENGINEERING

One way to obtain resistant cultivars is the above mentioned introgression of resistance genes into elite inbred lines for diploid hybrid breeding. However, the resistances from the wild species summarized here are not only important for conventional breeding but can also be applied through genetic engineering. The use of genetic modified organisms (GMOs) can be problematic due to regional differences in political regulations especially in the EU (Eckerstorfer et al., 2019) and consumer acceptance (McComas et al., 2014), but genetic engineering also brings great advantages due to the significantly faster and more precise application. For example Cis-genesis was used for the development of the cultivar 'Fortuna', which carries the genes *Rpi-blb1* and *Rpi-blb2* from *S. bulbocastanum* through *Agrobacterium*-mediated transformation (Storck et al., 2011). Another example would be the Innate® potato cultivars, which carry a late blight resistance gene from *S. venturii* (*Rpi-vnt1*), as well as other quality relevant traits from wild potato species (Richael, 2021). The Cis-genesis approach in particular could considerably minimize problems with disease infestation. It allows fast stacking of several R genes from multiple gene clusters (Zhu et al., 2012) without the significant drawback of linkage drag around introgressed resistance genes, as is often the case in conventional R gene introgression. Quantitative resistance in potato cultivars arises from the interaction of genes that induce some degree of tolerance against pathogens without complete prevention of infection (Poland et al., 2009) but also in combination with R genes both broken and still functional (Stewart et al., 2003). If quantitative and durable resistance can be developed by genetic engineering is still open for debate.

## 8 | CONCLUSION

As has been shown, there is a wealth of untapped potential for new impulses to *P. infestans* resistance breeding using the newly identified donor species. Future breeding and research should focus on localization and functional analysis of these genes. In order to equip cultivars with durable resistance, it is of vital importance to stack resistance genes from different sources as well as include quantitative resistance, which is generally more durable than individual monogenic resistance genes.

In addition, breeders should focus on finding new ways to implement resistances quickly. One such way could be breeding at the diploid level as has been described above. This method has the potential benefit that segregating populations derived from crosses with improved inbred lines not only help to map and characterize resistance but also already deliver material of higher quality for breeding resistant cultivars. The development of an inbred line based $F_1$ seed propagated potato crop would also enable fast and easy stacking and exchange of resistance genes. Although there is still much initial research needed for diploid potato breeding, it could become one possible gateway for the development of future cultivars. Thereby, diploid as well as tetraploid cultivars resulting from chromosome duplication could be used. Due to current regulations, genetic modification technologies are not yet an alternative way, even if organic farming could benefit strongly from the merits of Cis-genesis (Gheysen & Custers, 2017). It may be worthwhile to re-evaluate in order to harness the technology for the development of a more sustainable

agricultural practice (Waters et al., 2021). All methods must ultimately serve the same goal to make the cultivars capable for future agriculture with much higher standards in terms of sustainability, carbon-neutrality and reduced input of synthetic pesticides.

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## CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

## AUTHOR CONTRIBUTIONS

JB and RG developed the idea and wrote the manuscript in equal parts. RU and TH read and edited the draft version. All authors read and approved the final version of the manuscript.

## DATA AVAILABILITY STATEMENT

All the data we used for this review came from the articles cited correspondingly.

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## REFERENCES

Andrivon, D. (1996). The origin of *Phytophthora infestans* populations present in Europe in the 1840s: A critical review of historical and scientific evidence. *Plant Pathology*, *45*(6), 1027–1035. https://doi.org/10.1046/j.1365-3059.1996.d01-196.x

Bachem, C. W., van Eck, H. J., & Vries, M. E. D. (2019). Understanding genetic load in potato for hybrid diploid breeding. *Molecular Plant*, *12*(7), 896–898. https://doi.org/10.1016/j.molp.2019.05.015

Bachmann-Pfabe, S., Hammann, T., Kruse, J., & Dehmer, K. J. (2019). Screening of wild potato genetic resources for combined resistance to late blight on tubers and pale potato cyst nematodes. *Euphytica*, *215*(3), 1–15. https://doi.org/10.1007/s10681-019-2364-y

Bethke, P. C., Halterman, D. A., & Jansky, S. (2017). Are we getting better at using wild potato species in light of new tools? *Crop Science*, *57*, 1241–1258. https://doi.org/10.2135/cropsci2016.10.0889

Bhardwaj, V., Srivastava, D. A. K., Sharma, S., Kumar, V., Kaushhik, S. K., Singh, R., Singh, R. K., & Chakrabarti, S. K. (2018). Late blight resistance status in wild potato species against Indian population of *Phytophthora infestans*. *Indian Journal of Horticulture*, *75*, 99–104. https://doi.org/10.5958/0974-0112.2018.00017.8

Birhman, R. K., & Hosaka, K. (2000). Production of inbred progenies of diploid potatoes using an S-locus inhibitor (Sli) gene, and their characterization. *Genome*, *43*, 495–502. https://doi.org/10.1139/g00-012

Bormann, C. A., Rickert, A. M., Castillo Ruiz, R. A., Paal, J., Lübeck, J., Strahwald, J., Buhr, K., & Gebhardt, C. (2004). Tagging quantitative trait loci for maturity-corrected late blight resistance in tetraploid potato with PCR-based candidate gene markers. *Molecular Plant-Microbe Interactions*, *17*, 1126–1138. https://doi.org/10.1094/MPMI.2004.17.10.1126

Bradshaw, J. E. (2021). Domestication to twenty-first-century potato cultivars. In J. E. Bradshaw (Ed.), *Potato breeding: Theory and practice* (pp. 3–51). Springer. https://doi.org/10.1007/978-3-030-64414-7_1

Bradshaw, J. E., Bryan, G. J., Lees, A. K., McLean, K., & Solomon-Blackburn, R. M. (2006). Mapping the R10 and R11 genes for resistance to late blight (*Phytophthora infestans*) present in the potato (*Solanum tuberosum*) R-gene differentials of black. *Theoretical and Applied Genetics*, *112*(4), 744–751. https://doi.org/10.1007/s00122-005-0179-9

Bradshaw, J. E., Bryan, G. J., & Ramsay, G. (2006). Genetic resources (including wild and cultivated *Solanum* species) and Progress in their utilisation in potato breeding. *Potato Research*, *49*, 49–65. https://doi.org/10.1007/s11540-006-9002-5

Bradshaw, J. E., Hackett, C. A., Lowe, R., McLean, K., Stewart, H. E., Tierney, I., Vilaro, M. D. R., & Bryan, G. J. (2006). Detection of a quantitative trait locus for both foliage and tuber resistance to late blight [*Phytophthora infestans* (Mont.) de Bary] on chromosome 4 of a dihaploid potato clone (*Solanum tuberosum* subsp. *tuberosum*). *Theoretical and Applied Genetics*, *113*(5), 943–951. https://doi.org/10.1007/s00122-006-0353-8

Budin, K. Z. (2002). Genetic foci of *Solanum* species, Petota Dumort, resistant to *Phytophthora infestans* (Mont.) De Bary. *Genetic Resources and Crop Evolution*, *49*, 229–235. https://doi.org/10.1023/A:1015549214779

Cappadocia, M., & Cheng, D. S. K. (1986). Self-compatibility in doubled haploids and their hybrids, regenerated via anther culture in self-incompatible *Solanum chacoense* Bitt. *Theoretical and Applied Genetics*, *72*, 66–69. https://doi.org/10.1007/BF00261456

Chakrabarti, S. K., Singh, B. P., Thakur, G., Tiwari, J. K., Kaushik, S. K., Sharma, S., & Bhardwaj, V. (2014). QTL analysis of late blight resistance in a diploid potato family of *Solanum spegazzinii* × *S. chacoense*. *Potato Research*, *57*, 1–11. https://doi.org/10.1007/s11540-014-9249-1

Champouret, N. (2010). *Functional genomics of Phytophthora infestans effectors and Solanum resistance genes*Doctoral dissertation. Wageningen University.

Chen, X., Lewandowska, D., Armstrong, M. R., Baker, K., Lim, T. Y., Bayer, M., Harrower, B., McLean, K., Jupe, F., Witek, K., Lees, A. K., Jones, J. D., Bryan, G. L., & Hein, I. (2018). Identification and rapid mapping of a gene conferring broad-spectrum late blight resistance in the diploid potato species *Solanum verrucosum* through DNA capture technologies. *Theoretical and Applied Genetics*, *131*, 1287–1297. https://doi.org/10.1007/s00122-018-3078-6

Chung, Y. S., Kim, C., & Jansky, S. (2017). New source of bacterial soft rot resistance in wild potato (*Solanum chacoense*) tubers. *Genetic Resources and Crop Evolution*, *64*(8), 1963–1969. https://doi.org/10.1007/s10722-017-0487-3

Clot, C. R., Polzer, C., Prodhomme, C., Schuit, C., Engelen, C. J. M., Hutten, R. C. B., & Eck, H. J. (2020). The origin and widespread occurrence of Sli-based self-compatibility in potato. *Theoretical and Applied Genetics*, *133*(9), 2713–2728. https://doi.org/10.1007/s00122-020-03627-8

Collins, A., Milbourne, D., Ramsay, L., Meyer, R., Chatot-Balandras, C., Oberhagemann, P., De Jong, W., Gebhardt, C., Bonnel, E., & Waugh, R. (1999). QTL for field resistance to late blight in potato are strongly correlated with maturity and vigour. *Molecular Breeding*, *5*, 387–398. https://doi.org/10.1023/A:1009601427062

Colon, L. T., & Budding, D. J. (1988). Resistance to late blight (*Phytophthora infestans*) in ten wild *Solanum* species. *Euphytica*, *39*(S3), 77–86. https://doi.org/10.1007/BF00043370

Cook, D. E., Mesarich, C. H., & Thomma, B. P. H. J. (2015). Understanding plant immunity as a surveillance system to detect invasion. *Annual Review of Phytopathology*, *53*, 541–563. https://doi.org/10.1146/annurev-phyto-080614-120114

Costanzo, S., Simko, I., Christ, B. J., & Haynes, K. G. (2005). QTL analysis of late blight resistance in a diploid potato family of *Solanum phureja* x *S. Stenotomum*. *Theoretical and Applied Genetics*, *111*(3), 609–617. https://doi.org/10.1007/s00122-005-2053-1

Danan, S., Chauvin, J. E., Caromel, B., Moal, J. D., Pellé, R., & Lefebvre, V. (2009). Major-effect QTLs for stem and foliage resistance to late blight

in the wild potato relatives *Solanum sparsipilum* and *S. spegazzinii* are mapped to chromosome X. *Theoretical and Applied Genetics*, *119*, 705–719. https://doi.org/10.1007/s00122-009-1081-7

Danan, S., Veyrieras, J. B., & Lefebvre, V. (2011). Construction of a potato consensus map and QTL meta-analysis offer new insights into the genetic architecture of late blight resistance and plant maturity traits. *BMC Plant Biology*, *11*, 1–16. https://doi.org/10.1186/1471-2229-11-16

De Jong, H., & Rowe, P. (1971). Inbreeding in cultivated diploid potatoes. *Potato Research*, *14*(2), 74–83. https://doi.org/10.1007/BF02355931

Dionne, L. A. (1963). Studies on the use of *Solanum acaule* as a bridge between *Solanum tuberosum* and species in the series Bulbocastana, Cardiophylla and Pinnatisecta. *Euphytica*, *12*(3), 263–269. https://doi.org/10.1007/BF00027461

Douches, D. S., Kirk, W. W., Bertram, M. A., Coombs, J. J., & Niemira, B. A. (2002). Foliar and tuber assessment of late blight (*Phytophthora infestans* (Mont.) de Bary) reaction in cultivated potato (*Solanum tuberosum* L.). *Potato Research*, *45*, 215–224. https://doi.org/10.1007/BF02736116

Du, Y., Weide, R., Zhao, Z., Msimuko, P., Govers, F., & Bouwmeester, K. (2018). RXLR effector diversity in *Phytophthora infestans* isolates determines recognition by potato resistance proteins; the case study AVR1 and R1. *Studies in Mycology*, *89*, 85–93. https://doi.org/10.1016/j.simyco.2018.01.003

Duan, Y., Duan, S., Armstrong, M. R., Xu, J., Zheng, J., Hu, J., Chen, X., Hein, I., Li, G., & Jin, L. (2020). Comparative transcriptome profiling reveals compatible and incompatible patterns of potato toward *Phytophthora infestans*. *G3: Genes, Genomes, Genetics*, *10*, 623–634. https://doi.org/10.1534/g3.119.400818

Eckerstorfer, M. F., Engelhard, M., Heissenberger, A., Simon, S., & Teichmann, H. (2019). Plants developed by new genetic modification techniques-comparison of existing regulatory frameworks in the EU and non-EU countries. *Frontiers in Bioengineering and Biotechnology*, *7*, 1–16. https://doi.org/10.3389/fbioe.2019.00026

Eggers, E., van der Burgt, A., van Heusden, S. A. W., & Vries, M. E. D. (2021). Neofunctionalisation of the Sli gene leads to self-compatibility and facilitates precision breeding in potato. *Nature Communications*, *12*(4141), 1–9. https://doi.org/10.1038/s41467-021-24267-6

El-Kharbotly, A., Palomino-Sánchez, C., Salamini, F., Jacobsen, E., & Gebhardt, C. (1996). R6 and R7 alleles of potato conferring race-specific resistance to *Phytophthora infestans* (Mont.) de Bary identified genetic loci clustering with the R3 locus on chromosome XI. *Theoretical and Applied Genetics*, *92*, 880–884. https://doi.org/10.1007/s001220050206

El-Kharbotly, A., Leonards-Schippers, C., Huigen, D. J., Jacobsen, E., Pereira, A., Stiekema, W. J., Salamini, F., & Gebhardt, C. (1994). Segregation analysis and RFLP mapping of the R1 and R3 alleles conferring race-specific resistance to *Phytophthora infestans* in progeny of dihaploid potato parents. *MGG Molecular & General Genetics*, *242*(6), 749–754. https://doi.org/10.1007/BF00283432

Endelman, J. B., & Jansky, S. H. (2016). Genetic mapping with an inbred line-derived F2 population in potato. *Theoretical and Applied Genetics*, *129*(5), 935–943. https://doi.org/10.1007/s00122-016-2673-7

Ewing, E. E., Šimko, I., Smart, C. D., Bonierbale, M. W., Mizubuti, E. S. G., May, G. D., & Fry, W. E. (2000). Genetic mapping from field tests of qualitative and quantitative resistance to *Phytophthora infestans* in a population derived from *Solanum tuberosum* and *Solanum berthaultii*. *Molecular Breeding*, *6*, 25–36. https://doi.org/10.1023/A:1009648408198

FAO. (2020). *World food and agriculture - statistical yearbook 2020*. FAO. https://doi.org/10.4060/cb1329en

Foster, S. J., Park, T.-H., Pel, M., Brigneti, G., Śliwka, J., Jagger, L., van der Vossen, E., & Jones, J. D. G. (2009). *Rpi-vnt1.1*, a *tm-2*$^2$ homolog from *Solanum venturii*, confers resistance to potato late blight. *Molecular Plant-Microbe Interactions*, *22*, 589–600. https://doi.org/10.1094/MPMI-22-5-0589

Fry, W. (2008). *Phytophthora infestans*: The plant (and R gene) destroyer. *Molecular Plant Pathology*, *9*, 385–402. https://doi.org/10.1111/j.1364-3703.2007.00465.x

Gabriel, J., Coca, A., Plata, G., & Parlevliet, J. E. (2007). Characterization of the resistance to *Phytophthora infestans* in local potato cultivars in Bolivia. *Euphytica*, *153*, 321–328. https://doi.org/10.1007/s10681-006-9237-x

Gheysen, G., & Custers, R. (2017). Why organic farming should embrace co-existence with cisgenic late blight–resistant potato. *Sustainability*, *9*, 172. https://doi.org/10.3390/su9020172

Ghislain, M., Trognitz, B., Del Herrera, M. R., Solis, J., Casallo, G., Vásquez, C., Hurtado, O., Castillo, R., Portal, R., & Orrillo, M. (2001). Genetic loci associated with field resistance to late blight in offspring of *Solanum phureja* and *S. tuberosum* grown under short-day conditions. *Theoretical and Applied Genetics*, *103*, 433–442. https://doi.org/10.1007/s00122-001-0545-1

Graebner, R. C., Haynes, K., Charlton, B. A., Yilma, S., & Sathuvalli, V. (2022). Evaluation of yield and quality traits in russet-chipper and 4x-2x crosses in potato (*Solanum tuberosum* L.). *American Journal of Potato Research*, *99*, 48–57. https://doi.org/10.1007/s12230-021-09858-9

Grünwald, N. J., & Flier, W. G. (2005). The biology of *Phytophthora infestans* at its center of origin. *Annual Review of Phytopathology*, *43*, 171–190. https://doi.org/10.1146/annurev.phyto.43.040204.135906

Haas, B. J., Kamoun, S., Zody, M. C., Jiang, R. H. Y., Handsaker, R. E., Cano, L. M., Grabherr, M., Kodira, C. D., Raffaele, S., Torto-Alalibo, T., Bozkurt, T. O., Ah-Fong, A. M. V., Alvarado, L., Anderson, V. L., Armstrong, M. R., Avrova, A., Baxter, L., Beynon, J., Boevink, P. C., … Nusbaum, C. (2009). Genome sequence and analysis of the Irish potato famine pathogen *Phytophthora infestans*. *Nature*, *461*(7262), 393–398. https://doi.org/10.1038/nature08358

Hanneman, R. E., & Peloquin, S. J. (1968). Ploidy levels of progency from diploid-tetraploid crosses in the potato. *American Potato Journal*, *45*, 255–261. https://doi.org/10.1007/BF02849919

Haverkort, A. J., Boonekamp, P. M., Hutten, R., Jacobsen, E., Lotz, L. A. P., Kessel, G. J. T., Vossen, J. H., & Visser, R. G. F. (2016). Durable late blight resistance in potato through dynamic varieties obtained by Cisgenesis: Scientific and societal advances in the DuRPh project. *Potato Research*, *59*, 35–66. https://doi.org/10.1007/s11540-015-9312-6

Hawkes, J. G. (1990). *The potato: Evolution, biodiversity and genetic resources*. Smithsonian Institution Press.

Hawkes, J. G. (1994). Origins of cultivated potatoes and species relationships. In *Potato genetics*. CAB International.

Haynes, K. G., & Qu, X. (2016). Late blight and early blight resistance from *Solanum hougasii* Introgressed into *Solanum tuberosum*. *American Journal of Potato Research*, *93*, 86–95. https://doi.org/10.1007/s12230-015-9492-2

Haynes, K. G., Qu, X., & Christ, B. J. (2014). Two cycles of recurrent maternal half-sib selection reduce foliar late blight in a diploid hybrid *Solanum phureja-S. stenotomum* population by two-thirds. *American Journal of Potato Research*, *91*, 254–259. https://doi.org/10.1007/s12230-013-9345-9

Hein, I., Birch, P. R. J., Danan, S., Lefebvre, V., Odeny, D. A., Gebhardt, C., Trognitz, F., & Bryan, G. J. (2009). Progress in mapping and cloning qualitative and quantitative resistance against *Phytophthora infestans* in potato and its wild relatives. *Potato Research*, *52*(3), 215–227. https://doi.org/10.1007/s11540-009-9129-2

Hein, I., McLean, K., Chalhoub, B., & Bryan, G. J. (2007). Generation and screening of a BAC library from a diploid potato clone to unravel durable late blight resistance on linkage group IV. *International Journal of Plant Genomics*, *2007*, 1–5. https://doi.org/10.1155/2007/51421

Helgeson, J. P., Pohlman, J. D., Austin, S., Haberlach, G. T., Wielgus, S. M., Ronis, D., Zambolim, L., Tooley, P., McGrath, J. M., James, R. V., & Stevenson, W. R. (1998). Somatic hybrids between *Solanum bulbocastanum* and potato: A new source of resistance to late blight. *Theoretical and Applied Genetics*, *96*(6–7), 738–742. https://doi.org/10.1007/s001220050796

Hermsen, J. G. T., & Ramanna, M. S. (1973). Double-bridge hybrids of *Solanum bulbocastanum* and cultivars of *Solanum tuberosum*. *Euphytica*, *22*(3), 457–466. https://doi.org/10.1007/BF00036641

Hosaka, K., & Hanneman, R. E. (1998). Genetics of self-compatibility in a self-incompatible wild diploid potato species *Solanum chacoense*. 2. Localization of an S locus inhibitor (*Sli*) gene on the potato genome using DNA markers. *Euphytica*, *103*, 265–271. https://doi.org/10.1023/A:1018380725160

Hosaka, K., & Sanetomo, R. (2020). Creation of a highly homozygous diploid potato using the S locus inhibitor (*Sli*) gene. *Euphytica*, *216*(11), 1–16. https://doi.org/10.1007/s10681-020-02699-3

Hougas, R. W., & Peloquin, S. J. (1958). The potential of potato haploids in breeding and genetic research. *American Potato Journal*, *35*, 701–707. https://doi.org/10.1007/BF02855564

Huang, S. (2005). *Discovery and characterization of the major late blight resistance complex in potato*Doctoral dissertation. Wageningen University.

Huang, S., van der Vossen, E. A. G., Kuang, H., Vleeshouwers, V. G. A. A., Zhang, N., Borm, T. J. A., Van Eck, H. J., Baker, B., Jacobsen, E., & Visser, R. G. F. (2005). Comparative genomics enabled the isolation of the *R3a* late blight resistance gene in potato. *Plant Journal*, *42*, 251–261. https://doi.org/10.1111/j.1365-313X.2005.02365.x

Huang, S., Vleeshouwers, V. G. A. A., Werij, J. S., Hutten, R. C. B., Van Eck, H. J., Visser, R. G. F., & Jacobsen, E. (2004). The *R3* resistance to *Phytophthora infestans* in potato is conferred by two closely linked R genes with distinct specificities. *Molecular Plant-Microbe Interactions*, *17*, 428–435. https://doi.org/10.1094/MPMI.2004.17.4.428

Hulbert, S. H., Webb, C. A., & Smith, S. M. (2001). Resistance gene complexes: Evolution and utilization. *Annual Review of Phytopathology*, *39*, 285–312. https://doi.org/10.1146/annurev.phyto.39.1.285

Irikura, Y., & Sakaguchi, S. (1972). Induction of 12-chromosome plants from anther culture in a tuberous *Solanum*. *Potato Research*, *15*, 170–173. https://doi.org/10.1007/BF02355964

Jackson, S. A., & Hanneman, R. E. (1999). Crossability between cultivated and wild tuber-and non-tuber-bearing *solanums*. *Euphytica*, *109*, 51–67. https://doi.org/10.1023/A:1003710817938

Jacobs, M. M. J., Vosman, B., Vleeshouwers, V. G. A. A., Visser, R. G. F., Henken, B., & van den Berg, R. G. (2010). A novel approach to locate *Phytophthora infestans* resistance genes on the potato genetic map. *Theoretical and Applied Genetics*, *120*(4), 785–796. https://doi.org/10.1007/s00122-009-1199-7

Jacobsen, E. (1981). Polyploidization in leaf callus tissue and in regenerated plants of dihaploid potato. *Plant Cell, Tissue and Organ Culture*, *1*, 77–84. https://doi.org/10.1007/BF02318906

Jakuczun, H., & Wasilewicz-Flis, I. (2004). New sources of potato resistance to *Phytophthora infestans* at the diploid level. *Plant Breeding and Seed Science*, *50*, 137–145.

Jansky, S. (2006). Overcoming hybridization barriers in potato. *Plant Breeding*, *125*, 1–12. https://doi.org/10.1111/j.1439-0523.2006.01178.x

Jansky, S., & Hamernik, A. (2009). The introgression of 2× 1EBN *Solanum* species into the cultivated potato using *Solanum verrucosum* as a bridge. *Genetic Resources and Crop Evolution*, *56*(8), 1107–1115. https://doi.org/10.1007/s10722-009-9433-3

Jansky, S. H., Charkowski, A. O., Douches, D. S., Gusmini, G., Richael, C., Bethke, P. C., Spooner, D. M., Novy, R. G., De Jong, H., De Jong, W. S., Bamberg, J. B., Thompson, A. L., Bizimungu, B., Holm, D. G., Brown, C. R., Haynes, K. G., Sathuvalli, V. R., Veilleux, R. E., Miller, J. C., … Jiang, J. (2016). Reinventing potato as a diploid inbred line-based crop. *Crop Science*, *56*(4), 1412–1422. https://doi.org/10.2135/cropsci2015.12.0740

Jansky, S. H., Chung, Y. S., & Kittipadukal, P. (2014). M6: A diploid potato inbred line for use in breeding and genetics research. *Journal of Plant Registrations*, *8*, 195–199. https://doi.org/10.3198/jpr2013.05.0024crg

Jansky, S. H., & Peloquin, S. J. (2006). Advantages of wild diploid *Solanum* species over cultivated diploid relatives in potato breeding programs. *Genetic Resources and Crop Evolution*, *53*(4), 669–674. https://doi.org/10.1007/s10722-004-2949-7

Jo, K.-R., Arens, M., Kim, T.-J., Jongsma, M. A., Visser, R. G. F., Jacobsen, E., & Vossen, J. H. (2011). Mapping of the *S. demissum* late blight resistance gene R8 to a new locus on chromosome IX. *Theoretical and Applied Genetics*, *123*, 1331–1340. https://doi.org/10.1007/s00122-011-1670-0

Johnston, S. A., den Nijs, T. P. M., Peloquin, S. J., & Hanneman, R. E. (1980). The significance of genic balance to endosperm development in interspecific crosses. *Theoretical and Applied Genetics*, *57*, 5–9. https://doi.org/10.1007/BF00276002

Johnstone, F. E. (1939). Chromosome doubling in potatoes induced by colchicine treatment. *American Potato Journal*, *16*(11), 288–304. https://doi.org/10.1007/BF02861918

Jones, J., Foster, S., Chu, Z., Park, T.-H., van der Vossen, E., Pel, M., & Visser, R. (2009). Late blight resistance genes and methods. International application published under the patent cooperation treaty (PCT).

Jones, J. D. G., & Dangl, J. L. (2006). The plant immune system. *Nature*, *444*(7117), 323–329. https://doi.org/10.1038/nature05286

Jupe, F., Witek, K., Verweij, W., Śliwka, J., Pritchard, L., Etherington, G. J., Maclean, D., Cock, P. J., Leggett, R. M., Bryan, G. J., Cardle, L., Hein, I., & Jones, J. D. (2013). Resistance gene enrichment sequencing (RenSeq) enables reannotation of the NB-LRR gene family from sequenced plant genomes and rapid mapping of resistance loci in segregating populations. *The Plant Journal*, *76*(3), 530–544. https://doi.org/10.1111/tpj.12307

Kaiser, N., Manrique-Carpintero, N. C., DiFonzo, C., Coombs, J., & Douches, D. (2020). Mapping *Solanum chacoense* mediated Colorado potato beetle (*Leptinotarsa decemlineata*) resistance in a self-compatible F2 diploid population. *Theoretical and Applied Genetics*, *133*(9), 2583–2603. https://doi.org/10.1007/s00122-020-03619-8

Karki, H. S., Jansky, S. H., & Halterman, D. A. (2021). Screening of wild potatoes identifies new sources of late blight resistance. *Plant Disease*, *105*, 368–376. https://doi.org/10.1094/PDIS-06-20-1367-RE

Khiutti, A., Spooner, D. M., Jansky, S. H., & Halterman, D. A. (2015). Testing taxonomic predictivity of foliar and tuber resistance to *Phytophthora infestans* in wild relatives of potato. *Phytopathology*, *105*(9), 1198–1205. https://doi.org/10.1094/PHYTO-02-15-0046-R

Kuhl, J. C., Hanneman, R. E., & Havey, M. J. (2001). Characterization and mapping of Rpi1, a late-blight resistance locus from diploid (1EBN) Mexican Solanum pinnatisectum. *Molecular Genetics and Genomics*, *265*(6), 977–985. https://doi.org/10.1007/s004380100490

Leisner, C., Hamilton, J., Crisovan, E., Manrique-Carpintero, N., Marand, A., Newton, L., Pham, G. M., Jiang, J., Douches, D. S., Jansky, S. H., & Buell, C. (2018). Genome sequence of M6, a diploid inbred clone of the high-glycoalkaloid-producing tuber-bearing potato species *Solanum chacoense*, reveals residual heterozygosity. *The Plant Journal*, *94*(3), 562–570. https://doi.org/10.1111/tpj.13857

Leonards-Schippers, C., Gieffers, W., Salamini, F., & Gebhardt, C. (1992). The *R1* gene conferring race-specific resistance to *Phytophthora infestans* in potato is located on potato chromosome V. *MGG Molecular & General Genetics*, *233*, 278–283. https://doi.org/10.1007/BF00587589

Li, G., Huang, S., Guo, X., Li, Y., Yang, Y., Guo, Z., Kuang, H., Rietman, H., Bergervoet, M., Vleeshouwers, V. G. G. A., van der Vossen, E. A. G., Qu, D., Visser, R. F. G., Jacobsen, E., & Vossen, J. H. (2011). Cloning and characterization of *R3b*; members of the R3 superfamily of late

blight resistance genes show sequence and functional divergence. *Molecular Plant-Microbe Interactions*, *24*, 1132–1142. https://doi.org/10.1094/MPMI-11-10-0276

Li, X., Van Eck, H. J., Rouppe Van Der Voort, J. N. A. M., Huigen, D. J., Stam, P., & Jacobsen, E. (1998). Autotetraploids and genetic mapping using common AFLP markers: The *R2* allele conferring resistance to *Phytophthora infestans* mapped on potato chromosome 4. *Theoretical and Applied Genetics*, *96*(8), 1121–1128. https://doi.org/10.1007/s001220050847

Lian, Q., Tang, D., Bai, Z., Qi, J., Lu, F., Huan, S., & Zhang, C. (2019). Acquisition of deleterious mutations during potato polyploidization. *Journal of Integrative Plant Biology*, *61*, 7–11. https://doi.org/10.1111/jipb.12748

Lin, X., Armstrong, M., Baker, K., Wouters, D., Visser, R. G. F., Wolters, P. J., Hein, I., & Vleeshouwers, V. G. A. A. (2020). RLP/K enrichment sequencing; a novel method to identify receptor-like protein (RLP) and receptor-like kinase (RLK) genes. *New Phytologist*, *227*(4), 1264–1276. https://doi.org/10.1111/nph.16608

Lindhout, P., de Vries, M., ter Maat, M., Ying, S., Viquez-Zamora, M., & van Heusden, S. (2016). Hybrid potato breeding for improved varieties. *Achieving Sustainable Cultivation of Potatoes*, *1*, 1–24. https://doi.org/10.19103/AS.2016.0016.04

Lindhout, P., Meijer, D., Schotte, T., Hutten, R. C., Visser, R. G., & Eck, H. J. V. (2011). Towards $F_1$ hybrid seed potato breeding. *Potato Research*, *54*(4), 301–312. https://doi.org/10.1007/s11540-011-9196-z

Lokossou, A. A., Park, T. H., van Arkel, G., Arens, M., Ruyter-Spira, C., Morales, J., Whisson, S. C., Birch, P. R. J., Visser, R. G. F., Jacobsen, E., & van der Vossen, E. A. G. (2009). Exploiting knowledge of R/Avr genes to rapidly clone a new LZ-NBS-LRR family of late blight resistance genes from potato linkage group IV. *Molecular Plant-Microbe Interactions*, *22*, 630–641. https://doi.org/10.1094/MPMI-22-6-0630

Lokossou, A. A., Rietman, H., Wang, M., Krenek, P., van der Schoot, H., Henken, B., Hoekstra, R., Vleeshouwers, V. G. G. A., van der Vossen, E. A. G., Visser, R. G. F., Jacobsen, E., & Vosman, B. (2010). Diversity, distribution, and evolution of *Solanum bulbocastanum* late blight resistance genes. *Molecular Plant-Microbe Interactions*, *23*, 1206–1216. https://doi.org/10.1094/MPMI-23-9-1206

Luo, M., Sun, X., Qi, Y., Zhou, J., Wu, X., & Tian, Z. (2021). *Phytophthora infestans* RXLR effector Pi04089 perturbs diverse defense-related genes to suppress host immunity. *BMC Plant Biology*, *21*, 1–15. https://doi.org/10.1186/s12870-021-03364-0

Manrique-Carpintero, N., Islam, M. S., Enciso-Rodríguez, F., Rosenzweig, N., Coombs, J., & Douches, D. S. (2020). Mapping *Solanum berthaultii*-based late blight (*Phytophthora infestans*) resistance in a diploid population. *American Journal of Potato Research*, *97*, 596–604. https://doi.org/10.1007/s12230-020-09808-x

Marks, G. E. (1966). The origin and significance of intraspecific polyploidy: Experimental evidence from *Solanum chacoense*. *Evolution*, *20*, 552–557. https://doi.org/10.2307/2406589

Mayton, H., Griffiths, H., Simko, I., Cheng, S., Lorenzen, J., De Jong, W., & Fry, W. E. (2010). Foliar and tuber late blight resistance in a *Solanum tuberosum* breeding population. *Plant Breeding*, *129*, 197–201. https://doi.org/10.1111/j.1439-0523.2009.01671.x

Mayton, H., Rauscher, G., Simko, I., & Fry, W. E. (2011). Evaluation of the RPi-ber late blight resistance gene for tuber resistance in the field and laboratory. *Plant Breeding*, *130*, 464–468. https://doi.org/10.1111/j.1439-0523.2010.01836.x

McCauley, D. (2021). The worlds first diploid recombinant inbred potato population. *CSA News*, *66*, 6–11. https://doi.org/10.1002/csan.20602

McComas, K. A., Besley, J. C., & Steinhardt, J. (2014). Factors influencing U.S. consumer support for genetic modification to prevent crop disease. *Appetite*, *78*, 8–14. https://doi.org/10.1016/j.appet.2014.02.006

Meade, F., Hutten, R., Wagener, S., Prigge, V., Dalton, E., Kirk, H. G., Griffin, D., & Milbourne, D. (2020). Detection of novel QTLs for late blight resistance derived from the wild potato species *Solanum microdontum* and *Solanum pampasense*. *Genes*, *11*(7), 1–18. https://doi.org/10.3390/genes11070732

Meksem, K., Leister, D., Peleman, J., Zabeau, M., Salamini, F., & Gebhardt, C. (1995). A high-resolution map of the vicinity of the *R1* locus on chromosome V of potato based on RFLP and AFLP markers. *MGG Molecular & General Genetics*, *249*, 74–81. https://doi.org/10.1007/BF00290238

Mendiburu, A. O., & Peloquin, S. J. (1977). The significance of 2n gametes in potato breeding. *Theoretical and Applied Genetics*, *49*, 53–61. https://doi.org/10.1007/BF00275164

Michelmore, R. W., & Meyers, B. C. (1998). Clusters of resistance genes in plants evolve by divergent selection and a birth-and-death process. *Genome Research*, *8*, 1113–1130. https://doi.org/10.1101/gr.8.11.1113

Millam, S., Payne, L. A., & Mackay, G. R. (1995). The integration of protoplast fusion-derived material into a potato breeding programme—A review of progress and problems. In *The methodology of plant genetic manipulation: Criteria for decision making* (pp. 451–455). Springer. https://doi.org/10.1007/978-94-011-0357-2_55

Monino-Lopez, D., Nijenhuis, M., Kodde, L., Kamoun, S., Salehian, H., Schentsnyi, K., Stam, R., Lokossou, A., Abd-El-Haliem, A., Visser, R. G. F., & Vossen, J. H. (2021). Allelic variants of the NLR protein Rpi-chc1 differentially recognize members of the *Phytophthora infestans* PexRD12/31 effector superfamily through the leucine-rich repeat domain. *Plant Journal*, *107*, 182–197. https://doi.org/10.1111/tpj.15284

Muratova, O. A., Beketova, M. P., Kuznetsova, M. A., Rogozina, E. V., & Khavkin, E. E. (2020). South American species *Solanum alandiae* card. And *S. okadae* Hawkes et Hjerting as potential sources of genes for potato late blight resistance. *Proceedings on Applied Botany, Genetics and Breeding*, *181*, 73–83. https://doi.org/10.30901/2227-8834-2020-1-73-83

Nachtigall, M., König, J., & Thieme, R. (2018). Mapping of a novel, major late blight resistance locus in the diploid (1EBN) Mexican *Solanum pinnatisectum* Dunal on chromosome VII. *Plant Breeding*, *137*, 433–442. https://doi.org/10.1111/pbr.12580

Naess, S. K., Bradeen, J. M., Wielgus, S. M., Haberlach, G. T., McGrath, J. M., & Helgeson, J. P. (2000). Resistance to late blight in *Solanum bulbocastanum* is mapped to chromosome 8. *Theoretical and Applied Genetics*, *101*(5–6), 697–704. https://doi.org/10.1007/s001220051533

Nechwatal, J., & Zellner, M. (2015). Potential suitability of various leaf treatment products as copper substitutes for the control of late blight (*Phytophthora infestans*) in organic potato farming. *Potato Research*, *58*(3), 261–276. https://doi.org/10.1007/s11540-015-9302-8

Nowicki, M., Foolad, M. R., Nowakowska, M., & Kozik, E. U. (2012). Potato and tomato late blight caused by *Phytophthora infestans*: An overview of pathology and resistance breeding. *Plant Disease*, *96*, 4–17. https://doi.org/10.1094/PDIS-05-11-0458

Oosumi, T., Rockhold, D. R., Maccree, M. M., Deahl, K. L., McCue, K. F., & Belknap, W. R. (2009). Gene *Rpi-bt1* from *Solanum bulbocastanum* confers resistance to late blight in transgenic potatoes. *American Journal of Potato Research*, *86*(6), 456–465. https://doi.org/10.1007/s12230-009-9100-4

Ortiz, R. (2020). Genomic-led potato breeding for increasing genetic gains: Achievements and outlook. *Crop Breeding, Genetics and Genomics*, *2*, 1–25. https://doi.org/10.20900/cbgg20200010

Pandey, S. K., Sarkar, D., Sharma, S., & Chandel, P. (2010). Integration of somatic fusion into potato breeding: Problems and perspectives. *Potato Journal*, *37*, 9–20.

Park, T. H., Foster, S., Brigneti, G., & Jones, J. D. G. (2009). Two distinct potato late blight resistance genes from *Solanum berthaultii* are located

on chromosome 10. *Euphytica*, *165*, 269–278. https://doi.org/10.1007/s10681-008-9784-4

Park, T. H., Gros, J., Sikkema, A., Vleeshouwers, V. G. A. A., Muskens, M., Allefs, S., Jacobsen, E., Visser, R. G. F., & van der Vossen, E. A. G. (2005). The late blight resistance locus *Rpi-blb3* from *Solanum bulbocastanum* belongs to a major late blight R gene cluster on chromosome 4 of potato. *Molecular Plant-Microbe Interactions*, *18*, 722–729. https://doi.org/10.1094/MPMI-18-0722

Park, T. H., Vleeshouwers, V. G. A. A., Huigen, D. J., van der Vossen, E. A. G., Van Eck, H. J., & Visser, R. G. F. (2005). Characterization and high-resolution mapping of a late blight resistance locus similar to *R2* in potato. *Theoretical and Applied Genetics*, *111*(3), 591–597. https://doi.org/10.1007/s00122-005-2050-4

Park, T. H., Vleeshouwers, V. G. A. A., Hutten, R. C. B., Van Eck, H. J., van der Vossen, E., Jacobsen, E., & Visser, R. G. F. (2005). High-resolution mapping and analysis of the resistance locus *Rpi-abpt* against *Phytophthora infestans* in potato. *Molecular Breeding*, *16*, 33–43. https://doi.org/10.1007/s11032-005-1925-z

Park, T. H., Vleeshouwers, V. G. A. A., Jacobsen, E., van der Vossen, E., & Visser, R. G. F. (2009). Molecular breeding for resistance to *Phytophthora infestans* (Mont.) de Bary in potato (*Solanum tuberosum* L.): A perspective of cisgenesis. *Plant Breeding*, *128*, 109–117. https://doi.org/10.1111/j.1439-0523.2008.01619.x

Park, T. H., Vleeshouwers, V. G. A. A., Kim, J.-B., Hutten, R. C. B., & Visser, R. G. F. (2005). Dissection of foliage and tuber late blight resistance in mapping populations of potato. *Euphytica*, *143*(1–2), 75–83. https://doi.org/10.1007/s10681-005-2658-0

Pel, M. A. (2010). *Mapping, isolation and characterization of genes responsible for late blight resistance in potato*Doctoral dissertation. Wageningen University.

Pel, M. A., Foster, S. J., Park, T. H., Rietman, H., Ven Arkel, G., Jones, J. D. G., Van Eck, H. J., Jacobsen, E., Visser, R. G. F., & van der Vossen, E. A. G. (2009). Mapping and cloning of late bright resistance genes from *Solanum venturii* using an interspecific candidate gene approach. *Molecular Plant-Microbe Interactions*, *22*, 601–615. https://doi.org/10.1094/MPMI-22-5-0601

Phumichai, C., Mori, M., Kobayashi, A., Kamijima, O., & Kazuyoshi, H. (2005). Toward the development of highly homozygous diploid potato lines using the self-compatibility controlling *Sli* gene. *Genome*, *48*, 977–984. https://doi.org/10.1139/G05-066

Platt, H. W., & Tai, G. (1998). Relationship between resistance to late blight in potato foliage and tubers of cultivars and breeding selections with different resistance levels. *American Journal of Potato Research*, *75*(4), 173–178. https://doi.org/10.1007/bf02853569

Poland, J. A., Balint-Kurti, P. J., Wisser, R. J., Pratt, R. C., & Nelson, R. J. (2009). Shades of gray: The world of quantitative disease resistance. *Trends in Plant Science*, *14*, 21–29. https://doi.org/10.1016/j.tplants.2008.10.006

Ramsay, G., Stewart, H. E., De Jong, W., Bradshaw, J. E., & Mackay, G. R. (1999). Introgression of late blight resistance into *Solanum tuberosum*. In *Genetics and breeding for crop quality and resistance* (pp. 25–32). Springer Netherlands. https://doi.org/10.1007/978-94-011-4475-9_3

Rauscher, G., Simko, I., Mayton, H., Bonierbale, M., Smart, C. D., Grünwald, N. J., Greenland, A., & Fry, W. E. (2010). Quantitative resistance to late blight from *Solanum berthaultii* cosegregates with R piber: Insights in stability through isolates and environment. *Theoretical and Applied Genetics*, *121*(8), 1553–1567. https://doi.org/10.1007/s00122-010-1410-x

Rauscher, G. M., Smart, C. D., Simko, I., Bonierbale, M., Mayton, H., Greenland, A., & Fry, W. E. (2006). Characterization and mapping of *Rpi-ber*, a novel potato late blight resistance gene from *Solanum berthaultii*. *Theoretical and Applied Genetics*, *112*, 674–687. https://doi.org/10.1007/s00122-005-0171-4

Rehman, M., Liu, L., Wang, Q., Saleem, M. H., Bashir, S., Ullah, S., & Peng, D. (2019). Copper environmental toxicology, recent advances, and future outlook: A review. *Environmental Science and Pollution Research*, *26*, 18003–18016. https://doi.org/10.1007/s11356-019-05073-6

Richael, C. M. (2021). Development of the genetically modified innate® potato. *Plant Breeding Reviews*, *44*, 57–78. https://doi.org/10.1002/9781119717003.ch3

Rietman, H. (2011). *Putting the Phytophthora infestans genome sequence at work; multiple novel avirulence and potato resistance gene candidates revealed*Doctoral dissertation. Wageningen University.

Rietman, H., Bijsterbosch, G., Cano, L. M., Lee, H. R., Vossen, J. H., Jacobsen, E., Visser, R. G. F., Kamoun, S., & Vleeshouwers, V. G. A. A. (2012). Qualitative and quantitative late blight resistance in the potato cultivar Sarpo Mira is determined by the perception of five distinct RXLR effectors. *Molecular Plant-Microbe Interactions*, *25*(7), 910–919. https://doi.org/10.1094/MPMI-01-12-0010-R

Rodewald, J., & Trognitz, B. (2013). *Solanum* resistance genes against *Phytophthora infestans* and their corresponding avirulence genes. *Molecular Plant Pathology*, *14*, 740–757. https://doi.org/10.1111/mpp.12036

Ruiz de Galarreta, J. I., Carrasco, A., Salazar, A., Barrena, I., Iturritxa, E., Marquinez, R., Legorburu, F. J., & Ritter, E. (1998). Wild *Solanum* species as resistance sources against different pathogens of potato. *Potato Research*, *41*, 57–68. https://doi.org/10.1007/BF02360262

Sandbrink, J. M., Colon, L. T., Wolters, P. J. C. C., & Stiekema, W. J. (2000). Two related genotypes of *Solanum microdontum* carry different segregating alleles for field resistance to *Phytophthora infestans*. *Molecular Breeding*, *6*, 215–225. https://doi.org/10.1023/A:1009697318518

Schellenberger, R., Touchard, M., Clément, C., Baillieul, F., Cordelier, S., Crouzet, J., & Dorey, S. (2019). Apoplastic invasion patterns triggering plant immunity: Plasma membrane sensing at the frontline. *Molecular Plant Pathology*, *20*, 1602–1616. https://doi.org/10.1111/mpp.12857

Simko, I., Costanzo, S., Ramanjulu, V., Christ, B. J., & Haynes, K. G. (2006). Mapping polygenes for tuber resistance to late blight in a diploid *Solanum phureja* x *S. stenotomum* hybrid population. *Plant Breeding*, *125*(4), 385–389. https://doi.org/10.1111/j.1439-0523.2006.01232.x

Śliwka, J., Jakuczun, H., Chmielarz, M., Hara-Skrzypiec, A., Tomczyńska, I., Kilian, A., & Zimnoch-Guzowska, E. (2012a). Late blight resistance gene from *Solanum ruiz-ceballosii* is located on potato chromosome X and linked to violet flower colour. *BMC Genetics*, *13*(11), 1–12. https://doi.org/10.1186/1471-2156-13-11

Śliwka, J., Jakuczun, H., Chmielarz, M., Hara-Skrzypiec, A., Tomczyńska, I., Kilian, A., & Zimnoch-Guzowska, E. (2012b). A resistance gene against potato late blight originating from *Solanum* × *michoacanum* maps to potato chromosome VII. *Theoretical and Applied Genetics*, *124*, 397–406. https://doi.org/10.1007/s00122-011-1715-4

Śliwka, J., Jakuczun, H., Lebecka, R., Marczewski, W., Gebhardt, C., & Zimnoch-Guzowska, E. (2006). The novel, major locus *Rpi-phu1* for late blight resistance maps to potato chromosome IX and is not correlated with long vegetation period. *Theoretical and Applied Genetics*, *113*(4), 685–695. https://doi.org/10.1007/s00122-006-0336-9

Smilde, W. D., Brigneti, G., Jagger, L., Perkins, S., & Jones, J. D. G. (2005). *Solanum mochiquense* chromosome IX carries a novel late blight resistance gene *Rpi-moc1*. *Theoretical and Applied Genetics*, *110*, 252–258. https://doi.org/10.1007/s00122-004-1820-8

Song, J., Bradeen, J. M., Naess, S. K., Raasch, J. A., Wielgus, S. M., Haberlach, G. T., Liu, J., Kuang, H., Austin-Phillips, S., Buell, C. R., Helgeson, J. P., & Jiang, J. (2003). Gene RB cloned from *Solanum bulbocastanum* confers broad spectrum resistance to potato late blight. *Proceedings of the National Academy of Sciences of the United States of America*, *100*(16), 9128–9133. https://doi.org/10.1073/pnas.1533501100

Sørensen, K. K., Madsen, M. H., Kirk, H. G., Madsen, D. K., & Torp, A. M. (2006). Linkage and quantitative trait locus mapping of foliage late

blight resistance in the wild species *Solanum vernei*. *Plant Breeding*, *125*(3), 268–276. https://doi.org/10.1111/j.1439-0523.2006.01219.x

Spooner, D. M., Ghislain, M., Simon, R., Jansky, S. H., & Gavrilenko, T. (2014). Systematics, diversity, genetics, and evolution of wild and cultivated potatoes. *The Botanical Review*, *80*(4), 283–383. https://doi.org/10.1007/s12229-014-9146-y

Spooner, D. M., Ruess, H., Arbizu, C. I., Rodríguez, F., & Solís-Lemus, C. (2018). Greatly reduced phylogenetic structure in the cultivated potato clade (*Solanum* section *Petota* pro parte). *American Journal of Botany*, *105*, 60–70. https://doi.org/10.1002/ajb2.1008

Spooner, D. M., Van Den Berg, R. G., & Miller, J. T. (2001). Species and series boundaries of *Solanum* series *Longipedicellata* (Solanaceae) and phenetically similar species in ser. *Demissa* and ser. *Tuberosa*: Implications for a practical taxonomy of section *Petota*. *American Journal of Botany*, *88*, 113–130. https://doi.org/10.2307/2657132

Stefańczyk, E., Plich, J., Janiszewska, M., Smyda-Dajmund, P., Sobkowiak, S., & Śliwka, J. (2020). Marker-assisted pyramiding of potato late blight resistance genes *Rpi-rzc1* and *Rpi-phu1* on di- and tetraploid levels. *Molecular Breeding*, *40*(9), 1–12. https://doi.org/10.1007/s11032-020-01169-x

Stewart, H. E., Bradshaw, J. E., & Pande, B. (2003). The effect of the presence of R-genes for resistance to late blight (*Phytophthora infestans*) of potato (*Solanum tuberosum*) on the underlying level of field resistance. *Plant Pathology*, *52*, 193–198. https://doi.org/10.1046/j.1365-3059.2003.00811.x

Storck, T., Böhme, T., & Schultheiss, H. (2011). In H. T. A. M. Schepers (Ed.), *Fortuna et al.: Status and perspectives of GM approaches to fight late blight* (pp. 45–48). Thirteenth EuroBlight workshop.

Su, Y., Viquez-Zamora, M., Uil, D. D., Sinnige, J., Kruyt, H., Vossen, J., & Lindhout, P. (2020). Introgression of genes for resistance against *Phytophthora infestans* in diploid potato. *American Journal of Potato Research*, *97*, 33–42. https://doi.org/10.1007/s12230-019-09741-8

Swaminathan, M. S. (1951). Notes on induced polyploids in the tuber-bearing *Solanum* species and their crossability with *Solanum tuberosum*. *American Potato Journal*, *28*, 472–489. https://doi.org/10.1007/BF02854980

Szczerbakowa, A., Tarwacka, J., Oskiera, M., Jakuczun, H., & Wielgat, B. (2010). Somatic hybridization between the diploids of *S.* × *Michoacanum* and *S.* tuberosum. *Acta Physiologiae Plantarum*, *32*, 867–873. https://doi.org/10.1007/s11738-010-0472-3

Tan, M. Y. A., Hutten, R. C. B., Celis, C., Park, T. H., Niks, R. E., Visser, R. G. F., & Van Eck, H. J. (2008). The *Rpi-mcd1* locus from *Solanum microdontum* involved in resistance to *Phytophthora infestans*, causing a delay in infection, maps on potato chromosome 4 in a cluster of NBS-LRR genes. *Molecular Plant-Microbe Interactions*, *21*, 909–918. https://doi.org/10.1094/MPMI-21-7-0909

Thieme, R., Rakosy-Tican, E., Gavrilenko, T., Antonova, O., Schubert, J., Nachtigall, M., Heimbach, U., & Thieme, T. (2008). Novel somatic hybrids (*Solanum tuberosum* L. + *Solanum tarnii*) and their fertile BC1 progenies express extreme resistance to potato virus Y and late blight. *Theoretical and Applied Genetics*, *116*, 691–700. https://doi.org/10.1007/s00122-007-0702-2

Thieme, R., Rakosy-Tican, E., Nachtigall, M., Schubert, J., Hammann, T., Antonova, O., Gavrilenko, T., Heimbach, U., & Thieme, T. (2010). Characterization of the multiple resistance traits of somatic hybrids between *Solanum cardiophyllum* Lindl. And two commercial potato cultivars. *Plant Cell Reports*, *29*, 1187–1201. https://doi.org/10.1007/s00299-010-0905-x

Tiwari, J. K., Devi, S., Sharma, S., Chandel, P., Rawat, S., & Singh, B. P. (2015). Allele mining in *Solanum* germplasm: Cloning and characterization of RB-homologous gene fragments from late blight resistant wild potato species. *Plant Molecular Biology Reporter*, *33*(5), 1584–1598. https://doi.org/10.1007/s11105-015-0859-9

Tiwari, J. K., Siddappa, S., Singh, B. P., Kaushik, S. K., Chakrabarti, S. K., Bhardwaj, V., & Chandel, P. (2013). Molecular markers for late blight resistance breeding of potato: An update. *Plant Breeding*, *132*(3), 237–245. https://doi.org/10.1111/pbr.12053

Trognitz, F., Manosalva, P., Gysin, R., Niño-Liu, D., Simon, R., Herrera, M. D. R., Trognitz, B., Ghislain, M., & Nelson, R. (2002). Plant defense genes associated with quantitative resistance to potato late blight in *Solanum phureja* x dihaploid *S. tuberosum* hybrids. *Molecular Plant-Microbe Interactions*, *15*, 587–597. https://doi.org/10.1094/MPMI.2002.15.6.587

USABlight. (2021). A National Project on Tomato & Potato Late Blight. Retrieved from https://usablight.org/

van der Vossen, E., Gros, J., Sikkema, A., Muskens, M., Wouters, D., Wolters, P., Pereira, A., & Allefs, S. (2005). The *Rpi-blb2* gene from *Solanum bulbocastanum* is an *Mi-1* gene homolog conferring broad-spectrum late blight resistance in potato. *Plant Journal*, *44*, 208–222. https://doi.org/10.1111/j.1365-313X.2005.02527.x

van der Vossen, E., Sikkema, A., Hekkert, B. T. L., Gros, J., Stevens, P., Muskens, M., Wouters, D., Pereira, A., Stiekema, W., & Allefs, S. (2003). An ancient R gene from the wild potato species *Solanum bulbocastanum* confers broad-spectrum resistance to *Phytophthora infestans* in cultivated potato and tomato. *Plant Journal*, *36*(6), 867–882. https://doi.org/10.1046/j.1365-313X.2003.01934.x

van Lieshout, N., van der Burgt, A., de Vries, M. E., Ter Maat, M., Eickholt, D., Esselink, D., van Kaauwen, M. P., Kodde, L. P., Visser, R. G., Lindhout, P., & Finkers, R. (2020). Solyntus, the new highly contiguous reference genome for potato (*Solanum tuberosum*). *Genes, Genomes, Genetics*, *10*, 3489–3495. https://doi.org/10.1534/g3.120.401550

van Poppel, P. M. J. A. (2009). *The Phytophthora infestans avirulence gene PiaAvr4 and its potato counterpart R4*Doctoral dissertation. Wageningen University.

Verzaux, E., Budding, D., de Vetten, N., Niks, R. E., Vleeshouwers, V. G. A. A., van der Vossen, E. A. G., Jacobsen, E., & Visser, R. G. F. (2011). High resolution mapping of a novel late blight resistance gene *Rpi-avl1*, from the wild Bolivian species *Solanum avilesii*. *American Journal of Potato Research*, *88*(6), 511–519. https://doi.org/10.1007/s12230-011-9218-z

Verzaux, E. C. (2010). *Resistance and susceptibility to late blight in Solanum: Gene mapping, cloning and stacking*Doctoral dissertation. Wageningen University.

Villamon, F. G., Spooner, D. M., Orrillo, M., Mihovilovich, E., Pérez, W., & Bonierbale, M. (2005). Late blight resistance linkages in a novel cross of the wild potato species *Solanum paucissectum* (series *Piurana*). *Theoretical and Applied Genetics*, *111*(6), 1201–1214. https://doi.org/10.1007/s00122-005-0053-9

Vleeshouwers, V. G., van Dooijeweert, W., Paul Keizer, L. C., Sijpkes, L., Govers, F., & Colon, L. T. (1999). A laboratory assay for *Phytophthora infestans* resistance in various *Solanum* species reflects the field situation. *European Journal of Plant Pathology*, *105*, 241–250. https://doi.org/10.1023/A:1008710700363

Vleeshouwers, V. G. A. A., Rietman, H., Krenek, P., Champouret, N., Young, C., Oh, S. K., Wang, M., Bouwmeester, K., Vosmanm, B., Visser, R. G. F., Jacobsen, E., Govers, F., Kamoun, S., & van der Vossen, E. A. G. (2008). Effector genomics accelerates discovery and functional profiling of potato disease resistance and *Phytophthora Infestans* avirulence genes. *PLoS ONE*, *3*(8), 1–10. https://doi.org/10.1371/journal.pone.0002875

Vossen, J., Nijenhuis, M., Arens-De Reuver, M., van der Vossen, E., Jacobsen, E., & Visser, R. (2017). Cloning and exploitation of a functional R-gene from *Solanum chacoense*. *United State Patent*, *2*(12), 1–89.

Wang, M., Allefs, S., Van Den Berg, R. G., Vleeshouwers, V. G. A. A., van der Vossen, E. A. G., & Vosman, B. (2008). Allele mining in *Solanum*: Conserved homologues of *Rpi-blb1* are identified in *Solanum stoloniferum*. *Theoretical and Applied Genetics*, *116*(7), 933–943. https://doi.org/10.1007/s00122-008-0725-3

Waters, S., Ramos, A., Culler, A. H., Hunst, P., Zeph, L., Gast, R., Mahadeo, D., Sottosanto, J., Huber, S., Shan, G., Chakravarthy, S., & Goodwin, L. (2021). Recommendations for science-based safety assessment of genetically modified (GM) plants for food and feed uses. *Journal of Regulatory Science*, *9*, 16–21. https://doi.org/10.21423/jrs-v09i1waters

Weese, T. L., & Bohs, L. (2007). A three-gene phylogeny of the genus *Solanum* (Solanaceae). *Systematic Botany*, *32*, 445–463. https://doi.org/10.1600/036364407781179671

Weymers, P. S. V., Baker, K., Chen, X., Harrower, B., Cooke, D. E., Gilroy, E. M., Birch, P. R. J., Thilliez, G. J. A., Lees, A. K., Lynott, J. S., Armstrong, M. R., McKenzie, G., Bryan, G. J., & Hein, I. (2016). Utilizing "Omic" technologies to identify and prioritize novel sources of resistance to the oomycete pathogen *Phytophthora infestans* in potato germplasm collections. *Frontiers in Plant Science*, *7*, 672. https://doi.org/10.3389/fpls.2016.00672

Whisson, S. C., Boevink, P. C., Wang, S., & Birch, P. R. J. (2016). The cell biology of late blight disease. *Current Opinion in Microbiology*, *34*, 127–135. https://doi.org/10.1016/j.mib.2016.09.002

Witek, K., Jupe, F., Witek, A. I., Baker, D., Clark, M. D., & Jones, J. D. G. (2016). Accelerated cloning of a potato late blight-resistance gene using RenSeq and SMRT sequencing. *Nature Biotechnology*, *34*, 656–660. https://doi.org/10.1038/nbt.3540

Woodham-Smith, C. (1962). *The great hunger. Ireland 1845–1849*. Hamilton.

Yang, L., Wang, D., Xu, Y., Zhao, H., Wang, L., Cao, X., Chen, Y., & Chen, Q. (2017). A new resistance gene against potato late blight originating from *Solanum pinnatisectum* located on potato chromosome 7. *Frontiers in Plant Science*, *8*, 1–10. https://doi.org/10.3389/fpls.2017.01729

Yermishin, A. P., Polyukhovich, Y. V., Voronkova, E. V., & Savchuk, A. V. (2014). Production of hybrids between the 2EBN bridge species *Solanum verrucosum* and 1EBN diploid potato species. *American Journal of Potato Research*, *91*, 610–617. https://doi.org/10.1007/s12230-014-9385-9

Yin, J., Gu, B., Huang, G., Tian, Y., Quan, J., Lindqvist-Kreuze, H., & Shan, W. (2017). Conserved RXLR effector genes of *Phytophthora infestans* expressed at the early stage of potato infection are suppressive to host defense. *Frontiers in Plant Science*, *8*(12), 1–11. https://doi.org/10.3389/fpls.2017.02155

Zhang, C., Wang, P., Tang, D., Yang, Z., Lu, F., Qi, J., Tawari, N. R., Shang, Y., Li, C., & Huang, S. (2019). The genetic basis of inbreeding depression in potato. *Nature Genetics*, *51*, 374–378. https://doi.org/10.1038/s41588-018-0319-1

Zhou, Q., Tang, D., Huang, W., Yang, Z., Zhang, Y., Hamilton, J. P., Visser, R. G. F., Bachem, C. W. B., Buell, C. R., Zhang, Z., Zhang, C., & Huang, S. (2020). Haplotype-resolved genome analyses of a heterozygous diploid potato. *Nature Genetics*, *52*, 118–123. https://doi.org/10.1038/s41588-020-0699-x

Zhu, S. (2014). *R gene stacking by trans- and cisgenesis to achieve durable late blight resistance in potato*Doctoral dissertation. Wageningen University.

Zhu, S., Li, Y., Vossen, J. H., Visser, R. G. F., & Jacobsen, E. (2012). Functional stacking of three resistance genes against *Phytophthora infestans* in potato. *Transgenic Research*, *21*, 89–99. https://doi.org/10.1007/s11248-011-9510-1

Zlesak, D. C., & Thill, C. A. (2004). Foliar resistance to *Phytophthora infestans* (Mont.) de Bary (US-8) in 13 Mexican and south American *Solanum* species having EBNs of 1, 2, and 4 and implications for breeding. *American Journal of Potato Research*, *81*, 421–429. https://doi.org/10.1007/BF02870203

Zoteyeva, N., Chrzanowska, M., Flis, B., & Zimnoch-Guzowska, E. (2012). Resistance to pathogens of the potato accessions from the collection of N. I. Vavilov Institute of Plant Industry (VIR). *American Journal of Potato Research*, *89*, 277–293. https://doi.org/10.1007/s12230-012-9252-5

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## 2.2 Insights into the genetic basis of the pre-breeding potato clones developed at the Julius Kühn Institute for high and durable late blight resistance

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# Insights into the genetic basis of the pre-breeding potato clones developed at the Julius Kühn Institute for high and durable late blight resistance

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**Abstract**

Due to the high yield losses caused by late blight in potato cultivation, the development of resistant pre-breeding material is of great importance for cultivar breeding. The gene pool of the Julius Kühn Institute (JKI) includes a large collection of resistant clones whose resistance has not yet been analysed in detail with markers for relevant resistance genes. A panel of 52 pre-breeding potato clones developed at the JKI *via* interspecific crosses and highly resistant to late blight were tested for the presence of seven resistance genes (*Rpi-blb1/Rpi-sto1*, *Rpi-blb2*, *Rpi-blb3/R2/Rpi-abpt*, *R1*, *R3a*, *R3b*, *Rpi-phu1*) and one QTL allele (*QTL_phu-stn*) from *Solanum* species *S. bulbocastanum*, *S. demissum*, *S. phureja* and *S. stoloniferum*, respectively. Molecular marker assays based on sequence-specific primers revealed that 36 of the 52 pre-breeding clones carried either 1, 2, 3 or 4 resistance genes introgressed from these wild *Solanum* species. Results indicate that these resistance genes were retained over generations of breeding. Although highly resistant to late blight, 16 pre-breeding clones did not carry any of these resistance genes. Resistance in the gene pool may, thus, be based not only on individual resistance genes but also on QTL effects. Results help to better understand both inheritance and expression of late blight resistance of this unique gene pool and may be used for breeding programmes.

## Introduction

Potato late blight, caused by *Phytophthora infestans* (Mont.) de Bary, leads to high yield losses worldwide (Dowley *et al.*, 2008; Wiik, 2014). At the former Institute of Potato Research (now Julius Kühn Institute (JKI), Groß Lüsewitz, Germany), a long-term pre-breeding programme for durable *P. infestans* resistance has been run since the 1950s. Initially, crosses were made with resistant wild *Solanum* species to introgress resistance into the cultivated gene pool. In particular, accessions of *S. demissum*, *S. okadae*, *S. phureja*, *S. sparsipilum*, *S. stoloniferum*, *S. tuberosum* ssp. *andigena*, *S. vernei* and *S. bulbocastanum* were used as resistant progenitors. Progenies were backcrossed several times with common cultivars to select clones combining resistance and acceptable agronomic and qualitative traits. Thus, a unique gene pool was developed over decades. By using gene-specific markers, tracing the transmission of resistance genes from wild species in the course of a breeding programme became possible. In a marker-assisted approach, we here report the presence of known late blight resistance genes in the JKI potato gene pool and draw conclusions on the genetic basis of late blight resistance in this gene pool.

## Experimental

A total of 52 pre-breeding clones highly resistant to *P. infestans* were used for this study (online Supplementary Table S1). They originated from crosses carried out between 2001 and 2014 and represent higher backcross generations of BC5, BC6 or BC7. Additionally, eight common cultivars were included, five of which were described as susceptible ('Adretta', 'Belana', 'Gala', 'Krone', 'Princess') and three as moderately resistant ('Sarpo Mira', 'Alanis', 'Otolia'). Field resistance was evaluated in a randomized block design with two replications over 3 years at the JKI experimental station in Groß Lüsewitz. Plants were inoculated in early July with a *P. infestans* suspension containing races collected from the field over years. The field assessment was carried out twice a week until maturity. The relative

**Table 1.** Molecular markers used to detect corresponding late blight resistance genes

| Gene/QTL | Origin | Marker | Forward/reverse primer | Chromosomal location, expected size (bp) of amplicon | Annealing temperature (° C)/touch down | Reference |
|---|---|---|---|---|---|---|
| *Rpi-blb1/ Rpi-sto1* | *S. bulbocastanum* | BLB 1/1′ | F: CACGAGTGCCCTTTTCTGAC R: ACAATTGAATTTTTAGACTT | 8, 213 | 60–50 | Colton *et al.* (2006) |
| | *S. stoloniferum* | Sto1F/R | F: ACCAAGGCCACAAGATTCTC R: CCTGCGGTTCGGTTAATACA | 8, 890 | 68–58 | Zhu *et al.* (2012) |
| *Rpi-blb2* | *S. bulbocastanum* | BLB2F/R | F: GGACTGGGTAACGACAATCC R: AGCACGAGTTCCCCTAATGC | 6, 773 | 60–50 | Wang *et al.* (2008); Lokossou *et al.* (2010) |
| *Rpi-blb3/R2/ Rpi-abpt* | *S. bulbocastanum* | BLB3F/R | F: AGCTTTTTGAGTGTGTAATTGG R: GTAACTACGGACTCGAGGG | 4, 305 | 60–50 | Zhu *et al.* (2012) |
| | *S. demissum* | R2F/R | F: ATGGCTGATGCCTTTCTATCATTTGC R: TCACAACATATAATTCCGCTTC | 4, 2500 | 60–50 (27 cycles) | Kim *et al.* (2012) |
| | *S. demissum* | R2-F1/R3 | F: GCTCCTGATACGATCCATG R: ACGGCTTCTTGAATGAA | 4, 686 | 50 | Kim *et al.* (2012) |
| *R1* | *S. demissum* | 76–2sf2/ 76-2SR | F: CACTCGTGACATATCCTCACTA R: CAACCCTGGCATGCCACG | 5, 1400 | 60–50 | Ballvora *et al.* (2002) |
| *R3a* | *S. demissum* | SHa-F/R | F: ATCGTTGTCATGCTATGAGATTGTT R: CTTCAAGGTAGTGGGCAGTATGCTT | 11, 982 | 68–57 | Huang *et al.* (2005) |
| *R3b* | *S. demissum* | R3b-F4/R5 | F: GTCGATGAATGCTATGTTTCTCGAGA R: ACCAGTTTCTTGCAATTCCAGATTG | 11, 378 | 55 | Rietman (2011) |
| *Rpi-phu1* | *S. phureja* | GP94F/R | F: ATGTATCACAATCACATTCTTGCTC R: TGTAAAACCAACAAGTAGTGTTGC | 9, 300 | 45–35 | Śliwka *et al.* (2006) |
| *QTL_phu-stn* | *S. phureja* | GP198F-1/R | F: TTTGCTTACTCTTGTTGTATG R: TCACTTTGGTGCTTCTGTCG | 3, 450 | 60–50 (25 cycles) | Wickramasinghe *et al.* (2009) |

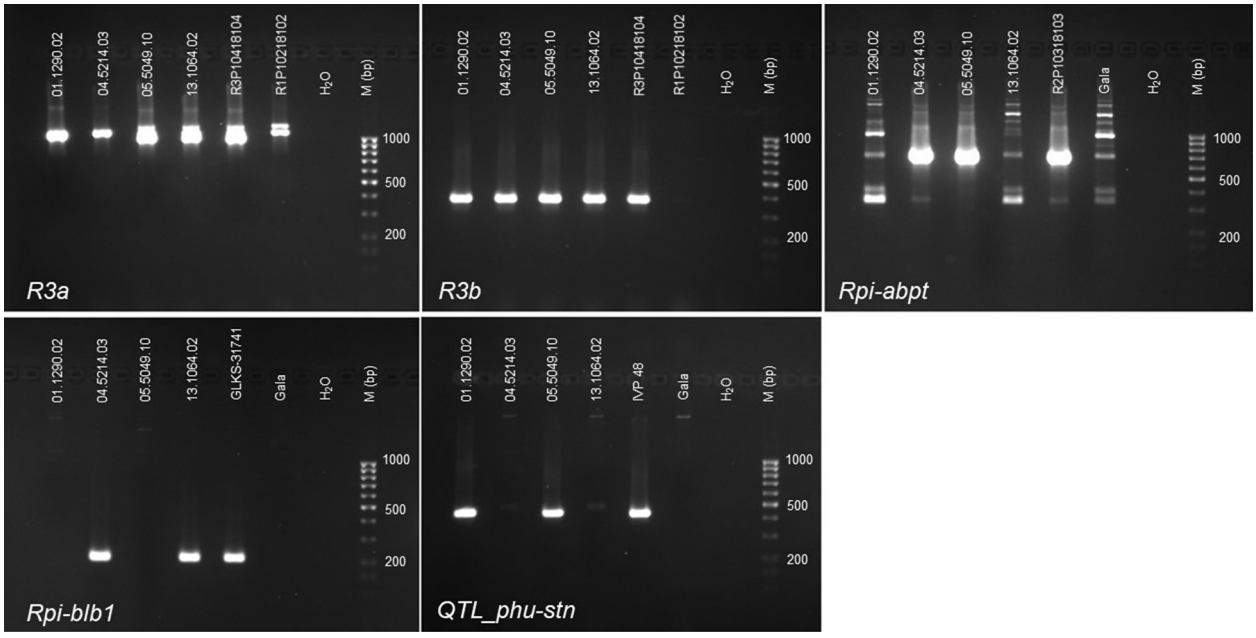


**Fig. 1.** Detection of *R3a*, *R3b*, *Rpi-abpt*, *Rpi-blb1* and *QTL_phu-stn* in the clones 01.1290.02, 04.5214.03, 05.5049.10 and 13.1064.02 using gene-specific markers. Every last line (M) is a 100 bp ladder (AppliChem; Darmstadt, Germany). *R3a* and *R3b*: positive control R3P10418104, negative control R1P10218102 *Rpi-abpt*: positive control R2P10318103, negative control 'Gala' *Rpi-blb1*: positive control GLKS-31741, negative control 'Gala' *QTL_phu-stn*: positive control IVP 48, negative control 'Gala'.

area under the disease progress curve was calculated and converted into scores from 1 (highly resistant) to 9 (highly susceptible) according to OEPP/EPPO (2021).

Plants for marker analysis were cultivated in a greenhouse for 4 weeks and DNA was extracted from young leaves using the DNeasy Plant Pro Kit (Qiagen; Hilden, Germany). Eleven pairs of gene-specific PCR primers for seven known resistance genes and one QTL allele were used (Table 1). These markers were selected based on the resistance genes coming from the wild progenitors. The PCR reactions of 20 µl consisted of 20 ng template DNA, 0.4 µM of each primer and 10 µl Red HS Taq Master Mix (Biozym; Hessisch Oldendorf, Germany). The PCR products were visualized by agarose gel electrophoresis.

## Discussion

In total, 36 of 52 clones tested yielded PCR amplicons for up to four resistance genes for seven of the eight genes tested (online Supplementary Table S1).

The resistance gene *R1* was detected in six clones, eight clones were positive for *Rpi-blb3/R2/Rpi-abpt*, 13 for *R3a* and 27 for *R3b*. All eight cultivars contained the genes *R3a* and *R3b*, in cultivar 'Alanis' the genes *R1* and *Rpi-blb2* were observed as well.

The resistance genes *R1* to *R11* from the wild species *S. demissum* were frequently used in potato breeding due to their early discovery (Vleeshouwers *et al.*, 2011). The hypothesis that they continue to occur in many cultivars for this reason is confirmed by the present study. Markers indicative for *R3* genes were found in many clones and in all cultivars, indicating that these genes have remained for a long time in breeding germplasms after they had been overcome by the pathogen. For example, Rakosy-Tican *et al.* (2020) detected *R3a* and *R3b* in 'Quarta', 'Baltica' and 'Sapro Mira' and *R3b* in 'Romanze'.

*Rpi-blb1/Rpi-sto1* was detected in four clones. According to Van der Vossen *et al.* (2003), *Rpi-blb1/Rpi-sto1* provides broad-spectrum resistance and thus makes an important contribution to broaden the genetic base for resistance.

Since *Rpi-phu1* from *S. phureja* does not appear in any of the clones, it may not have entered the gene pool or got lost by selection or genetic drift. *QTL_phu-stn* was detected in five clones. Costanzo *et al.* (2005) first described this QTL and Wickramasinghe *et al.* (2009) developed a marker. The present study is, to our knowledge, the first to investigate the presence of this QTL in potato breeding germplasm. *Rpi-blb2* was determined in only one clone, which is not surprising since crosses between *S. tuberosum* and *S. bulbocastanum* are difficult to achieve.

In the older clones from 2001 to 2003, markers for up to two genes per clone were detected. The 2004 and 2005 clones contained markers for up to four genes per clone. The most recent clones in this study showed markers for up to three genes (Fig. 1, online Supplementary Table S1).

The results indicate that the JKI potato gene pool contains resistance genes introgressed from wild species in the past, which had been maintained over generations of breeding. These genes, with exception of *R3a* and *R3b*, which were also found in susceptible cultivars, in addition to QTLs with smaller effects, are presumably involved in the high resistance properties of a large part of the gene pool. Already broken resistances inherited from *S. demissum* may still contribute to increase the resistance level (Stewart *et al.*, 2003). Additionally, it was shown that durable resistance properties of crop plants can be achieved by stacking of resistance genes (Zhu *et al.*, 2012; Haverkort *et al.*, 2016; Ghislain *et al.*, 2019; Stefańczyk *et al.*, 2020). Rogozina *et al.* (2021) found the resistance level to be correlated to the number of genes. In the present study, some clones carried just one or none of the analysed genes, whilst showing high resistance levels (online

Supplementary Table S1). Late blight resistance of the gene pool under survey appears, thus, not solely based on individual major resistance genes, but also on quantitative effects. In a meta-analysis focused on quantitative *P. infestans* resistance, QTLs for resistance were found to be located on all 12 chromosomes (Danan *et al.*, 2011). Whether a similar situation is present in the JKI potato gene pool remains to be analysed.

**Supplementary material.** The supplementary material for this article can be found at https://doi.org/10.1017/S1479262121000447

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## References

**Ballvora A, Ercolano MR, Weiß J, Meksem K, Bormann CA, Oberhagemann P, Salamini F and Gebhardt C** (2002) The R1 gene for potato resistance to late blight (*Phytophthora infestans*) belongs to the leucine zipper/NBS/LRR class of plant resistance genes. *The Plant Journal* **30**, 361–371.

**Colton LM, Groza HI, Wielgus SM and Jiang J** (2006) Marker-assisted selection for the broad-spectrum potato late blight resistance conferred by gene RB derived from a wild potato species. *Crop Science* **46**, 589–594.

**Costanzo S, Simko I, Christ BJ and Haynes KG** (2005) QTL analysis of late blight resistance in a diploid potato family of *Solanum phureja* × *S. stenotomum*. *Theoretical and Applied Genetics* **111**, 609–617.

**Danan S, Veyrieras JB and Lefebvre V** (2011) Construction of a potato consensus map and QTL meta-analysis offer new insights into the genetic architecture of late blight resistance and plant maturity traits. *BMC Plant Biology* **11**, 1–16.

**Dowley LJ, Grant J and Griffin D** (2008) Yield losses caused by late blight (*Phytophthora infestans* (Mont.) de Bary) in potato crops in Ireland. *Irish Journal of Agriculture and Food Research* **47**, 69–78.

**Ghislain M, Byarugaba AA, Magembe E, Njoroge A, Rivera C, Román ML, Tovar JC, Gamboa S, Forbes GA, Kreuze JF, Barekye A and Kiggundu A** (2019) Stacking three late blight resistance genes from wild species directly into African highland potato varieties confers complete field resistance to local blight races. *Plant Biotechnology Journal* **17**, 1119–1129.

**Haverkort AJ, Boonekamp PM, Hutten R, Jacobsen E, Lotz LAP, Kessel GJT, Vossen JH and Visser RGF** (2016) Durable late blight resistance in potato through dynamic varieties obtained by cisgenesis: scientific and societal advances in the DuRPh project. *Potato Research* **59**, 35–66.

**Huang S, van der Vossen EAG, Kuang H, Vleeshouwers VGAA, Zhang N, Borm TJA, van Eck HJ, Baker B, Jacobsen E and Visser RGF** (2005) Comparative genomics enabled the isolation of the R3a late blight resistance gene in potato. *The Plant Journal* **42**, 251–261.

**Kim HJ, Lee HR, Jo KR, Mortazavian SMM, Huigen DJ, Evenhuis B, Kessel G, Visser RGF, Jacobsen E and Vossen JH** (2012) Broad spectrum late blight resistance in potato differential set plants MaR8 and MaR9 is conferred by multiple stacked R genes. *Theoretical and Applied Genetics* **124**, 923–935.

**Lokossou AA, Rietman H, Wang M, Krenek P, van der Schoot H, Henken B, Hoekstra R, Vleeshouwers VGAA, van der Vossen EAG, Visser RGF, Jacobsen E and Vosman B**. (2010) Diversity, distribution, and evolution of *Solanum bulbocastanum* late blight resistance genes. *Molecular Plant-Microbe Interactions Journal* **23**, 1206–1216.

**OEPP/EPPO** (2021) PP 1/002(5) *Phytophthora infestans* on potato. *Bulletin OEPP/EPPO Bulletin* **51**, 79–82.

**Rakosy-Tican E, Thieme R, König J, Nachtigall M, Hammann T, Denes TE, Kruppa K and Molnár-Láng M** (2020) Introgression of two broad-spectrum late blight resistance genes, *Rpi-Blb*1 and *Rpi-Blb*3, from *Solanum bulbocastanum* dun plus race-specific R genes into potato pre-breeding lines. *Frontiers in Plant Science* **11**, 699.

**Rietman H** (2011) *Putting the Phytophthora Infestans Genome Sequence at Work; Identification of Many New R and Avr Genes in Solanum* (PhD thesis), Wageningen University, Wageningen, The Netherlands.

**Rogozina EV, Beketova MP, Muratova OA, Kuznetsova MA and Khavkin EE** (2021) Stacking resistance genes in multiparental interspecific potato hybrids to anticipate late blight outbreaks. *Agronomy* **11**, 1–31.

**Śliwka J, Jakuczun H, Lebecka R, Marczewski W, Gebhardt C and Zimnoch-Guzowska E** (2006) The novel, major locus Rpi-phu1 for late blight resistance maps to potato chromosome IX and is not correlated with long vegetation period. *Theoretical and Applied Genetics* **113**, 685–695.

**Stefańczyk E, Plich J, Janiszewska M, Smyda-Dajmund P, Sobkowiak S and Śliwka J** (2020) Marker-assisted pyramiding of potato late blight resistance genes Rpi-rzc1 and Rpi-phu1 on di-and tetraploid levels. *Molecular Breeding* **40**, 1–12.

**Stewart HE, Bradshaw JE and Pande B** (2003) The effect of the presence of R-genes for resistance to late blight (*Phytophthora infestans*) of potato (*Solanum tuberosum*) on the underlying level of field resistance. *Plant Pathology* **52**, 193–198.

**Van der Vossen E, Sikkema A, Hekkert BtL, Gros J, Stevens P, Muskens M, Wouters D, Pereira A, Stiekema W and Allefs S** (2003) An ancient R gene from the wild potato species *Solanum bulbocastanum* confers broad-spectrum resistance to *Phytophthora infestans* in cultivated potato and tomato. *The Plant Journal* **36**, 867–882.

**Vleeshouwers VGAA, Raffaele S, Vossen JH, Champouret N, Oliva R, Segretin ME, Rietmann H, Cano LM, Lokossou A, Kessel G, Pel MA and Kamoun S** (2011) Understanding and exploiting late blight resistance in the age of effectors. *Annual Review of Phytopathology* **49**, 507–531.

**Wang M, Allefs S, van den Berg RG, Vleeshouwers VGAA, van der Vossen EAG and Vosman B** (2008) Allele mining in *Solanum*: conserved homologues of *Rpi-blb*1 are identified in *Solanum stoloniferum*. *Theoretical and Applied Genetics* **116**, 933–943.

**Wickramasinghe WMDK, Qu XS, Costanzo S, Haynes KG and Christ BJ** (2009) Development of PCR-based markers linked to quantitative resistance to late blight in a diploid hybrid potato population of *Solanum phureja* × *S. stenotomum*. *American Journal of Potato Research* **86**, 188–195.

**Wiik L** (2014) Potato late blight and tuber yield: results from 30 years of field trials. *Potato Research* **57**, 77–98.

**Zhu S, Li Y, Vossen JH, Visser RGF and Jacobsen E** (2012) Functional stacking of three resistance genes against *Phytophthora infestans* in potato. *Transgenic Research* **21**, 89–99.

**Table S1** Cultivars and pre-breeding clones with high level of late blight resistance after three years of field assessment (1 = highly resistant, 9 = highly susceptible) and detection of their resistance genes using gene-specific markers. The first two digits of the clones indicate the year of crossing

| **Potato clone** | **Field resistance to late blight** | **Resistance genes (n)** | **Positive marker assay for resistance gene(s)** |
|---|---|---|---|
| Adretta | 6 | 2 | *R3a, R3b* |
| Belana | 6* | 2 | *R3a, R3b* |
| Gala | 6* | 2 | *R3a, R3b* |
| Krone | 5* | 2 | *R3a, R3b* |
| Princess | 7 | 2 | *R3a, R3b* |
| Sarpo Mira | 2 | 2 | *R3a, R3b* |
| Alanis | 3* | 4 | *Rpi-blb2, R1, R3a, R3b* |
| Otolia | 4* | 2 | *R3a, R3b* |
| 01.1343.01 | 1 | 1 | *R3b* |
| 01.1290.02 | 3 | 2 | *R3b, QTL_phu-stn* |
| 03.5067.01 | 2 | 0 | |
| 03.5115.05 | 3 | 1 | *R3b* |
| 03.5131.01 | 4 | 2 | *Rpi-blb1/Rpi-sto1, R3b* |
| 04.1465.03 | 3 | 2 | *R3a, R3b* |
| 04.5170.02 | 1 | 1 | *Rpi-blb2* |
| 04.5182.06 | 3 | 2 | *R1, R3b* |
| 04.5197.01 | 2 | 2 | *Rpi-blb3/R2/Rpi-abpt, QTL_phu-stn* |
| 04.5207.07 | 4 | 4 | *R1, R3a, R3b, QTL_phu-stn* |
| 04.5211.01 | 2 | 3 | *Rpi-blb3/R2/Rpi-abpt, R3b, QTL_phu-stn* |
| 04.5214.03 | 2 | 3 | *Rpi-blb1/Rpi-sto1, Rpi-blb3/R2/Rpi-abpt, R3b* |
| 04.5214.04 | 4 | 2 | *Rpi-blb3/R2/Rpi-abpt, R3b* |
| 04.5224.01 | 4 | 2 | *R3a, R3b* |
| 04.5228.07 | 2 | 1 | *Rpi-blb3/R2/Rpi-abpt* |
| 04.5230.04 | 4 | 0 | |
| 04.5233.03 | 3 | 0 | |
| 05.5049.10 | 4 | 4 | *Rpi-blb3/R2/Rpi-abpt, R3a, R3b, QTL_phu-stn* |
| 05.5161.05 | 4 | 2 | *R3a, R3b* |
| 07.1018.05 | 4 | 2 | *Rpi-blb3/R2/Rpi-abpt, R3b* |
| 07.1084.07 | 4 | 2 | *Rpi-blb3/R2/Rpi-abpt, R3b* |
| 08.1115.08 | 4 | 0 | |
| 08.1115.12 | 4 | 0 | |
| 08.1132.01 | 2 | 2 | *R3a, R3b* |
| 08.1149.11 | 4 | 2 | *R3a, R3b* |
| 08.1160.01 | 3 | 0 | |
| 08.1179.07 | 2 | 0 | |
| 09.1239.01 | 2 | 2 | *R3a, R3b* |
| 10.1017.05 | 2 | 2 | *R1, R3b* |
| 11.1005.03 | 2 | 2 | *Rpi-blb3/R2/Rpi-abpt, R3a* |
| 11.1006.11 | 2 | 0 | |
| 11.1021.02 | 3 | 2 | *R3b, QTL_phu-stn* |
| 11.1029.01 | 3 | 1 | *QTL_phu-stn* |
| 11.1044.02 | 2 | 1 | *QTL_phu-stn* |

| | | | |
|---|---|---|---|
| 11.1052.07 | 2 | 0 | |
| 11.1053.03 | 3 | 2 | *Rpi-blb1/Rpi-sto1, R3b* |
| 11.1055.01 | 2 | 0 | |
| 12.1009.07 | 3 | 0 | |
| 12.1010.09 | 2 | 0 | |
| 12.1013.03 | 2 | 1 | *R3b* |
| 12.1022.03 | 3 | 0 | |
| 12.1024.03 | 3 | 0 | |
| 13.1042.05 | 3 | 2 | *R3a, R3b* |
| 13.1047.01 | 3 | 0 | |
| 13.1057.01 | 3 | 2 | *R3a, R3b* |
| 13.1064.02 | 2 | 3 | *Rpi-blb1/Rpi-sto1, R3a, R3b* |
| 13.1093.05 | 2 | 1 | *R1* |
| 14.1016.03 | 3 | 2 | *R3a, R3b* |
| 14.1023.02 | 2 | 1 | *R1* |
| 14.1025.04 | 3 | 0 | |
| 14.1029.01 | 2 | 1 | *Rpi-blb3/R2/Rpi-abpt* |
| 14.1078.02 | 2 | 2 | *R1, R3b* |
| GLKS-31741 (*blb41*) | | | Positive control *Rpi-blb1/Rpi-sto1, Rpi-blb3/R2/Rpi-abpt* |
| Bionica | | | Positive control *Rpi-blb2* |
| Toluca | | | Positive control *Rpi-blb2* |
| R1 P 102 18102 | | | Positive control *R1* |
| R2 P 103 18103 | | | Positive control *Rpi-blb3/R2/Rpi-abpt* |
| R3 P 104 18104 | | | Positive control *R3a, R3b* |
| Sto 30602/1 | | | Positive control *Rpi-blb1/Rpi-sto1* |
| *S. phureja* IVP 48 | | | Positive control *Rpi-phu1, QTL_phu-stn* |

*Federal Plant Variety Office

## 2.3 Pre-breeding bei der Kartoffel (*Solanum tuberosum*) zur Verbesserung der Resistenz gegen *Phytophthora infestans*

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Originalarbeit

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# Pre-breeding bei der Kartoffel (*Solanum tuberosum*) zur Verbesserung der Resistenz gegen *Phytophthora infestans*

Pre-breeding of potato (*Solanum tuberosum*) to improve resistance against *Phytophthora infestans*




## Zusammenfassung

Die Kraut- und Knollenfäule (*Phytophthora infestans* Mont. de Bary) verursacht in der Kartoffelproduktion jährlich enorme Ernteverluste. Bislang gibt es dennoch keine zugelassene Sorte, die eine stabile Resistenz mit sich bringt. Am Julius Kühn-Institut konnten in den letzten Jahren neue Zuchtstämme entwickelt werden, die sich bereits in umfangreichen Resistenzuntersuchungen bewährt haben. Damit einhergehend wurden anhand einer genomweiten Assoziationsstudie mit 265 Pre-breeding-Stämmen und zugelassenen Sorten neun Marker für fünf QTL auf den Chromosomen 1, 7, 10 und 11 identifiziert, die mit der Resistenz in Zusammenhang stehen. Diese Ergebnisse können in Zukunft dazu beitragen, die Entwicklung von resistenten Sorten zu vereinfachen.


**Stichwörter:** *Phytophthora infestans*, Kraut- und Knollenfäule, *Solanum tuberosum*, Kartoffel, genomweite Assoziationsstudie


## Abstract

Late blight (*Phytophthora infestans* Mont. de Bary) causes high yield losses in potato production every year. However, to date there is no approved variety that provides stable resistance. In recent years, pre-breeding clones have been developed at the Julius Kühn Institute that have proven their value in extensive resistance tests. This was accompanied by a genome-wide association study involving 265 pre-breeding clones and approved varieties, respectively, which identified nine markers for five QTL on chromosomes 1, 7, 10, and 11 that are associated with the resistance. These results may help to develop resistant varieties in the future.


**Key words:** *Phytophthora infestans,* late blight, *Solanum tuberosum*, potato, genome-wide association study

## Einleitung

Nach wie vor gehört die Kartoffel (*Solanum tuberosum* L.) zu den wichtigsten Nahrungspflanzen weltweit. Dennoch ist ihre Ertragsstabilität vor allem durch Krankheiten wie die Kraut- und Knollenfäule (Abb. 1–4), hervorgerufen durch den Erreger *Phytophthora infestans* (*P.i.*), gefährdet. Bislang mangelt es trotz jahrzehntelanger Forschung an Sorten, welche die zahlreichen für Kartoffeln vermarktungsrelevanten Eigenschaften mit einer hinreichend hohen und dauerhaften Widerstandsfähigkeit gegen *P. infestans* vereinen würden. Im Jahr 2019 waren in Deutschland sieben Sorten mit der Boniturnote 3 (Noten von 1 (geringe Anfälligkeit) bis 9 (hohe Anfälligkeit)) für den konventionellen Anbau und eine Sorte mit der Note 4 für den ökologischen Anbau registriert (Bundessortenamt, 2019). Die Züchtung auf *P.i.*-Resistenz wird dadurch erschwert, dass

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**Abb. 1.** Gegen Krautfäule anfällige und resistente Stämme im Vergleich vier Wochen nach der Inokulation mit *P. infestans*.

**Abb. 2.** Krautfäulebefall im Blatttest sechs Tage nach der Inokulation mit *P. infestans*. Die fünf Blätter der ersten Reihe stammen von einem resistenten Genotyp, die Blätter der Reihen zwei und drei entstammen hoch anfälligen Genotypen.

Resistenzen gegen Krautfäule einerseits und Knollenfäule andererseits nach bisherigen Erkenntnissen unabhängig voneinander vererbt werden (Mayton et al., 2010). Im letzten Jahrhundert gab es einige vielversprechende Ansätze für die Nutzung sogenannter R-Gene gegen Krautfäule, die jeweils eine hohe Resistenzausprägung ihrer Träger bedingten. Für diesen qualitativ ausgeprägten Typ der Resistenz sind insgesamt 11 R-Gene, die aus der Wildart *S. demissum* stammen und in die Kulturkartoffel eingekreuzt wurden, beschrieben worden (Black et al., 1953; Malcolmson & Black, 1966; Malcolmson, 1969). Nachdem inzwischen diese Resistenzen jedoch alle von entsprechenden Pathotypen des sehr anpassungsfähigen Erregers gebrochen worden sind

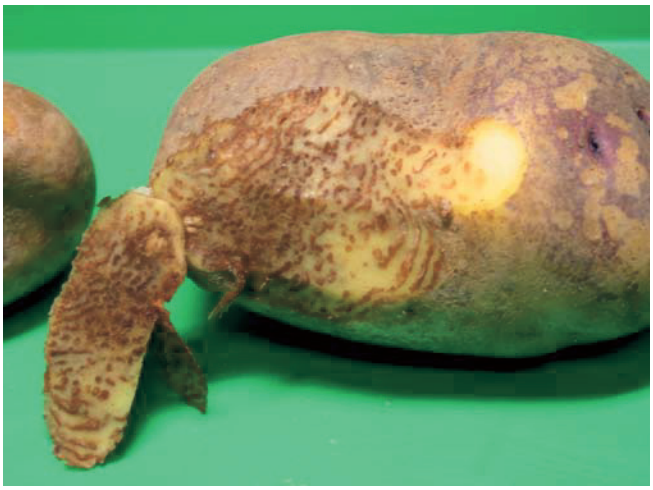

**Abb. 3.** Knollenfäulebefall an einer ganzen Knolle eines anfälligen Genotyps 14 Tage nach der Inokulation mit *P. infestans* mithilfe des Tauchtests.

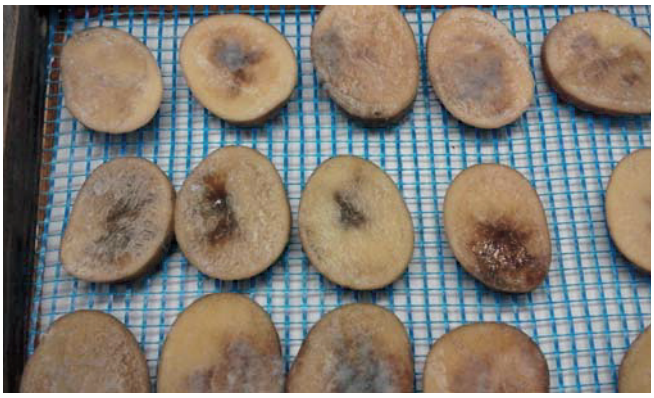

**Abb. 4.** Knollenfäulebefall im Scheibentest sechs Tage nach der Inokulation mit *P. infestans*. Die Scheiben aus Reihe eins und drei stammen von anfälligen Genotypen, dagegen sind in Reihe zwei Scheiben eines resistenten Genotyps gezeigt.

(Collins et al., 1999; Hein et al., 2009), steht heute der quantitativ vererbte Typ der Resistenz im Fokus der Forschung, der durch die Beteiligung mehrerer bis vieler Gene mit jeweils unvollständiger Resistenzwirkung und längere Beständigkeit der Gesamtwirkung gegenüber der Pathogenpopulation gekennzeichnet ist. Am Julius Kühn-Institut (JKI) in Groß Lüsewitz wurden explizit für den ökologischen Anbau, bei dem die Bekämpfung von *P.i.* aufgrund der geltenden Beschränkung im Einsatz von Kupferpräparaten auf maximal 6 kg $Cu^{2+}$ je Hektar und Jahr besonders schwierig ist (Verordnung (EG) Nr. 889/2008), im Rahmen eines BÖLN-Projekts (2810 OE 121) von 2012 bis 2018 ältere und jüngere Pre-breeding-Stämme des JKI hinsichtlich ihrer Resistenz- und Qualitätseigenschaften untersucht. Zudem wurde anhand von Sorten und Zuchtstämmen eine genomweite Assoziationsstudie durchgeführt, um QTL und entsprechende Marker für die quantitative *P.i.*-Resistenz der Zuchtstämme zu identifizieren.

## Material und Methoden

### *Pflanzenmaterial*

Insgesamt wurden zwischen 2012 und 2018 102 Sorten (Tab. S1), 67 ältere JKI-Pre-breeding-Stämme sowie 166 innerhalb des Projektes am JKI bzw. an der Bayerischen Landesanstalt für Landwirtschaft (LfL) entwickelte Stämme untersucht.

### *Bewertung der P.i.-Resistenz*

Die Bewertung der *P.i.*-Resistenz erfolgte durch Erfassung des Befalls nach der Inokulation je Stamm oder Sorte mit vier Methoden: Feldprüfung, Einzelblatttest, Tauchtest und Scheibentest. Alle Methoden wurden je Stamm bzw. Sorte in drei aufeinander folgenden Jahren durchgeführt.

Feldprüfung. Die Erfassung des Krautfäulebefalls erfolgte in einer vollständig randomisierten Blockanlage mit je zwei Wiederholungen à fünf Pflanzen je Stamm bzw. Sorte. Als Windschutz diente ein Mantel aus Hanfpflanzen. Zum Blühende der Sorte ‘Adretta‘ wurde jeweils eine Pflanze je Versuchsparzelle mit 5 ml einer *P.i.*-Suspension verschiedener Pathotypen inokuliert, deren Zusammensetzung jedes Jahr mit neu gesammeltem Erregermaterial ergänzt wurde ($1{,}2 \times 10^4$ Sporangien/ml, Darsow, 2008). Anschließend erfolgte die Bonitur des Befalls in Prozent befallener Krautfläche jeder Parzelle unter Ausschluss der inokulierten Pflanze alle drei bis vier Tage, bis ein Befall von 100 % erreicht war, bzw. bis zur Abreife des jeweiligen Stammes. Anhand dieser Boniturен wurden rAUDPC-Werte (relative Area Under Disease Progress Curve; Fry, 1978; Colon, 1994) berechnet. Da die Krautfäuleresistenz häufig in Zusammenhang mit einer späten Abreife steht, wurden die rAUDPC-Werte anschließend nach Truberg et al. (2009) reifekorrigiert und als ΔrAUDPC-Werte dargestellt.

Einzelblatttest. Kurz vor der Inokulation im Feldversuch wurden jeweils fünf Blätter verschiedener Pflanzen eines Stammes entnommen und im Labor je 20 µl *P.i.*-Suspension auf die Blattunterseite getropft. Nach 24 h wurden die Blätter gedreht und für weitere fünf Tage bei 16 °C, 95 % relativer Feuchte (RF) und 150 Lux inkubiert. Die Bonitur erfolgte anhand der nekrotisierten Blattfläche und der Mycelbildung auf der Blattunterseite (Tab. 1).

Tauchtest. Beim Tauchtest wird die Widerstandsfähigkeit der gesamten Knolle gegenüber Knollenfäule ermittelt. Dafür wurden je Stamm 15 Knollen in eine *P.i.*-Suspension (2000 Sporangien/ml) getaucht und für 24 h in Dunkelheit bei 19 °C/100 % RF inkubiert. Anschließend erfolgte eine 14-tägige Inkubation bei 16 °C/85 % RF in Dunkelheit. Der Befall mit Knollenfäule wurde einzelknollenweise erfasst und als Mittelwert je Stamm zusam-

**Tab. 1. Bonitурskala für den Einzelblatttest.** Die Bonitur erfolgte sechs Tage nach der Inokulation mit *P. infestans*.

| Note | Luftmyzel | Nekrotisierung |
|---|---|---|
| 1 | Kein Myzel | Keine Nekrosen |
| 2 | Leichte Symptome erkennbar | Punktförmige Nekrosen |
| 3 | bis zu 4 % der Fläche mit Myzel bedeckt | 2–4 mm große Nekrosen |
| 4 | 5–12 % der Fläche mit Myzel bedeckt | 5–12 % Zerstörung der Fläche |
| 5 | 13–30 % der Fläche mit Myzel bedeckt | 13–30 % Zerstörung der Fläche |
| 6 | 31–55 % der Fläche mit Myzel bedeckt | 31–55 % Zerstörung der Fläche |
| 7 | 56–78 % der Fläche mit Myzel bedeckt | 56–78 % Zerstörung der Fläche |
| 8 | 79–96 % der Fläche mit Myzel bedeckt | 79–96 % Zerstörung der Fläche |
| 9 | 97–100 % der Fläche mit Myzel bedeckt | 97–100 % Zerstörung der Fläche |

**Tab. 2. Bonitурskala für den Tauchtest.** Die Bonitur erfolgte 14 Tage nach der Inokulation mit *P. infestans*.

| Note | Verbräunung der Knollenoberfläche |
|---|---|
| 1 | Keine Verbräunung |
| 2 | Leichte Verbräunung erkennbar |
| 3 | bis zu 4 % der Fläche verbräunt |
| 4 | 5–15 % der Fläche verbräunt |
| 5 | 16–37 % der Fläche verbräunt |
| 6 | 38–57 % der Fläche verbräunt |
| 7 | 58–75 % der Fläche verbräunt |
| 8 | 76–93 % der Fläche verbräunt |
| 9 | 94–100 % der Fläche verbräunt |



mengefasst (Tab. 2). Knollen, die keinen oder sehr geringen Befall (Note 2) zeigten, wurden nach 14 Tagen erneut bonitiert und gingen mit halber Gewichtung in den Index ein (Darsow, 2008). Diese zweite Bonitur diente dem Auffinden von Knollen, die bei der ersten Bonitur so schwach befallen waren, dass der Befall nicht zu erkennen war. Um diesen späten und im Lager deutlich weniger gefährlichen Befall nicht zu überwerten, erfolgte die Gewichtung im Index mit dem Faktor 0,5.

Scheibentest. Um auch die Resistenzeigenschaften des Knollenmarks zu bewerten, wurde ein Scheibentest zu zwei Zeitpunkten mit vier Knollen je Stamm und Konzentrationsstufe durchgeführt. Von jeder Knolle wurde jeweils eine Scheibe an beiden Terminen mit je 20 µL einer niedrig (1.900 Sporangien/ml) bzw. einer hoch (15.000 Sporangien/ml) konzentrierten *P.i.*-Suspension inokuliert. Nach 24 h wurden die Scheiben gedreht und anschließend für weitere fünf Tage bei 16°C/95 % RF inkubiert. Für die Bonitur wurden die Scheiben mit jener *P.i.*-Konzentration gewertet, die eine Differenzierung des Befalls ermöglichte (Tab. 3).

Die Auswertungen der Laboruntersuchungen wurden neben den ΔrAUDPC-Werten für die Selektion von geeigneten Zuchtstämmen verwendet. Es wurde zudem geprüft, ob die Ergebnisse der verschiedenen Tests nach Pearson miteinander korrelieren. Prüfglieder, die sowohl in der Feldprüfung als auch in den Labortests eine hinreichende *P.i.*-Resistenz zeigten (durchschnittliche Boniturnoten < 5, ΔrAUDPC-Werte < 0), wurden im dritten Versuchsjahr auch hinsichtlich ihrer Speiseeignung untersucht (Daten unveröffentlicht).

### *Statistische Analyse der phänotypischen Daten und genomweite Assoziationsstudie*

Die Auswertung der Labor- und Felddaten durch eine Varianzanalyse mit einem gemischten linearen Modell erfolgte mit dem Programm „R“. Hierbei wurden die Jahre als Umwelten betrachtet:

$$y_{ijk} = \mu + G_i + E_j + GxE_{ij} + \varepsilon_{ijk}$$

$y_{ijk}$ = ΔrAUDPC-Wert bzw. Note des Scheiben- Blatt- oder Tauchtests des i-ten Stamms in der j-ten Umwelt und der k-ten Wiederholung
$G_i$ = i-ter Stamm
$E_j$ = Umwelt j für drei verschiedene Jahre
$GxE_{ij}$ = Interaktion des Stammes und der Umwelt
$\varepsilon_{ijk}$ = Restfehler

**Tab. 3. Bonitурskala für den Scheibentest.** Die Bonitur erfolgte sechs Tage nach der Inokulation mit *P. infestans*.

| Note | Luftmyzel | Verbräunung |
|---|---|---|
| 1 | Kein Myzel | Keine Verbräunung |
| 2 | Leichte Symptome erkennbar | Leichte Verbräunung erkennbar |
| 3 | bis zu 5 % der Fläche mit Myzel bedeckt | bis zu 14 % der Fläche verbräunt |
| 4 | 6–12 % (Mittel 9 %) der Fläche mit Myzel bedeckt | 15–24 % der Fläche verbräunt |
| 5 | 13–40 % (Mittel 25 %) der Fläche mit Myzel bedeckt | 25–44 % der Fläche verbräunt |
| 6 | 31–60 % (Mittel 43 %) der Fläche mit Myzel bedeckt | 45–66 % der Fläche verbräunt |
| 7 | 50–85 % (Mittel 62 %) der Fläche mit Myzel bedeckt | 67–82 % der Fläche verbräunt |
| 8 | 75–96 % (Mittel 85 %) der Fläche mit Myzel bedeckt | 83–96 % der Fläche verbräunt |
| 9 | 93–100 % (Mittel 96 %) der Fläche mit Myzel bedeckt | 97–100 % der Fläche verbräunt |

Die Heritabilität des Merkmals ΔrAUDPC wurde nach Holland et al. (2003) berechnet.

Um molekulare Marker für die quantitative *P.i.*-Resistenz der JKI-Zuchtstämme zu identifizieren, wurde von 265 ausgewählten Stämmen und Sorten Blattmaterial entnommen und nach der CTAB-Methode (Stein et al., 2001) DNA extrahiert.

Anschließend erfolgte die Genotypisierung mit der DArTSeq Plattform (Erhalt von DArT und SNP Markern) durch Diversity Arrays Technology Pty Ltd, Canberra, Australien (https://www.diversityarrays.com/). Marker mit einer Minor-Allelfrequenz < 5 % oder einem Anteil an doppelten Nullallelen > 20 % wurden nicht berücksichtigt. Fehlende Markerdaten wurden mit der K-Nearest Neighbours-Methode ersetzt (Batista & Monard, 2002).

Für die Assoziationsstudie wurden LS-Means (Least Square Means) der ΔrAUDPC-Werte berechnet und mit den Daten der Genotypisierung als Alleldosis in R mit dem Modell „Diplo-additive“ (Paket „GWASpoly“ nach Rosyara et al., 2016) verrechnet.

## Ergebnisse

### *Bewertung von P.i.-resistentem Zuchtmaterial für den ökologischen Anbau*

Über jeweils drei Jahre wurden Sorten sowie ältere und neuere Pre-breeding-Stämme erfolgreich in ihrer *P.i.*-Resistenz charakterisiert.

In Abbildung 5 sind Boxplots von 103 Prüfgliedern der Jahre 2015–2017 in ihren ΔrAUDPC-Werten und ihren Reifegruppen im Vergleich gezeigt. Negative ΔrAUDPC-Werte (unterhalb der roten Linie) weisen einen besonders niedrigen reifekorrigierten Krautfäulebefall auf. Der Vergleich zeigt, dass der überwiegende Teil der JKI Stämme deutlich geringer befallen wurde als die meisten zugelassenen Sorten und Zuchtstämme anderer Herkunft und zudem ein großer Teil der relativ resistenten JKI-Stämme der frühen bis mittelfrühen Reifegruppe angehörte. Von den Sorten zeigten mit wenigen Ausnahmen diejenigen einen geringen Befall, die spät abreiften (Abb. 5).

Auch die Ergebnisse der Labortests wiesen große Unterschiede zwischen den Sorten und Zuchtstämmen auf. Bei sechs Stämmen war eine besonders geringe Ausbreitung der Kraut- und Knollenfäule zu beobachten. Zugleich konnten diese Stämme frühen bis mittelfrühen Reifegruppen zugeordnet werden. Die Sorten wiesen auch bei den Labortests eine erhöhte Anfälligkeit auf (Tab. 4). Eine Ausnahme stellte die Sorte ‘Sarpo Mira‘ dar, die zwar gute Resistenzeigenschaften mit sich bringt, aber für den deutschen Markt deutlich zu spät abreift.

Die Ergebnisse der verschiedenen Labortests und der Feldprüfung wiesen eine hohe Korrelation auf (Tab. 5). Einzig die Reife war mit keinem weiteren Merkmal korreliert.

Bei der Testung auf Speiseeignung schnitt der Stamm 12797/9 vergleichsweise gut ab. Die übrigen Stämme waren insgesamt für Speisezwecke wenig geeignet.

### *Phänotypisierung und genomweite Assoziationsstudie*

Die Varianzanalyse ergab, dass die Stämme in ihren Laborwerten und ΔrAUDPC-Werten signifikante Unterschiede aufwiesen. Die Heritabilität der für die Assoziationsstudie genutzten ΔrAUDPC-Werte lag bei $h^2 = 0{,}80$.

Für die Assoziationsstudien wurden nach einer Filterung insgesamt 27.710 polymorphe Marker genutzt. In Abbildung 6 ist die Verteilung der Marker über die 12 Chromosomen der Kulturkartoffel dargestellt. Neun Marker mit geringen Markereffekten zwischen −0,13 und 0,12 waren mit dem Merkmal ΔrAUDPC-Wert assoziiert ($-\log_{10}(p) > 3{,}5$). Sie befinden sich auf den Chromosomen 1, 7, 10 und 11 (Abb. 6).

## Diskussion

Die Ergebnisse zeigen, dass Stämme entwickelt werden konnten, die sich in ihrer *P.i.*-Resistenz deutlich von den derzeit zugelassenen Sorten unterscheiden. Ein Stamm (12797/9) zeigte gute Ergebnisse auch bei der Speisewertprüfung. Dies verdeutlicht, dass das Einkreuzen von

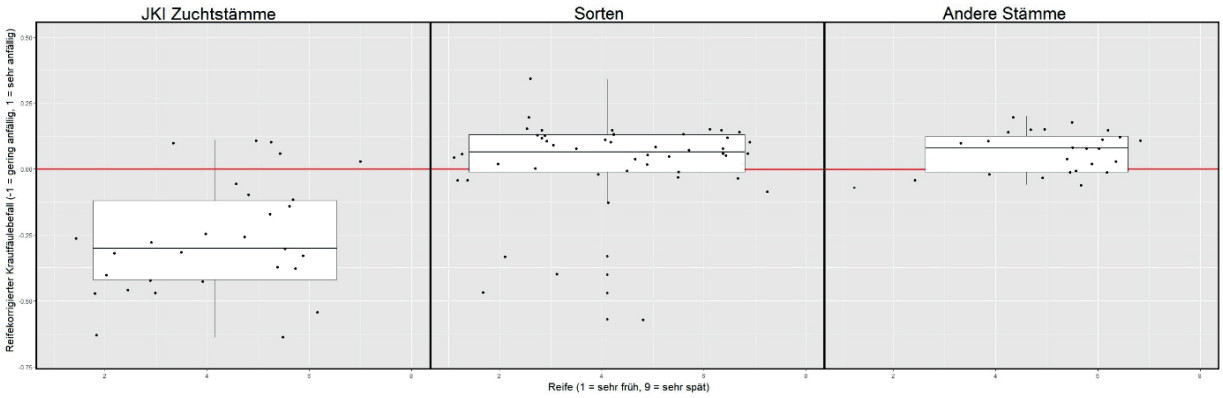


**Abb. 5.** **ΔrAUDPC-Werte und Reifeboniturnoten von Sorten und Zuchtstämmen im Mittel von drei Jahren.** Die Boxplots zeigen jeweils den Median (dicke waagerechte Linie), das obere und untere Quartil (dünne waagerechte Linien) sowie Minimum und Maximum (Ende der Whisker) unter Ausschluss der Ausreißer. In Rot ist die Nulllinie dargestellt.

**Tab. 4.** ***Pi.*-Befall an drei älteren und drei neu entwickelten Zuchtstämmen sowie vier Sorten im dreijährigen Mittel.** Boniturskalen [a)] 1 = kein Befall, 9 = Blattfläche vollständig nekrotisiert und mit Myzel bedeckt, [b)] 1 = kein Befall, 9 = 100 % Zerfall des Knollengewebes, [c)] 1 = kein Befall, 9 = Verbräunung der Scheiben, mit Mycel bedeckt, [d)] 1 = sehr früh, 9 = sehr spät

| Stamm bzw. Sorte | rAUDPC [%] | ΔrAUDPC [Index] | Blatttest [Note[a)]] | Knollentauchtest[Index[b)]] | Scheibentest [Note[c)]] | Reife [Note[d)]] |
|---|---|---|---|---|---|---|
| 12797/9 | 0 | −0,38 | 2,2 | 1,00 | 2,7 | 5,5 |
| 12.1022/3 | 2 | −0,38 | 1,2 | 2,10 | 2,4 | 4,1 |
| 12.1060/2 | 3 | −0,41 | 1,1 | 2,30 | 3,1 | 3,7 |
| GL-03.5129.06 | 3 | −0,24 | 1,4 | 1,00 | 2,1 | 5,3 |
| GL-04.5170.02 | 0 | −0,26 | 1,5 | 3,30 | 4,0 | 6,3 |
| GL-04.5230.06 | 7 | −0,23 | 1,3 | 1,55 | 3,0 | 3,9 |
| Adretta | 63 | 0,32 | 4,5 | 5,61 | 5,8 | 3,6 |
| Jelly | 40 | 0,14 | 3,4 | 5,10 | 7,3 | 6,3 |
| Princess | 54 | 0,26 | 6,0 | 4,10 | 7,6 | 5,6 |
| Sarpo Mira | 2 | −0,23 | 2,3 | 4,15 | 6,5 | 6,8 |
| Grenzdifferenz 5 % | 15 | 0,08 | 1,0 | 0,2 | 0,3 | |

**Tab. 5.** **Korrelation der mittleren Feld- und Laborergebnisse nach Pearson.**

| | Reife | rAUDPC | ΔrAUDPC | Blatttest | Tauchtest |
|---|---|---|---|---|---|
| rAUDPC | −0,70 | | | | |
| ΔrAUDPC | 0,00 | 0,90*** | | | |
| Blatttest | −0,03 | 0,65*** | 0,71*** | | |
| Tauchtest | 0,07 | 0,61*** | 0,57*** | 0,53*** | |
| Scheibentest | −0,05 | 0,55*** | 0,60*** | 0,66*** | 0,58*** |

*** p < 0,001

Sorten zur Verbesserung der agronomischen Merkmale der Pre-breeding-Stämme in den nächsten Jahren eine wichtige Rolle spielt, um diese in einer anschließenden Sortenzüchtung verwenden zu können.

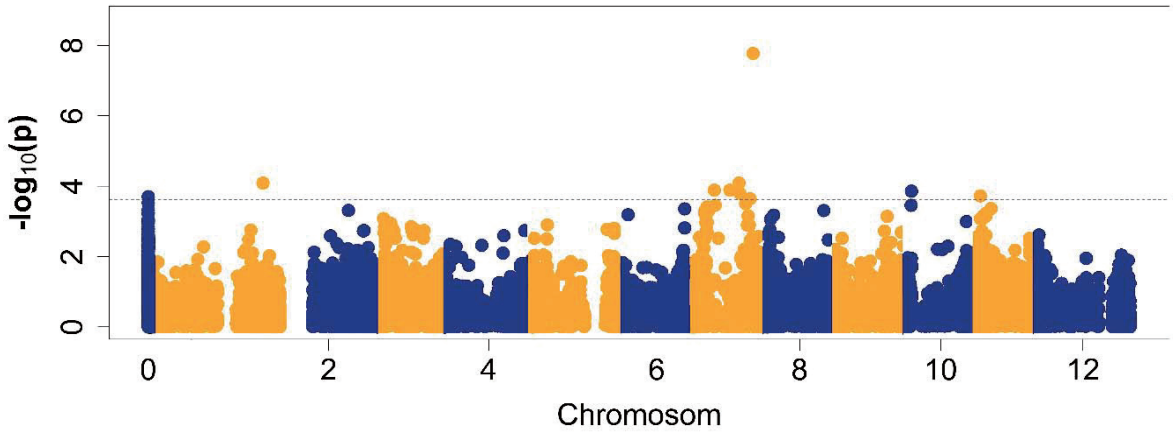


**Abb. 6. Manhattan-Plot (diplo-additive) für das Merkmal ΔrAUDPC.** Das Signifikanzniveau ((-$\log_{10}$(p)> 3,5) wurde durch die Kontrolle der False Discovery Rate von 5 % festgelegt. Die Differenzierung der Chromosomen ist durch die abwechselnde Färbung gegeben.



Da die Ergebnisse der Feld- und Labortests stark miteinander korrelieren, wäre es denkbar den Testumfang für zukünftige Stämme zu reduzieren. Eine Möglichkeit wäre, statt je zwei Tests für Kraut- und Knollenfäule nur noch jeweils einen Test zu verwenden.

Die genomweite Assoziationsstudie zeigt fünf QTL mit kleinen Effekten für das Merkmal *P.i.*-Resistenz der untersuchten Zuchtstämme auf. Diese niedrige Zahl an Resistenzfaktoren wirft die Frage auf, ob es sich bei den QTL um R-Gene handeln könnte. Gegen eine solche Annahme spricht die Pathotypen-Zusammensetzung des in dieser Studie verwendeten Inokulums, welches alle elf bekannten R-Gene aus *S. demissum* überwindet. Die in dieser Studie beobachteten, resistenzwirksamen QTL repräsentieren somit wahrscheinlich anderweitige Resistenzfaktoren. Die durch diese Faktoren bedingte Krautfäuleresistenz der betroffenen Zuchtstämme ist in unseren Feldprüfungen bislang über mindestens vier Jahre wirksam geblieben und dürfte somit einen dauerhaften Resistenztypus darstellen.

Danan et al. (2011) schließen aus ihrer Metaanalyse von 19 unabhängigen Studien zur QTL-Kartierung von *P.i.*-Resistenz, dass resistenzbedingte QTL auf allen zwölf Chromosomen des Kartoffelgenoms vorliegen. In den einzelnen Analysen wurden jeweils, wie auch in dieser Studie, nur vereinzelte QTL nachgewiesen. Daraus lässt sich ableiten, dass die gesamte genetische Diversität der Kartoffel und ihrer kreuzbaren Wildarten sehr viele verschiedenen Resistenzquellen bereithält und es weiterer Forschung bedarf, die Wirksamkeit und Dauerhaftigkeit der betreffenden QTL zu untersuchen und züchterisch zu erschließen.

Mithilfe von Markern, die mit dem Merkmal ΔrAUDPC assoziiert sind, wäre es denkbar, bereits Pflanzen im Sämlingsstadium (F1) auf *P.i*-Resistenz zu selektieren. Da sich die Assoziation in dieser Studie allerdings als schwach erwies, sind weitere Studien angedacht.

## Fazit

Die neuen Stämme bieten sich besonders für den ökologischen Landbau an, da die Bekämpfung von *P.i.* hier nur schwer möglich ist. Aber auch der konventionelle Kartoffelanbau könnte von neuen Sorten profitieren, deren Resistenzniveau durch Einkreuzung der hier beschriebenen Pre-breeding-Stämme verbessert ist. Die hierdurch mögliche Reduzierung der chemischen Pflanzenschutzmaßnahmen wäre in künftigen Versuchen zu thematisieren. Das Pre-breeding-Material kann zudem der Erweiterung des Genpools der europäischen Kulturkartoffel dienen, weil es bislang in der Sortenzüchtung nicht genutzte genetische Diversität aus *Solanum*-Wildarten enthält, die auf konventionellem züchterischem Weg eingekreuzt worden ist. Die zur Verfügung stehenden Zuchtstämme bieten eine Grundlage, in Zukunft Sorten mit verbesserter Resistenz gegen die Kraut- und Knollenfäule bei nicht zu später Abreife und guter Speiseeignung zu entwickeln.

Die in den bisherigen und folgenden Arbeiten generierten Daten zu molekularen Markern sollen in weiteren Analysen auch auf potentielle Zusammenhänge zur Knollenfäule untersucht werden. Überdies werden die beschriebenen sowie weitere Zuchtstämme und Neuzüchtungen neben der *P.i.*-Resistenz auch auf ihre Nährstoffeffizienz untersucht (Projekt EffiKar).

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## Erklärung zu Interessenskonflikten

Die Autoren erklären, dass keine Interessenskonflikte vorliegen.

## Literatur


Batista, G.E.A.P.A., M.C. Monard, 2002: A Study of *K*-Nearest Neighbour as an Imputation Method. HIS **87** (48), 1-10.

Black, W., C. Mastenbroek, W.R. Mills, L.C. Peterson, 1953: A proposal for an international nomenclature of races of *Phytophthora infestans* and of genes controlling immunity in *Solanum demissum* derivatives. Euphytica **2** (3), 173–179, DOI: 10.1007/BF00053724.

Bundessortenamt (Hrsg.), 2019: Beschreibende Sortenliste Kartoffel, **2019**, Hannover, ISSN: 14 30-97 77.

Collins, A., D. Milbourne, L. Ramsay, R. Meyer, C. Chatot-Balandras, P. Oberhagemann, W. De Jong, C. Gebhard, E. Bonnel, R. Waugh, 1999: QTL for field resistance to late blight in potato are strongly correlated with maturity and vigour. Molecular Breeding **5** (5), 387-398.

Colon, L., 1994: Resistance to *Phytophthora infestans* in *Solanum tuberosum* and wild *Solanum* species. Dissertation Agricultural University Wageningen, 1-159.

Danan, S., J.B. Veyrieras, V. Lefebvre, 2011: Construction of a potato consensus map and QTL meta-analysis offer new insights into the genetic architecture of late blight resistance and plant maturity traits. BMC Plant Biology **11** (1), 1–16, DOI: 10.1186/1471-2229-11-16.

Darsow, U., 2008: Vorlaufzüchtung der Kartoffel auf quantitative *Phytophthora*-Resistenz im ILK Groß Lüsewitz in der Ressortforschung des BMELV. Stand der Forschung und Züchtung. Mitteilungen aus dem Julius Kühn-Institut **415**, 1-128.

Fry, W.E., 1978: Quantification of general resistance of potato cultivars and fungicide effects for integrated control of potato late blight. Phytopathology **68** (11), 1650-1655.

Hein, I., P.R. Birch, S. Danan, V. Lefebvre, D.A. Odeny, C. Gebhardt, F. Trognitz, G.J. Bryan, 2009: Progress in mapping and cloning qualitative and quantitative resistance against *Phytophthora infestans* in potato and its wild relatives. Potato Research **52** (3), 215–227, DOI: 10.1007/s11540-009-9129-2.

Holland, J.B., W.E. Nyquist, C.T. Cervantes-Martínez, 2003: Estimating and interpreting heritability for plant breeding: an update. Plant Breeding Reviews **22**, 1-104.

Malcolmson, J.F., 1969: Races of *Phytophthora infestans* occurring in Great Britain. Transactions of the British Mycological Society **53** (3), 417–423, DOI: 10.1016/S0007-1536(69)80099-9.

Malcolmson, J.F., W. Black, 1966: New R genes in *Solanum demissum* Lindl. and their complementary races of *Phytophthora infestans* (Mont.) de Bary. Euphytica **15** (2), 199–203, DOI: 10.1007/BF00022324.

Mayton, H., H. Griffiths, I. Simko, S. Cheng, J. Lorenzen, W. De Jong, W.E. Fry, 2010: Foliar and tuber late blight resistance in a *Solanum tuberosum* breeding population. Plant Breeding **129** (2), 197–201, DOI: 10.1111/j.1439-0523.2009.01671.x.

Rosyara, U.R., W.S. De Jong, D.S. Douches, J.B. Endelman, 2016: Software for genome-wide association studies in autopolyploids and its application to potato. The Plant Genome **9** (2), DOI: 10.3835/plantgenome2015.08.0073.

Stein, N., G. Herren, B. Keller, 2001: A new DNA extraction method for high-throughput marker analysis in a large-genome species such as *Triticum aestivum*. Plant Breeding **120** (4), 354-356.

Truberg, B., T. Hammann, U. Darsow, H.P. Piepho, 2009: Empirischer Vergleich verschiedener Methoden zur Reifekorrektur von Daten zum Befall mit Krautfäule (*Phytophthora infestans* (Mont.) de Bary) in Selektionsexperimenten bei der Kartoffel (*Solanum tuberosum* subsp. *tuberosum*). Journal für Kulturpflanzen – Journal of Cultivated Plants **61** (3), 77-81.

## Anhang

**Tab. S1. Zwischen 2012 und 2018 untersuchte Kartoffelsorten.**

| lfd-Nr. | Sorte | lfd-Nr. | Sorte | lfd-Nr. | Sorte |
|---|---|---|---|---|---|
| 1 | Adretta | 35 | Eurobeta | 69 | Novago |
| 2 | Agila | 36 | Fidelia | 70 | Omega |
| 3 | Agria | 37 | Figaro | 71 | Opal |
| 4 | Allians | 38 | Flamingskost | 72 | Osira |
| 5 | Allora | 39 | Francisca | 73 | Preciosa |
| 6 | Alouette | 40 | Goldmarie | 74 | Princess |
| 7 | Ampera | 41 | Golf | 75 | Quadriga |
| 8 | Andrea | 42 | Grandifolia | 76 | Queen Anne |
| 9 | Annalena | 43 | Hansa | 77 | Ramona |
| 10 | Anuschka | 44 | Heidi | 78 | Red Fantasy |
| 11 | Axona | 45 | Husar | 79 | Regina |
| 12 | Baltic Cream | 46 | Jelly | 80 | Ribera |
| 13 | Barbara | 47 | Juligelb | 81 | Rita |
| 14 | Belana | 48 | Karlena | 82 | Salome |
| 15 | Belinda | 49 | Kifli | 83 | Salute |
| 16 | Bintje | 50 | Kolibri | 84 | Samson |
| 17 | Biogold | 51 | Königsmark | 85 | Sarpo Mira |
| 18 | Bionica | 52 | Kuras | 86 | Sirius |
| 19 | Birgit | 53 | Lady Claire | 87 | Solist |
| 20 | Blaue Sankt Galler | 54 | Laura | 88 | Solo |
| 21 | Blue Danube | 55 | Laurette | 89 | Sonja |
| 22 | Caprice | 56 | Linzer Speise | 90 | Soraya |
| 23 | Cardinia | 57 | Lisa | 91 | Stefanie |
| 24 | Carolus | 58 | Lolita | 92 | Steffi |
| 25 | Cascada | 59 | Margit | 93 | Tacoma |
| 26 | Colomba | 60 | Mariola | 94 | Talent |
| 27 | Connect | 61 | Mariska | 95 | Tessa |
| 28 | Cosma | 62 | Markies | 96 | Toluca |
| 29 | Diplomat | 63 | Marli | 97 | Tomensa |
| 30 | Ditta | 64 | Merlot | 98 | Torenia |
| 31 | Eersteling | 65 | Montana | 99 | Troja |
| 32 | Elfe | 66 | Musica | 100 | Twinner |
| 33 | Escort | 67 | Nicola | 101 | Vitabella |
| 34 | Esprit | 68 | Nordlicht | 102 | Wega |

## 2.4 Genome-wide association study of resistance to late blight based on Julius Kühn Institute pre-breeding potato clones

In Bearbeitung für die Einreichung.

**Genome-wide association study of resistance to late blight based on Julius Kühn Institute pre-breeding potato clones**

Abstract

Late blight remains one of the most devastating diseases in potato cultivation. For this reason, the Julius Kühn Institute has a late blight resistance breeding program since more than 60 years. A field trial was carried out with 200 genotypes including pre-breeding clones and cultivars, which were inoculated with a *Phytophthora infestans* suspension. Relative area under disease progress curves (rAUDPC) were calculated. In addition, detached leaves and tuber slices of 200 genotypes were inoculated with *P. infestans*. Scorings from 1 (no infestation) to 9 (full infestation) were made. Genome-wide association studies (GWAS) were carried out on the traits describing foliage and tuber blight infestation. Significant marker-trait associations for foliage blight were detected on chromosomes 9 and 11. From the 200 genotypes, 121 carried resistance loci either on chromosome 9 or 11, only one genotype carried resistance loci on both chromosome 9 and 11. Foliage blight scorings of the genotypes carrying resistance loci on chromosome 9 or 11 were 1.2 or 1.6, respectively, while scorings of genotypes carrying the susceptible alleles were 4.7 on average. Similar strong reductions in late blight infestation were found in the field trial. Although tuber blight infestation was largely reduced if genotypes carried resistance alleles on one of the two chromosomes, no significant marker-trait associations were identified for tuber blight. The stacking of different resistance alleles in breeding clones is a promising approach to obtain genotypes with durable late blight resistance. Results of the present study can help to develop such clones by marker-assisted selection.

Introduction

Potato cultivation is still characterised by high yield losses from late blight, caused by the oomycete *P. infestans*, which is still the most devastating pathogen in potato cultivation. Yield losses are particularly high in organic farming, where only copper formulations can be used for disease control. Infestation with late blight is manifested on the plant by brown spots on the shoot axis and leaves and a white mycelial layer on the underside of the leaves. Tubers show dark spots and become soft and mushy due to secondary infestation with bacteria (Arora et al. 2014). In addition to agronomic measures, the cultivation of resistant cultivars is one of the most promising ways to prevent blight. Resistance to *P. infestans* can be caused by individual

resistance genes (R genes, monogenic) as well as stacking of different R genes (pyramidization) or quantitative trait loci (QTL, polygenic). In the past, it was shown that monogenic resistances are quickly broken by adaptation of the pathogen (Bradshaw et al. 2006; Fry 2008; Hein et al. 2009). In the mid-20th century, much work was invested in the utilisation of resistance from *Solanum demissum*, in which eleven R genes were identified (Vleeshouwers et al. 2011). Unfortunately, the resistances were quickly broken here as well.

As an alternative to conventional breeding, it is possible to transfer several R genes from wild species at once to commercial cultivars by means of gene technology (cisgenesis). This has already been proven successful several times (Zhu et al. 2012; Haverkort et al. 2016; Ghislain et al. 2019; Stefańczyk et al. 2020) but the disadvantage here is that such plants fall under the EU genetic engineering legislation and therefore cannot be adapted by farmers in member countries. Hence, only breeding of cultivars with pyramided R genes and/or QTL can lead to stable resistances in new cultivars for the European market. At the Julius Kühn Institute (JKI), resistant pre-breeding material has been developed in a long-term breeding program for more than 60 years. At first, crosses were made with resistant accessions of wild species. These were then backcrossed up to seven times with cultivars to develop pre-breeding clones with improved agronomic values. The gene pool at JKI was previously investigated for the presence of various R genes from wild species (Blossei et al. 2021). Interestingly, some highly resistant breeding clones were identified, which carry none of the genes studied. Accordingly, it was hypothesised that QTL effects or other R genes must also have a strong influence on the resistance in this material. In the present article, genome-wide association studies (GWAS) were conducted using pre-breeding clones and cultivars to further investigate resistance in new JKI pre-breeding material.

## Material and Methods

### Plant Material and phenotypic data

The trials were carried out at the JKI's experimental field in Groß Lüsewitz, north-east Germany. For this purpose, 200 genotypes, including 161 breeding clones and 39 cultivars (Supplementary Table 1), were grown over three years in a randomised block design with two replications and ten plants per plot. The trials took place between 2018 and 2021.

At the end of flowering of the cultivar ‘Adretta’, one plant per experimental plot was inoculated with 5 ml of a *P. infestans* suspension of common field isolates, a composition which was

supplemented each year with newly collected pathogen material ($1.2 \times 10^4$ sporangia $ml^{-1}$, Darsow 2008). The infestation was assessed as the percentage of the infested foliage area of each plot, excluding the inoculated plant, every three to four days until an infestation of 100 % was reached, or until the respective clone had matured. Based on these assessments, relative area under disease progress curve (rAUDPC) values were calculated (Fry 1978; Colon 1994). Since late blight resistance is often associated with late maturity, the rAUDPC values were additionally maturity-corrected according to Truberg et al. (2009) and presented as ΔrAUDPC values.

In addition to field testing, detached leaf assays were carried out and tuber slice tests were used to investigate tuber blight resistance.

For the detached leaf assay, five leaves of different plants per plot were taken shortly before inoculation in the field trial and 20 µl drops of the *P. infestans* suspension were applied onto the underside of each leaf in the laboratory. After 24 h, the leaves were turned and incubated for another five days at 16 °C, 95 % relative humidity (RH) and 150 Lux. Scoring was based on the necrotic leaf area and mycelium formation on the underside of the leaf with scores from 1 (no infestation) to 9 (full infestation). The tuber slice test was performed on four tubers per plot. Slices from each tuber were inoculated with 20 µl of low (1,900 sporangia $ml^{-1}$) and high (15,000 sporangia $ml^{-1}$) concentrated *P. infestans* suspensions. After 24 h, the slices were rotated and then incubated for another five days at 16°C, 95 % RH. Scoring was based on mycelium formation, rotting and browning with scores from 1 (no infestation) to 9 (full infestation) for both concentrations. The mean value was used for evaluation.

Pearson's (1948) correlation coefficient between traits was calculated and the heritability of the phenotypic traits was calculated with PLABSTAT from 2011 according to Knapp and Bridges (1987).

DNA Extraction and Genotyping

DNA was extracted from young leaves using the NDeasy Plant Pro Kit from Qiagen and sent to LGC Genomics GmbH. LGC performed genotyping by sequencing (GBS) with 2 x 150 bp (NextSeq 500/550 v2) and ~ 1.5 million reads/sample with the enzyme combination PstI-ApeKI. The reference genome was accession GCA_000226075, strain DM1-3 516 R44 from the Potato Genome Sequencing Consortium (2011). A total of 21,312 single nucleotide polymorphisms (SNPs) were fully covered in 66 % of the samples with a minor allele frequency of 5 %. Of these, further 310 SNPs were removed since they had more than 4 alleles present.

Genome-wide association study

The calculation of the kinship matrix and population structure by principal component analysis as well as the calculation of GWAS were carried out with the R package GWASpoly (Rosyara et al. 2016). For GWAS, the first three principal components were used as cofactors. The genotypes were divided into the groups 'cultivar' and 'pre-breeding clone'. The 1-dom-alt model was used for all traits. The model assumes that the plants carrying only reference alleles are susceptible to late blight. Resistance is inherited by the alternative allele and the full dominance effect is assumed when only one alternative allele is present. Bonferroni correction ($\alpha$ = 0.05/number of SNPs) was used to account for multiple testing and to keep the rate of false positive QTL low. Manhattan plots showing $-\log_{10}$ (p-values) were generated and the explained percentage of phenotypic variance ($R^2$) was calculated with a regression of SNP marker dosage (0 = no alternative allele; 1 = one or more alternative alleles) on the resistance test results.

Results and Discussion

The phenotypic data show that the cultivars with mean values of 5.6 for the detached leaf assay, 0.717 for the rAUDPC values, 0.482 for the ΔrAUDPC values and 5.0 for the tuber slice test were much more susceptible to late blight than the pre-breeding clones with mean values of 2.0 for the detached leaf assay, 0.107 for the rAUDPC values, -0.079 for the ΔrAUDPC values and 2.7 for the tuber slice test (Supplementary Table 1).

Of the 161 clones, 133 showed high late blight resistance with ΔrAUDPC values < 0. The remaining 28 clones were proved to be susceptible with ΔrAUDPC values > 0. Of the 39 cultivars, only ‘Sarpo Mira’, ‘Bionica’ and ‘Toluca’ considered to be resistant according to their ΔrAUDPC values < 0. All three cultivars are known to carry resistance genes. The resistance genes *R3a, R3b, R4, Rpi-Smira1* and *Rpi-Smira2*/*R8* were found to be present in ‘Sarpo Mira’ (Rietman et al. 2012; Tomczyńska et al. 2014; Vossen et al. 2016). ‘Bionica’ carries the resistance genes *R2, R3a, R3b* and *Rpi-blb2*. In ‘Toluca’ the genes *R3a* and *Rpi-blb2* were identified (Haverkort et al. 2009; Haesaert et al. 2015).

The broad-sense heritability for foliage late blight resistance was 0.76 for the rAUDPC values, 0.73 for the ΔrAUDPC values and 0.68 for the detached leaf assay scores. The heritability for tuber blight resistance was 0.67.

Overall, there was a very high correlation between the results of the field test and the detached leaf assay (Table 1). The correlation between the tuber slice test and test for foliage blight was

lower, but still high. Inheritance of tuber blight resistance is potentially independent from foliar blight resistance (Douches et al. 2002; Mayton et al. 2010; Platt & Tai 1998), however, the lower correlation coefficients of the present study do not necessarily support the assumption of an independent inheritance within the present population.

Table 1 Pearson's correlation coefficients between relative area under disease progress curve (rAUDPC), the maturity-corrected ΔrAUDPC, detached leaf assay scores and the tuber slice tests

| | rAUDPC | ΔrAUDPC | Leaf | Slice |
|---|---|---|---|---|
| rAUDPC | 1 | 0.98 | 0.85 | 0.70 |
| drAUDPC | | 1 | 0.86 | 0.67 |
| Leaf | | | 1 | 0.68 |
| Slice | | | | 1 |

GWAS revealed for the detached leaf assay two significant marker-trait associations on chromosome 9 and nine markers significantly associated with late blight resistance on chromosome 11, explaining between 10.8 and 27.8 % of the phenotypic variance (Figure 1a, Supplementary Table 2). For ΔrAUDPC, there was one significant marker on chromosome 9 and 14 markers on chromosome 11 explaining between 9.3 and 19.8 % of phenotypic variance (Figure 1b, Supplementary Table 2). The same marker on chromosome 9 and 15 markers on chromosome 11 were significantly associated with rAUDPC and explained between 8.8 and 20.8 % of the phenotypic variance (Figure 1c, Supplementary Table 2). Among all marker-trait associations, one marker on chromosome 9 and nine on chromosome 11 turned out to be significant in all three tests. No significant marker-trait associations were detected in the tuber slice test (Figure 1d).

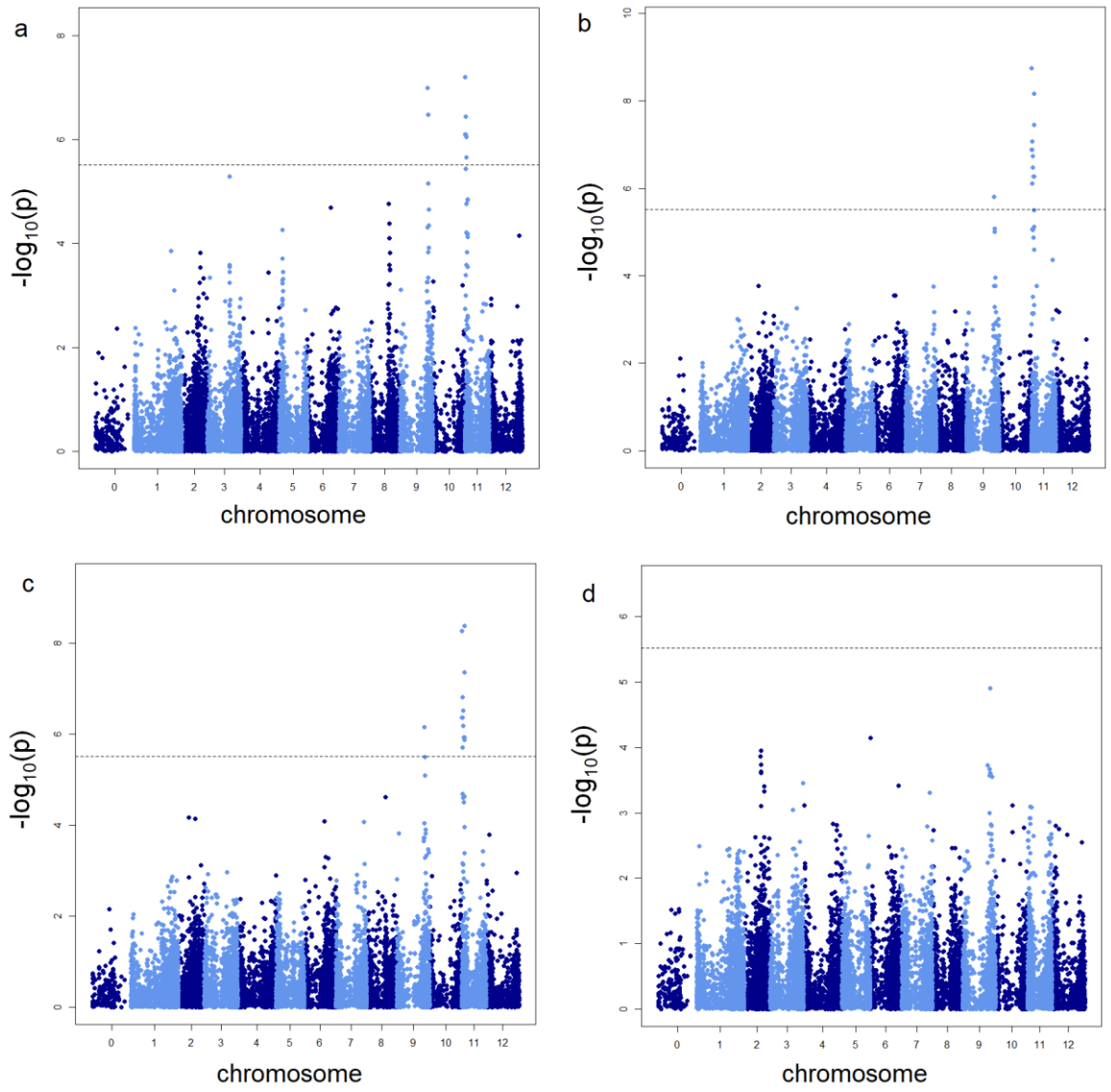


Figure 1 Manhattan plots for the detached leaf assay (a), ΔrAUDPC (b), rAUDPC (c) and tuber slice test (d).

Results show that 78 genotypes (38 cultivars and 40 clones) did not carry an alternative allele on the loci with highest -$\log_{10}$(p) values for the detached leaf assay and ΔrAUDPC on either chromosome 9 or 11. Of these 40 clones, 26 showed rAUDPC values >0 (Supplementary Table 1). On the marker locus at 51,556,194 bp on chromosome 9, 68 pre-breeding clones carried at least one alternative allele putatively associated with late blight resistance. On the locus at 159,849 bp on chromosome 11, 54 clones and the cultivar 'Sarpo Mira' carried at least one alternative allele. There was one clone that carried alternative alleles on both chromosomes. Overall, the genotypes that carried at least one alternative allele were found to be clearly more resistant than those without alternative alleles (Figure 2).

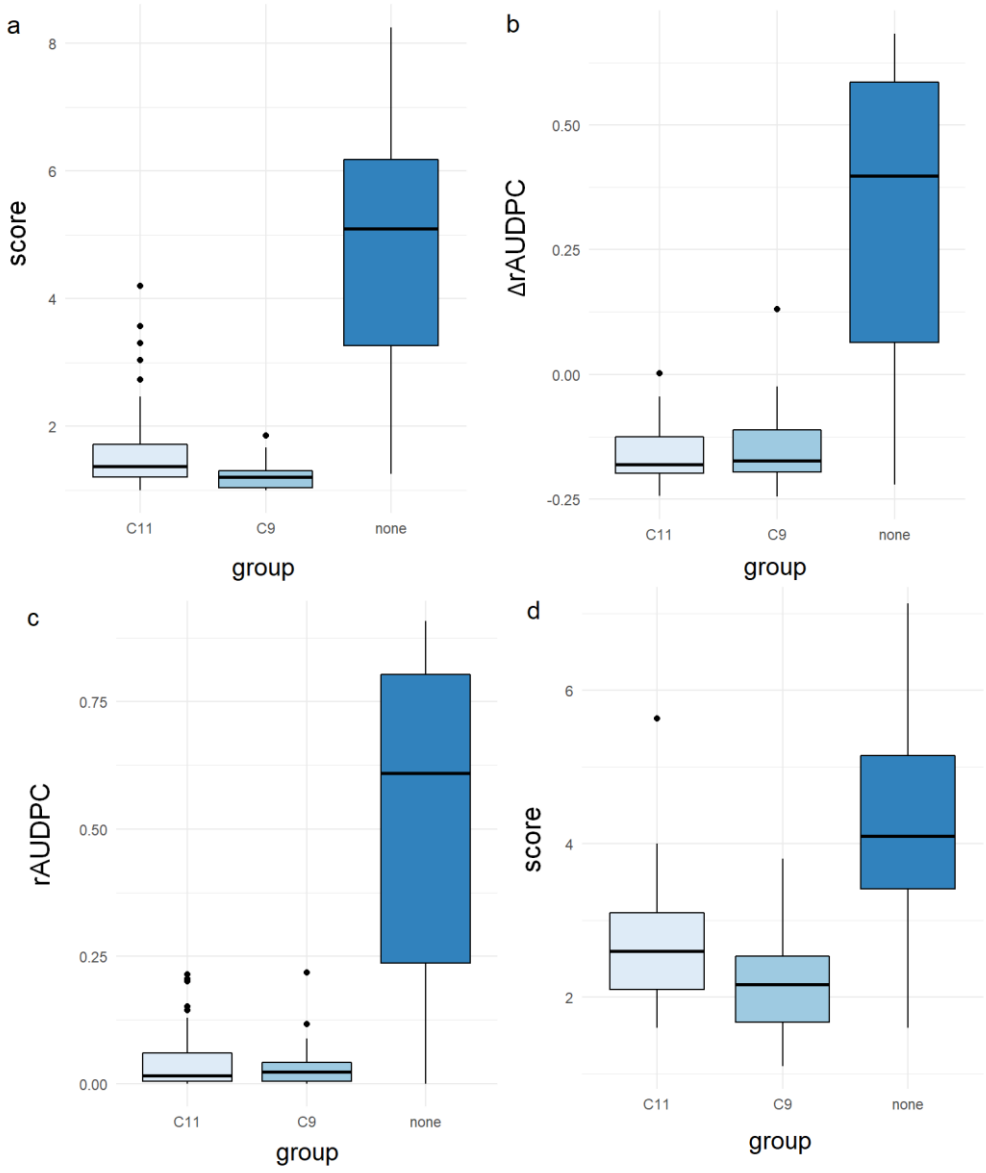


Figure 2 Boxplots for the scores of the detached leaf assay (a), ΔrAUDPC values (b), rAUDPC values (c) and the scores of the tuber slice test (d) divided into the groups carrying at least one alternative allele on chromosomes 11 (C11) and 9 (C9) or carrying no alternative allele.

There is no known resistant genes in the region of the markers significantly associated to late blight resistance on chromosome 9. The closest resistance gene is a nucleotide-binding site leucine-rich repeat (NBS-LRR) at 56.9 Mb (PGSC0003DMG400017146). The gene closest to the SNP at 51.6 Mb on chromosome 9 is an *Oxidoreductase* (PGSC0003DMG400016854), which is 16 kb apart from the SNP. The second significant SNP at 52.5 Mb is located within an *Oligonucleotide transporter* family gene (PGSC0003DMG400011396). According to the *S. tuberosum* reference sequence 3.0 (plants.ensemble.org), five NBS-LRR genes map in the region of significant marker-trait associations on chromosome 11 (PGSC0003DMG400013308, PGSC0003DMG401015682, PGSC0003DMG400046545, PGSC0003DMG400044423,

PGSC0003DMG400027325). The distance between the genes and the nearest significant SNP ranges between 75 and 642 kb. Linkage disequilibrium (LD) between all markers significantly associated with late blight resistance on chromosome 11 was considerably high (Figure 3). The region carrying five NBS-LLR genes and the 15 SNPs spans a distance of 4.58 Mb and harbours more than 400 additional SNPs. Vos et al. (2017) found large haploblocks with reduced LD decay spanning several Mb for introgressed regions. Probably the marker-trait association hotspot on chromosome 11 is such a region introgressed from wild potato in order to obtain late blight resistance.

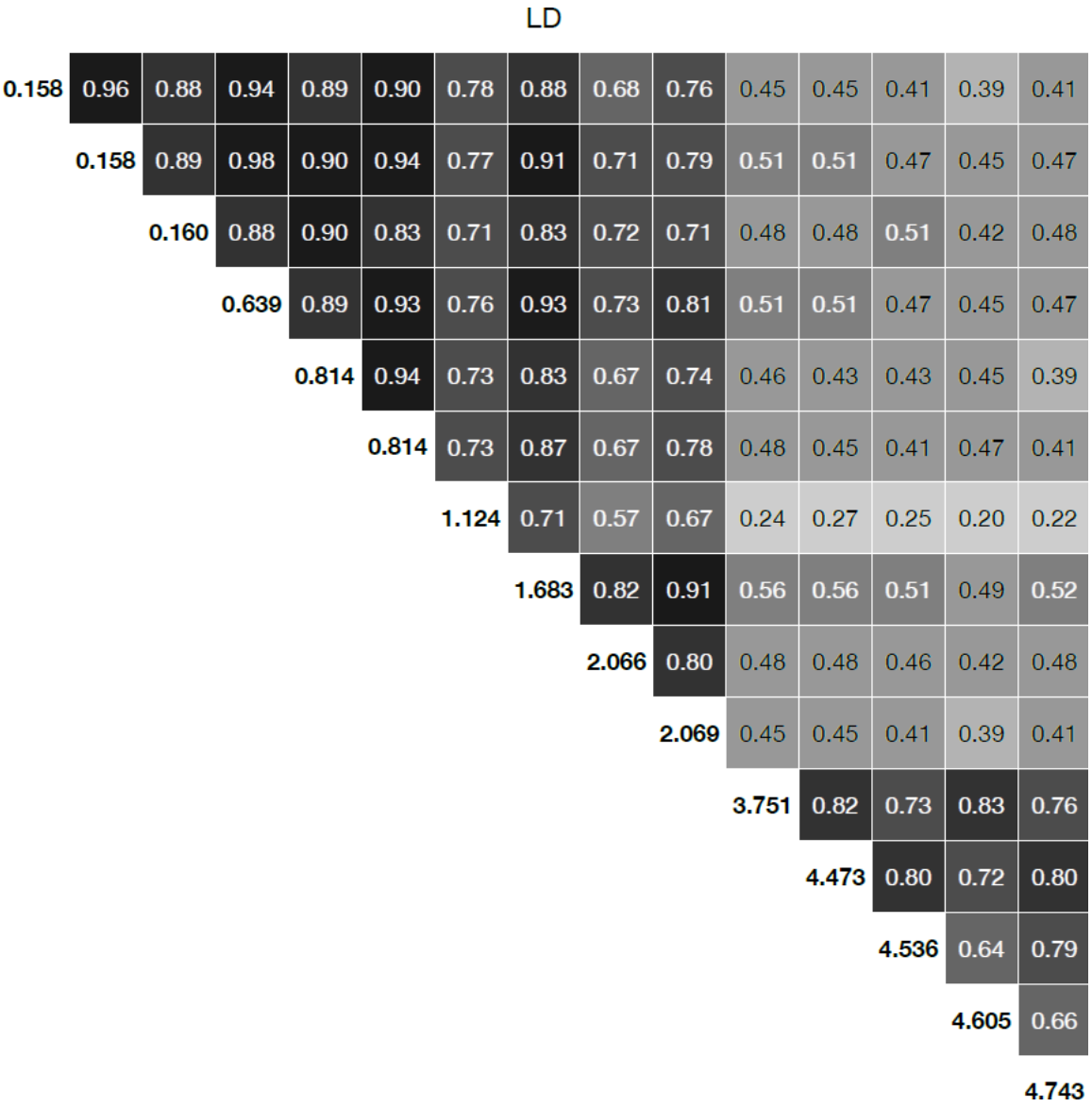


Figure 3 Linkage disequilibrium (LD, $r^2$) of the 15 significant marker-trait associations on chromosome 11.

Besides that some R genes and QTL against *P. infestans* from wild species have already been detected on chromosomes 9 and 11 in previous studies (Table 2 and 3). The marker-trait

association on chromosome 9 found in this work is at the end of the chromosome, so the R genes *Rpi-moc1*, *Rpi-vnt1*, *R8/Rpi-Smira2*, *R9a* and *Ph-3* located there could be related to the QTL. The genes *R8* and *R9a* are the most probable, since many crossings with *S. demissum* were done at the JKI in the 1950s.

It is known that most of the R genes from *S. demissum* are located at the end of chromosome 11 (Bakker et al. 2011), so that they are not suitable for the marker-trait association detected here. Besides *S. demissum*, also *S. phureja* was crossed in the gene pool, so that the marker-trait association found here may originate from *S. phureja*. The R gene *Rpi-Smira1* from 'Sarpo Mira', which was also used for many crosses, is also located on chromosome 11, but close to the gene *R3a* from *S. demissum* (Rietman et al. 2012), so this is rather unlikely. Nevertheless, the alternative allele on chromosome 11 was also detected in 'Sarpo Mira'.

Table 2 R genes and QTL against late blight on chromosome 9

| R gene/QTL | Species | Reference |
|---|---|---|
| *R9a, R8/Rpi-Smira2* | *S. demissum, S. tuberosum* cv. 'Sarpo Mira' | Jo et al. 2011 and 2015; Rietman et al. 2012 |
| *Rpi-edn2* | *S. edinense* | Verzaux, 2010 |
| *Rpi-moc1, Rpi-mcq1* | *S. mochiquense* | Smilde et al. 2005; Jones et a. 2009 |
| *Rpi-nrs1* | *S. neorossii* | Jones et a. 2009 |
| *Rpi-oka1, Rpi-oka2, Rpi-oka3* | *S. okadae* | Jones et a. 2009 |
| *Rpi-phu1* | *S. phureja* | Sliwka et al. 2006 |
| *Rpi-vnt1.1, Rpi-vnt1.2, Rpi-vnt1.3* | *S. venturii* | Foster et al. 2009 |
| *Rpi-ver1* | *S. verrucosum* | Chen et al. 2018 |
| *Ph-3* | *S. pimpinellifolium* | Zhang et al. 2014 |
| QTL | *S. chacoense* | Chakrabarti et al. 2014 |
| QTL | *S. microdontum* | Lin et al. 2020 |
| QTL | *S. vernei* | Sørensen et al. 2006 |

Table 3 R genes and QTL against late blight on chromosome 11

| R gene/QTL | Species | Reference |
|---|---|---|
| *Rpi-avl1* | *S. avilesii* | Verzaux et al. 2011 |
| *Rpi-cap1* | *S. capsicibaccatum* | Jacobs et al. 2010 |
| *Rpi-qum1* | *S. circaeifolium spp. quimense* | Verzaux, 2010 |
| *R3a, R3b, R5, R6, R7, R9, R10, R11* | *S. demissum* | El-Kharbotly et al. 1994; Huang, 2005 |
| *Rpi-edn3* | *S. edinense* | Verzaux, 2010 |
| *Rpi-pur1* | *S. piruae* | Rietman, 2011 |
| *Rpi-sto2* | *S. stoloniferum* | Champouret, 2010 |
| *Rpi-Smira1* | *S. tuberosum* cv. *Sarpo Mira* | Rietman et al. 2012 |
| *Rpi-vnt2* | *S. venturii* | Rietman 2011 |
| QTL | *S. berthaultii* | Ewing et al. 2000 |
| QTL | *S. pampasense* | Meade et al. 2020 |
| QTL | *S. paucissectum* | Villamon et al. 2005 |
| QTL | *S. phureja* | Ghislain et al. 2001 |
| QTL | *S. stenotomum* | Costanzo et al. 2005 |

The genome-wide association study conducted here on 200 genotypes revealed two significant marker-trait association on chromosome 9 explaining more than 20 % of the phenotypic variance and, in total, 15 significant markers on chromosome 11, each explaining more than 8 % of the phenotypic variance for foliage blight resistance. There are several NBS-LRR genes in the region of the 14 markers on chromosome 11. In addition, the well-known R genes *R8* and *R9a* on chromosome 9 are on the same arm as the significant markers, but with around 8 Mb still too far away to be the cause of the marker-trait associations (Jo et al. 2011 and 2015; Jiang et al. 2018). Lindqvist-Kreuze et al. (2014) also found a QTL in this region that is only 0.28 Mb away from the marker-trait association on chromosome 9 detected in this study. For the

future, it would be important to sequence these genes in resistant and susceptible genotypes and to establish gene expression patterns of leaves from potatoes infested with *P. infestation*.

## References


Arora, R. K., Sharma, S., & Singh, B. P. (2014). Late blight disease of potato and its management. *Potato Journal, 41*(1), 16-40.

Bakker, E., Borm, T., Prins, P., van der Vossen, E., Uenk, G., Arens, M., Boer, de J., Eck, van H., Muskens, M., Vossen, J., Linden, van der G., Ham, van R., Klein-Lankhorst, R., Visser, R., Smant, G., Bakker, J., & Goverse, A. (2011). A genome-wide genetic map of NB-LRR disease resistance loci in potato. *Theoretical and Applied Genetics, 123*(3), 493-508. https://doi.org/10.1007/s00122-011-1602-z

Bradshaw, J. E., Bryan, G. J., Lees, A. K., McLean, K., & Solomon-Blackburn, R. M. (2006). Mapping the *R10* and *R11* genes for resistance to late blight (*Phytophthora infestans*) present in the potato (*Solanum tuberosum*) R-gene differentials of Black. *Theoretical and Applied Genetics*, *112*(4), 744-751. https://doi.org/10.1007/s00122-005-0179-9

Blossei, J., Uptmoor, R., Thieme, R., Nachtigall, M., & Hammann, T. (2021). Insights into the genetic basis of the pre-breeding potato clones developed at the Julius Kühn Institute for high and durable late blight resistance. *Plant Genetic Resources, 19*(5), 461-464. https://doi.org/10.1017/S1479262121000447

Chakrabarti, S. K., Singh, B. P., Thakur, G., Tiwari, J. K., Kaushik, S. K., Sharma, S., & Bhardwaj, V. (2014). QTL analysis of late blight resistance in a diploid potato family of *Solanum spegazzinii* x *S. chacoense*. *Potato Research, 57*(1), 1–11. https://doi.org/10.1007/s11540-014-9249-1

Champouret, N. (2010). Functional genomics of *Phytophthora infestans* effectors and *Solanum* resistance genes. Doctoral dissertation. Wageningen University.

Chen, X., Lewandowska, D., Armstrong, M. R., Baker, K., Lim, T. Y., Bayer, M., Harrower, B., McLean, K., Jupe, F., Witek, K., Lees, A. K., Jones, J. D., Bryan, G. L., & Hein, I. (2018). Identification and rapid mapping of a gene conferring broad-spectrum late blight resistance in the diploid potato species *Solanum verrucosum* through DNA capture technologies. *Theoretical and Applied Genetics, 131*(6), 1287–1297. https://doi.org/10.1007/s00122-018-3078-6

Colon, L. (1994). Resistance to *Phytophthora infestans* in *Solanum tuberosum* and wild *Solanum* species. Wageningen University and Research.

Costanzo, S., Simko, I., Christ, B. J., & Haynes, K. G. (2005). QTL analysis of late blight resistance in a diploid potato family of *Solanum phureja* x *S. Stenotomum*. *Theoretical and Applied Genetics, 111*(3), 609–617. https://doi.org/10.1007/s00122-005-2053-1

Darsow, U. (2008). Pre-breeding for quantitative resistance of potato to late blight at the Institute of Agricultural Crops Gross Lüsewitz in the departmental research of BMELV-state of research and breeding. Mitteilungen aus dem Julius Kühn-Institut, 415.

Douches, D. S., Kirk, W. W., Bertram, M. A., Coombs, J. J., & Niemira, B. A. (2002). Foliar and tuber assessment of late blight (*Phytophthora infestans* (Mont.) de Bary) reaction in cultivated potato (*Solanum tuberosum* L.). *Potato Research*, *45*(2), 215-224. https://doi.org/10.1007/BF02736116

El-Kharbotly, A., Leonards-Schippers, C., Huigen, D. J., Jacobsen, E., Pereira, A., Stiekema, W. J., Salamini, F., & Gebhardt, C. (1994). Segregation analysis and RFLP mapping of the *R1* and *R3* alleles conferring race-specific resistance to *Phytophthora infestans* in progeny of dihaploid potato parents. *MGG Molecular & General Genetics, 242*(6), 749–754. https://doi.org/10.1007/BF00283432

Ewing, E. E., Šimko, I., Smart, C. D., Bonierbale, M. W., Mizubuti, E. S. G., May, G. D., & Fry, W. E. (2000). Genetic mapping from field tests of qualitative and quantitative resistance to *Phytophthora infestans* in a population derived from *Solanum tuberosum* and *Solanum berthaultii*. *Molecular Breeding, 6*(1), 25–36. https://doi.org/10.1023/A:1009648408198

Foster, S. J., Park, T.-H., Pel, M., Brigneti, G., ´Sliwka, J., Jagger, L., van der Vossen, E., & Jones, J. D. G. (2009). *Rpi-vnt1.1*, a tm-22 homolog from *Solanum venturii*, confers resistance to potato late blight. *Molecular Plant-Microbe Interactions, 22*(5), 589–600. https://doi.org/10.1094/MPMI-22-5-0589

Fry, W. (2008). *Phytophthora infestans*: the plant (and R gene) destroyer. *Molecular plant pathology*, *9*(3), 385-402. https://doi.org/10.1111/j.1364-3703.2007.00465.x

Fry, W. E. (1978). Quantification of general resistance of potato cultivars and fungicide effects for integrated control of potato late blight. *Phytopathology 68*(11), 1650-1655.

Ghislain, M., Byarugaba, A. A., Magembe, E., Njoroge, A., Rivera, C., Román, M. L., Tovar, J. C., Gamboa S., Forbes G. A., Kreuze, J. F., Barekye, A., & Kiggundu, A. (2019). Stacking three late blight resistance genes from wild species directly into African highland potato varieties confers complete field resistance to local blight races. *Plant Biotechnology Journal, 17*(6), 1119-1129. https://doi.org/10.1111/pbi.13042

Ghislain, M., Trognitz, B., Del Herrera, M. R., Solis, J., Casallo, G., Vásquez, C., Hurtado, O., Castillo, R., Portal, R., & Orrillo, M. (2001). Genetic loci associated with field resistance to late blight in offspring of *Solanum phureja* and *S. tuberosum* grown under short-day conditions. *Theoretical and Applied Genetics, 103*(2), 433–442. https://doi.org/10.1007/s00122-001-0545-1

Haesaert, G., Vossen, J. H., Custers, R., De Loose, M., Haverkort, A., Heremans, B., Hutton, B., Kessel, G., Landschoot, S., Droogenbroeck, B. van, Visser, R. G. F., & Gheysen, G. (2015). Transformation of the potato variety Desiree with single or multiple resistance genes increases resistance to late blight under field conditions. *Crop protection, 77*, 163-175. https://doi.org/10.1016/j.cropro.2015.07.018

Haverkort, A. J., Boonekamp, P. M., Hutten, R., Jacobsen, E., Lotz, L. A. P., Kessel, G. J. T., Vossen, J. H., & Visser, R. G. F. (2016). Durable late blight resistance in potato through dynamic varieties obtained by cisgenesis: scientific and societal advances in the DuRPh project. *Potato Research, 59*(1), 35-66. https://doi.org/10.1007/s11540-015-9312-6

Haverkort, A. J., Struik, P. C., Visser, R. G. F., & Jacobsen, E. J. P. R. (2009). Applied biotechnology to combat late blight in potato caused by *Phytophthora infestans*. *Potato Research, 52*(3), 249-264. https://doi.org/10.1007/s11540-009-9136-3

Hein, I., Birch, P. R., Danan, S., Lefebvre, V., Achieng Odeny, D., Gebhardt, C., Trognitz, F., & Bryan, G. J. (2009). Progress in mapping and cloning qualitative and quantitative resistance against *Phytophthora infestans* in potato and its wild relatives. *Potato Research, 52*(3), 215-227. https://doi.org/10.1007/s11540-009-9129-2

Huang, S. (2005). Discovery and characterization of the major late blight resistance complex in potato. Doctoral dissertation. Wageningen University.

Jacobs, M. M. J., Vosman, B., Vleeshouwers, V. G. A. A., Visser, R. G. F., Henken, B., & van den Berg, R. G. (2010). A novel approach to locate *Phytophthora infestans* resistance genes on the potato genetic map. *Theoretical and Applied Genetics, 120*(4), 785–796. https://doi.org/10.1007/s00122-009-1199-7

Jiang, R., Li, J., Tian, Z., Du, J., Armstrong, M., Baker, K., Lim, J. T.-Y., Vossen, J. H., He, Portal, L., Zhou, J., Bonierbale, M., Hein, I., Lindqvist-Kreuze, H., & Xie, C. (2018). Potato late blight field resistance from QTL dPI09c is conferred by the NB-LRR gene R8. *Journal of experimental botany, 69*(7), 1545-1555. https://doi.org/10.1093/jxb/ery021

Jo, K.-R., Arens, M., Kim, T.-J., Jongsma, M. A., Visser, R. G. F., Jacobsen, E., & Vossen, J. H. (2011). Mapping of the *S. demissum* late blight resistance gene *R8* to a new locus on chromosome IX. *Theoretical and Applied Genetics, 123*(8), 1331–1340. https://doi.org/10.1007/s00122-011-1670-0

Jo, K.-R., Visser, R. G., Jacobsen, E., & Vossen, J. H. (2015). Characterisation of the late blight resistance in potato differential MaR9 reveals a qualitative resistance gene, *R9a*, residing in a cluster of Tm-22 homologs on chromosome IX. *Theoretical and Applied Genetics, 128*(5), 931–941. https://doi.org/10.1007/s00122-015-2480-6

Jones, J., Foster, S., Chu, Z., Park, T.-H., van der Vossen, E., Pel, M., & Visser, R. (2009). Late blight resistance genes and methods. International application published under the patent cooperation treaty (PCT).

Knapp, S. J., & Bridges, W. C. (1987). Confidence interval estimators for heritability for several mating and experiment designs. *Theoretical and Applied Genetics, 73*(5), 759-763. https://doi.org/10.1007/BF00260787

Lin, X., Armstrong, M., Baker, K., Wouters, D., Visser, R. G. F., Wolters, P. J., Hein, I., & Vleeshouwers, V. G. A. A. (2020). RLP/K enrichment sequencing; a novel method to identify receptor-like protein (RLP) and receptor-like kinase (RLK) genes. *New Phytologist, 227*(4), 1264–1276. https://doi.org/10.1111/nph.16608

Lindqvist-Kreuze, H., Gastelo, M., Perez, W., Forbes, G. A., de Koeyer, D., & Bonierbale, M. (2014). Phenotypic stability and genome-wide association study of late blight resistance in potato genotypes adapted to the tropical highlands. *Phytopathology, 104*(6), 624-633. https://doi.org/10.1094/PHYTO-10-13-0270-R

Mayton, H., Griffiths, H., Simko, I., Cheng, S., Lorenzen, J., De Jong, W., & Fry, W. E. (2010). Foliar and tuber late blight resistance in a *Solanum tuberosum* breeding population. *Plant breeding, 129*(2), 197-201. https://doi.org/10.1111/j.1439-0523.2009.01671.x

Meade, F., Hutten, R., Wagener, S., Prigge, V., Dalton, E., Kirk, H. G., Griffin, D., & Milbourne, D. (2020). Detection of novel QTLs for late blight resistance derived from the wild potato species *Solanum microdontum* and *Solanum pampasense*. *Genes, 11*(7), 1–18. https://doi.org/10.3390/genes11070732

Pearson, K. (1948). Early Statistical Papers. Cambridge, England, University Press.

Platt, H. W., & Tai, G. (1998). Relationship between resistance to late blight in potato foliage and tubers of cultivars and breeding selections with different resistance levels. *American Journal of Potato Research, 75*(4), 173-178. https://doi.org/10.1007/BF02853569

Rietman, H. (2011). Putting the *Phytophthora infestans* genome sequence at work; multiple novel avirulence and potato resistance gene candidates revealed. Doctoral dissertation. Wageningen University.

Rietman, H., Bijsterbosch, G., Cano, L. M., Lee, H. R., Vossen, J. H., Jacobsen, E., Visser, R. G. F., Kamoun, S., & Vleeshouwers, V. G. A. A. (2012). Qualitative and quantitative late blight resistance in the potato cultivar Sarpo Mira is determined by the perception of five distinct RXLR effectors. *Molecular Plant-Microbe Interactions, 25*(7), 910–919. https://doi.org/10.1094/MPMI-01-12-0010-R

Rosyara, U. R., De Jong, W. S., Douches, D. S., & Endelman, J. B. (2016). Software for genome-wide association studies in autopolyploids and its application to potato. *The Plant Genome, 9*(2), 1-10. https://doi.org/10.3835/plantgenome2015.08.0073

Sliwka, J., Jakuczun, H., Lebecka, R., Marczewski, W., Gebhardt, C., & Zimnoch-Guzowska, E. (2006). The novel, major locus *Rpi-phu1* for late blight resistance maps to potato chromosome IX and is not correlated with long vegetation period. *Theoretical and Applied Genetics, 113*(4), 685–695. https://doi.org/10.1007/s00122-006-0336-

Smilde, W. D., Brigneti, G., Jagger, L., Perkins, S., & Jones, J. D. G. (2005). *Solanum mochiquense* chromosome IX carries a novel late blight resistance gene *Rpi-moc1*. *Theoretical and Applied Genetics, 110*(2), 252–258. https://doi.org/10.1007/s00122-004-1820-8

Sørensen, K. K., Madsen, M. H., Kirk, H. G., Madsen, D. K., & Torp, A. M. (2006). Linkage and quantitative trait locus mapping of foliage late blight resistance in the wild species *Solanum vernei*. *Plant Breeding, 125*(3), 268–276. https://doi.org/10.1111/j.1439-0523.2006.01219.x

Stefańczyk, E., Plich, J., Janiszewska, M., Smyda-Dajmund, P., Sobkowiak, S., & Śliwka, J. (2020). Marker-assisted pyramiding of potato late blight resistance genes *Rpi-rzc1* and *Rpi-phu1* on di-and tetraploid levels. *Molecular Breeding, 40*(9), 1-12. https://doi.org/10.1007/s11032-020-01169-x

The Potato Genome Sequencing Consortium (2011). Genome sequence and analysis of the tuber crop potato. *Nature 475*, 189–195. https://doi.org/10.1038/nature10158

Tomczyńska, I., Stefańczyk, E., Chmielarz, M., Karasiewicz, B., Kamiński, P., Jones, J. D., Lees, A. K., & Śliwka, J. (2014). A locus conferring effective late blight resistance in potato cultivar Sárpo Mira maps to chromosome XI. *Theoretical and applied genetics, 127*(3), 647-657. https://doi.org/10.1007/s00122-013-2248-9

Truberg, B., Hammann, T., Darsow, U., Piepho, H.P. (2009). Empirischer Vergleich verschiedener Methoden zur Reifekorrektur von Daten zum Befall mit Krautfaule (*Phytophthora infestans* (Mont.) de Bary) in Selektionsexperimenten bei der Kartoffel (*Solanum tuberosum* subsp. *tuberosum*). *Journal für Kulturpflanzen-Journal of Cultivated Plants, 61*, 77-81.

Verzaux, E. C. (2010). Resistance and susceptibility to late blight in *Solanum*: Gene mapping, cloning and stacking. Doctoral dissertation. Wageningen University.

Verzaux, E., Budding, D., de Vetten, N., Niks, R. E., Vleeshouwers, V. G. A. A., van der Vossen, E. A. G., Jacobsen, E., & Visser, R. G. F. (2011). High resolution mapping of a novel late blight resistance gene *Rpi-avl1*, from the wild Bolivian species *Solanum avilesii*. *American Journal of Potato Research, 88*(6), 511–519. https://doi.org/10.1007/s12230-011-9218-z

Villamon, F. G., Spooner, D. M., Orrillo, M., Mihovilovich, E., Pérez, W., & Bonierbale, M. (2005). Late blight resistance linkages in a novel cross of the wild potato species *Solanum paucissectum* (series Piurana). *Theoretical and Applied Genetics, 111*(6), 1201–1214. https://doi.org/10.1007/s00122-005-0053-9

Vleeshouwers, V. G., Raffaele, S., Vossen, J. H., Champouret, N., Oliva, R., Segretin, M. E., Rietman H., Cano, L. M., Lokossou, A., Kessel, G., Pel, M. A., & Kamoun, S. (2011). Understanding and exploiting late blight resistance in the age of effectors. *Annual review of phytopathology, 49*, 507-531. https://doi.org/10.1146/annurev-phyto-072910-095326

Vos, P. G., Paulo, M. J., Voorrips, R. E., Visser, R. G., van Eck, H. J., & van Eeuwijk, F. A. (2017). Evaluation of LD decay and various LD-decay estimators in simulated and SNP-array data of tetraploid potato. *Theoretical and Applied Genetics, 130*(1), 123-135. https://doi.org/10.1007/s00122-016-2798-8

Vossen, J. H., van Arkel, G., Bergervoet, M., Jo, K. R., Jacobsen, E., & Visser, R. G. (2016). The *Solanum demissum R8* late blight resistance gene is an Sw-5 homologue that has been deployed worldwide in late blight resistant varieties. *Theoretical and Applied Genetics, 129*(9), 1785-1796. https://doi.org/10.1007/s00122-016-2740-0

Zhang C, Liu L, Wang X, et al. 2014. The Ph-3 gene from *Solanum pimpinellifolium* encodes CC-NBS-LRR protein conferring resistance to *Phytophthora infestans*. *Theoretical and Applied Genetics 127*(6), 1353–1364. https://doi.org/10.1007/s00122-014-2303-1

Zhu, S., Li, Y., Vossen, J. H., Visser, R. G., & Jacobsen, E. (2012). Functional stacking of three resistance genes against *Phytophthora infestans* in potato. *Transgenic research, 21*(1), 89-99. https://doi.org/10.1007/s11248-011-9510-1

Supplementary Table 1 Phenotypic data of the pre-breeding clones and cultivars used for the genome-wide association study

| Clone/Cultivar | rAUDPC | ΔrAUDPC | Score detached leaf assay | Score tuber slice test |
|---|---|---|---|---|
| 131031/01 | 0.002 | -0.063 | 1.0 | 2.4 |
| 14.1022/07 | 0.004 | -0.084 | 1.3 | 2.4 |
| 14.1077/02 | 0.012 | -0.076 | 3.6 | 3.5 |
| 14.1081/01 | 0.000 | -0.221 | 1.2 | 2.5 |
| 14442/04 | 0.000 | -0.112 | 1.0 | 1.9 |
| 14442/06 | 0.017 | -0.096 | 1.0 | 2.7 |
| LfL_LL17_15176/01HC{Yes} | 0.000 | -0.124 | 1.5 | 3.6 |
| LfL_LL17_15176/05 | 0.000 | -0.112 | 1.8 | 2.8 |
| LfL_LL17_15207/01 | 0.000 | -0.136 | 1.4 | 2.6 |
| LL_15703/06 | 0.000 | -0.112 | 1.0 | 2.4 |
| LfL_ND17_16186/02 | 0.000 | -0.107 | 1.1 | 2.8 |
| LfL_ND17_16186/03 | 0.000 | -0.124 | 1.0 | 1.4 |
| LfL_ND17_16282/01 | 0.009 | -0.127 | 2.1 | 1.8 |
| LfL_FS17_16588/03 | 0.004 | -0.132 | 1.3 | 3.3 |
| LfL_LL17_16650/16 | 0.000 | -0.159 | 1.2 | 1.6 |
| LfL_LL17_16742/01 | 0.005 | -0.178 | 1.1 | 2.5 |
| GL_LL17_16.1056/02HC | 0.583 | 0.472 | 5.1 | 2.7 |
| GL_LL17_16.1061/01HC | 0.011 | -0.089 | 2.1 | 2.9 |
| GL_LL17_16.1089/01 | 0.237 | 0.172 | 3.6 | 3.7 |
| 12741/09 | 0.417 | 0.305 | 2.2 | 4.5 |
| 13414/05 | 0.004 | -0.084 | 1.0 | 2.0 |
| 13463/01 | 0.004 | -0.108 | 1.0 | 2.4 |
| 131051/03 | 0.017 | -0.059 | 3.2 | 3.3 |
| 14389Yes3/01 | 0.023 | -0.066 | 4.9 | 3.9 |
| 14508/08 | 0.000 | -0.088 | 1.0 | 1.9 |
| 14509/03 | 0.781 | 0.657 | 6.9 | 4.5 |
| 14547/04 | 0.196 | 0.037 | 6.1 | 3.7 |
| ND_15026-/01 | 0.000 | -0.124 | 1.0 | 2.2 |
| LL_15556blb3Y/01 | 0.029 | -0.036 | 3.2 | 2.9 |
| LfL_ND17_16177/02{Gro}{HC}{Yes} | 0.000 | -0.064 | 1.0 | 2.7 |
| LfL_ND17_16186/01 | 0.008 | -0.080 | 1.2 | 2.3 |
| LfL_Si17_16190-02 | 0.004 | -0.108 | 1.0 | 2.0 |
| LfL_Si17_16191-01 | 0.00 | -0.088 | 1.0 | 1.8 |
| LfL_Si17_16260-13 | 0.755 | 0.667 | 7.1 | 4.1 |
| LfL_ND17_16282/07 | 0.000 | -0.112 | 1.2 | 2.4 |
| LfL_Si17_16363-01 | 0.000 | -0.159 | 1.0 | 1.9 |
| LfL_Si17_16370-02 | 0.050 | -0.109 | 2.4 | 2.7 |
| LfL_ND17_16376/05 | 0.005 | -0.083 | 2.5 | 2.1 |
| GL_LL17_16.1017/03HE | 0.039 | -0.025 | 1.2 | 2.2 |
| GL_LL17_16.1032/03 | 0.013 | -0.146 | 1.0 | 1.8 |

| | | | | |
|---|---|---|---|---|
| GL_LL17_16.1098/01 | 0.004 | -0.179 | 1.0 | 2.2 |
| 14.1026/01 | 0.005 | -0.119 | 1.0 | 2.3 |
| 121011/1 | 0.005 | -0.084 | 1.4 | 2.0 |
| 14509/2 | 0.219 | 0.131 | 1.2 | 2.6 |
| 11574/1 | 0.349 | 0.201 | 4.5 | 3.7 |
| 12690/7 | 0.008 | -0.129 | 2.4 | 3.1 |
| 12741/1 | 0.009 | -0.068 | 2.5 | 3.1 |
| 12741/9 | 0.151 | 0.062 | 5.1 | 3.4 |
| 12797/9 | 0.000 | -0.112 | 1.4 | 2.7 |
| 13463/1 | 0.014 | -0.087 | 1.1 | 2.2 |
| 13465/1 | 0.431 | 0.271 | 7.5 | 4.0 |
| 131031/3 | 0.000 | -0.064 | 1.2 | 1.7 |
| 131051/3 | 0.026 | -0.064 | 3.4 | 2.6 |
| 14.1022/7 | 0.013 | -0.099 | 1.0 | 2.3 |
| 14.1026/1 | 0.003 | -0.121 | 1.0 | 2.2 |
| 14090/3 | 0.450 | 0.339 | 6.9 | 3.5 |
| 14389Yes3/1 | 0.016 | -0.084 | 6.4 | 3.9 |
| 14508/8 | 0.013 | -0.087 | 1.9 | 2.3 |
| 14794/1 | 0.005 | -0.155 | 4.5 | 3.7 |
| 94.7082.15 | 0.505 | 0.204 | 2.0 | 5.3 |
| 97.037.03 | 0.839 | 0.549 | 3.9 | 5.6 |
| 04.5233.03 | 0.034 | -0.209 | 1.8 | 2.5 |
| 15.1001.05 | 0.003 | -0.198 | 1.2 | 2.9 |
| 15.1005.01 | 0.041 | -0.190 | 1.2 | 2.6 |
| 15.1014.01 | 0.032 | -0.182 | 1.3 | 2.0 |
| 15.1028.05 | 0.078 | -0.126 | 1.5 | 1.9 |
| 15.1031.08 | 0.016 | -0.197 | 1.2 | 2.7 |
| 15.1033.26 | 0.034 | -0.184 | 1.6 | 2.1 |
| 15.1035.01 | 0.058 | -0.202 | 1.3 | 3.5 |
| 15.1039.01 | 0.133 | -0.085 | 1.7 | 3.8 |
| 15.1044.03 | 0.050 | -0.133 | 1.2 | 2.1 |
| 15.1045.04 | 0.028 | -0.186 | 1.1 | 2.5 |
| 16.1010.01 | 0.056 | -0.200 | 1.3 | 2.4 |
| 16.1016.17 | 0.005 | -0.244 | 1.7 | 2.0 |
| 16.1018.04 | 0.078 | -0.179 | 1.7 | 2.6 |
| 16.1042.03 | 0.044 | -0.205 | 1.3 | 2.1 |
| 16.1043.19 | 0.078 | -0.184 | 1.2 | 2.7 |
| 16.1061.01 | 0.206 | -0.045 | 2.7 | 2.5 |
| 16.1110.16 | 0.009 | -0.235 | 1.2 | 3.1 |
| 16.1017.01 | 0.028 | -0.218 | 1.5 | 2.4 |
| 16.1029.182 | 0.068 | -0.190 | 1.3 | 3.8 |
| 16.1029.265 | 0.019 | -0.221 | 1.4 | 2.0 |
| 16.1033.12 | 0.013 | -0.245 | 1.3 | 2.3 |
| 16.1082.01 | 0.065 | -0.188 | 1.8 | 2.7 |
| 16.1104.033 | 0.023 | -0.223 | 1.4 | 2.6 |
| 17.1002.01 | 0.201 | -0.050 | 3.3 | 3.8 |
| 17.1006.02 | 0.330 | 0.079 | 1.3 | 4.0 |

| | | | | |
|---|---|---|---|---|
| 17.1010.03 | 0.385 | 0.134 | 2.3 | 3.5 |
| 17.1014.03 | 0.035 | -0.211 | 1.3 | 2.1 |
| 17.1015.10 | 0.079 | -0.155 | 1.2 | 3.4 |
| 17.1017.02 | 0.000 | -0.244 | 1.4 | 3.1 |
| 17.1021.02 | 0.025 | -0.215 | 1.3 | 1.3 |
| 17.1022.04 | 0.031 | -0.216 | 1.3 | 1.4 |
| 17.1023.01 | 0.073 | -0.171 | 1.1 | 1.6 |
| 17.1025.02 | 0.023 | -0.194 | 1.1 | 1.6 |
| 17.1026.02 | 0.041 | -0.168 | 1.0 | 1.3 |
| 17.1027.02 | 0.129 | -0.097 | 1.4 | 2.3 |
| 17.1027.08 | 0.015 | -0.208 | 1.0 | 3.6 |
| 17.1035.01 | 0.012 | -0.239 | 1.5 | 4.0 |
| 17.1039.02 | 0.724 | 0.484 | 5.9 | 3.9 |
| 17.1044.02 | 0.117 | -0.127 | 1.9 | 1.4 |
| 17.1045.01 | 0.038 | -0.209 | 1.7 | 1.4 |
| 17.1048.01 | 0.088 | -0.163 | 1.1 | 1.3 |
| 17.1066.01 | 0.000 | -0.237 | 1.0 | 1.6 |
| 17.1070.03 | 0.144 | -0.088 | 1.4 | 1.6 |
| 17.1071.02 | 0.060 | -0.191 | 1.5 | 3.0 |
| 17.1073.01 | 0.060 | -0.177 | 1.8 | 3.1 |
| 17.1081.06 | 0.036 | -0.212 | 1.6 | 1.7 |
| 17.1082.01 | 0.013 | -0.207 | 1.3 | 2.8 |
| 17.1108.01 | 0.287 | 0.067 | 5.6 | 4.7 |
| 17.1078.04 | 0.729 | 0.499 | 4.7 | 2.6 |
| 17.1080.03 | 0.000 | -0.240 | 1.3 | 2.4 |
| 17.1086.01 | 0.837 | 0.611 | 4.3 | 4.0 |
| 16.1006.13 | 0.057 | -0.187 | 1.4 | 2.0 |
| 17.1059.05 | 0.012 | -0.214 | 1.2 | 1.3 |
| 16.1068.01 | 0.583 | 0.314 | 5.6 | 2.2 |
| 90.6684.04 | 0.403 | 0.197 | 2.9 | 4.4 |
| 09.1239.01 | 0.067 | -0.226 | 1.7 | 2.9 |
| 16.1076.07 | 0.282 | 0.068 | 1.5 | 1.6 |
| 15.1002.04 | 0.043 | -0.179 | 1.2 | 3.4 |
| 15.1011.10 | 0.238 | 0.019 | 3.6 | 3.2 |
| 15.1016.59 | 0.010 | -0.159 | 2.5 | 2.4 |
| 15.1017.03 | 0.061 | -0.137 | 1.4 | 2.9 |
| 15.1023.01 | 0.037 | -0.181 | 1.2 | 3.7 |
| 15.1031.03 | 0.041 | -0.176 | 1.2 | 3.6 |
| 15.1034.01 | 0.052 | -0.166 | 1.3 | 2.5 |
| 15.1045.08 | 0.037 | -0.178 | 1.2 | 2.2 |
| 15.1080.01 | 0.008 | -0.179 | 1.2 | 2.0 |
| 16.1011.05 | 0.055 | -0.169 | 4.2 | 3.4 |
| 16.1019.07 | 0.054 | -0.181 | 1.3 | 3.3 |
| 16.1020.07 | 0.049 | -0.177 | 1.3 | 3.5 |
| 16.1026.06 | 0.007 | -0.233 | 1.5 | 3.8 |
| 16.1027.03 | 0.029 | -0.197 | 1.2 | 1.9 |
| 16.1031.06 | 0.037 | -0.196 | 1.2 | 1.5 |

| | | | | |
|---|---|---|---|---|
| 16.1038.01 | 0.083 | -0.140 | 1.5 | 2.9 |
| 16.1039.55 | 0.281 | 0.056 | 1.6 | 2.4 |
| 16.1040.02 | 0.012 | -0.209 | 1.3 | 1.9 |
| 16.1046.29 | 0.035 | -0.177 | 1.2 | 3.3 |
| 16.1061.05 | 0.021 | -0.194 | 1.6 | 3.4 |
| 16.1087.02 | 0.017 | -0.222 | 1.7 | 2.1 |
| 16.1089.01 | 0.050 | -0.171 | 1.2 | 1.9 |
| 16.1091.02 | 0.036 | -0.196 | 1.2 | 3.8 |
| 16.1104.056 | 0.021 | -0.191 | 1.3 | 1.9 |
| 17.1002.07 | 0.214 | 0.002 | 1.3 | 2.6 |
| 17.1006.01 | 0.198 | -0.033 | 1.3 | 4.0 |
| 17.1011.03 | 0.151 | -0.072 | 1.2 | 2.4 |
| 17.1015.05 | 0.037 | -0.165 | 1.3 | 2.4 |
| 17.1018.01 | 0.004 | -0.199 | 1.1 | 2.3 |
| 17.1024.02 | 0.034 | -0.168 | 1.1 | 1.1 |
| 17.1026.03 | 0.034 | -0.185 | 1.1 | 1.5 |
| 17.1028.01 | 0.002 | -0.207 | 1.1 | 1.7 |
| 17.1029.01 | 0.015 | -0.183 | 1.1 | 1.6 |
| 17.1036.03 | 0.013 | -0.192 | 1.4 | 3.8 |
| 17.1044.01 | 0.007 | -0.198 | 1.1 | 1.4 |
| 17.1065.04 | 0.753 | 0.566 | 2.7 | 5.5 |
| 17.1067.04 | 0.072 | -0.140 | 1.9 | 2.9 |
| 17.1068.02 | 0.008 | -0.167 | 1.4 | 1.9 |
| 17.1073.08 | 0.003 | -0.195 | 1.4 | 2.8 |
| 17.1087.02 | 0.003 | -0.195 | 1.1 | 1.5 |
| 17.1078.08 | 0.630 | 0.413 | 5.8 | 2.8 |
| 16.1005.13 | 0.407 | 0.176 | 1.7 | 4.9 |
| Adretta | 0.819 | 0.575 | 7.3 | 6.2 |
| Adorata | 0.907 | 0.684 | 5.6 | 4.2 |
| Agria | 0.768 | 0.580 | 3.6 | 5.2 |
| Allians | 0.589 | 0.171 | 4.9 | 6.0 |
| Annegret | 0.870 | 0.606 | 6.6 | 4.1 |
| Baby Lou | 0.832 | 0.619 | 6.2 | 5.9 |
| Bionica | 0.197 | -0.175 | 5.4 | 6.2 |
| Blaue Anneliese | 0.544 | 0.349 | 4.2 | 5.3 |
| Cathi | 0.857 | 0.603 | 5.6 | 5.0 |
| Dukata | 0.816 | 0.628 | 6.1 | 5.9 |
| Emiliana | 0.854 | 0.604 | 5.0 | 5.9 |
| Escada | 0.784 | 0.558 | 6.5 | 4.2 |
| Ikarus | 0.787 | 0.560 | 6.2 | 4.7 |
| Innovator | 0.889 | 0.679 | 5.8 | 3.4 |
| Jelly | 0.648 | 0.384 | 5.2 | 6.3 |
| Jule | 0.738 | 0.529 | 6.6 | 4.7 |
| Karlena | 0.827 | 0.589 | 6.1 | 6.4 |
| Kuras | 0.445 | 0.172 | 4.2 | 5.0 |
| Lea | 0.831 | 0.569 | 6.5 | 3.5 |
| Lubeca | 0.799 | 0.546 | 5.1 | 6.4 |

| | | | | |
|---|---|---|---|---|
| Marta | 0.908 | 0.658 | 5.7 | 4.7 |
| Mary Ann | 0.813 | 0.597 | 8.3 | 4.6 |
| Nautilus | 0.794 | 0.517 | 4.8 | 6.8 |
| Olivia | 0.744 | 0.521 | 6.3 | 4.2 |
| Otolia | 0.230 | 0.100 | 3.8 | 5.3 |
| Papageno | 0.470 | 0.242 | 4.1 | 3.3 |
| Penni | 0.864 | 0.633 | 6.0 | 5.2 |
| Petra | 0.845 | 0.597 | 5.6 | 3.7 |
| Picus | 0.805 | 0.603 | 6.5 | 4.6 |
| Sandra | 0.817 | 0.600 | 6.3 | 4.5 |
| Sarpo Mira | 0.075 | -0.181 | 3.0 | 5.6 |
| Seresta | 0.772 | 0.574 | 6.5 | 3.3 |
| Solist | 0.786 | 0.481 | 4.9 | 7.1 |
| Solo | 0.774 | 0.545 | 6.5 | 4.7 |
| Tarzan | 0.763 | 0.560 | 7.0 | 4.1 |
| Toluca | 0.181 | -0.029 | 2.8 | 5.8 |
| Triton | 0.758 | 0.629 | 6.4 | 5.3 |
| Varuna | 0.872 | 0.660 | 5.8 | 5.0 |
| Virginia | 0.874 | 0.665 | 6.1 | 3.0 |

Supplementary Table 2 Results of the GWAS with the 1-dom-alt model

| Trait | Threshold | Marker | Chromosome | Position | Ref | Alt | Score | Effect | $R^2$ [%]* |
|---|---|---|---|---|---|---|---|---|---|
| Detached leaf assay | 5.52 | 9_51556194 | 9 | 51556194 | A | G | 7 | -1.97 | 27.8 |
| | 5.52 | 9_52489154 | 9 | 52489154 | A | G | 6.49 | -1.94 | 27.2 |
| | 5.52 | 11_158211 | 11 | 158211 | C | T | 6.1 | -1.61 | 11.1 |
| | 5.52 | 11_158263 | 11 | 158263 | C | T | 6.1 | -1.61 | 11.1 |
| | 5.52 | 11_159849 | 11 | 159849 | G | T | 7.21 | -1.7 | 10.8 |
| | 5.52 | 11_638647 | 11 | 638647 | A | G | 6.1 | -1.61 | 11.1 |
| | 5.52 | 11_814233 | 11 | 814233 | G | T | 6.1 | -1.61 | 11.1 |
| | 5.52 | 11_814343 | 11 | 814343 | C | T | 6.1 | -1.61 | 11.1 |
| | 5.52 | 11_1123733 | 11 | 1123733 | C | T | 6.45 | -1.69 | 10.9 |
| | 5.52 | 11_2065906 | 11 | 2065906 | A | G | 5.65 | -1.35 | 12.0 |
| | 5.52 | 11_2068637 | 11 | 2068637 | C | G | 6.05 | -1.5 | 11.0 |
| ΔrAUDPC | 5.52 | 9_51556194 | 9 | 51556194 | A | G | 5.81 | -0.25 | 19.8 |
| | 5.52 | 11_158211 | 11 | 158211 | C | T | 6.88 | -0.24 | 15.1 |
| | 5.52 | 11_158263 | 11 | 158263 | C | T | 6.88 | -0.24 | 15.1 |
| | 5.52 | 11_159849 | 11 | 159849 | G | T | 8.75 | -0.26 | 15.6 |
| | 5.52 | 11_638647 | 11 | 638647 | A | G | 6.88 | -0.24 | 15.1 |
| | 5.52 | 11_814233 | 11 | 814233 | G | T | 6.88 | -0.24 | 15.1 |
| | 5.52 | 11_814343 | 11 | 814343 | C | T | 6.88 | -0.24 | 15.1 |
| | 5.52 | 11_1123733 | 11 | 1123733 | C | T | 7.08 | -0.25 | 14.9 |
| | 5.52 | 11_1683052 | 11 | 1683052 | C | T | 6.11 | -0.22 | 14.7 |
| | 5.52 | 11_2065906 | 11 | 2065906 | A | G | 6.47 | -0.2 | 16.7 |
| | 5.52 | 11_2068637 | 11 | 2068637 | C | G | 6.73 | -0.22 | 14.7 |
| | 5.52 | 11_3751177 | 11 | 3751177 | A | G | 6.27 | -0.24 | 9.8 |
| | 5.52 | 11_4473431 | 11 | 4473431 | C | G | 6.27 | -0.24 | 9.8 |
| | 5.52 | 11_4604936 | 11 | 4604936 | A | T | 6.27 | -0.24 | 9.7 |
| | 5.52 | 11_4742648 | 11 | 4742648 | A | G | 8.17 | -0.25 | 9.3 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| rAUDPC | 5.52 | 9_51556194 | 9 | 51556194 | A | G | 6.15 | -25.52 | 20.8 |
| | 5.52 | 11_158211 | 11 | 158211 | C | T | 6.37 | -22.98 | 13.4 |
| | 5.52 | 11_158263 | 11 | 158263 | C | T | 6.37 | -22.98 | 13.4 |
| | 5.52 | 11_159849 | 11 | 159849 | G | T | 8.27 | -25.33 | 13.6 |
| | 5.52 | 11_638647 | 11 | 638647 | A | G | 6.37 | -22.98 | 13.4 |
| | 5.52 | 11_814233 | 11 | 814233 | G | T | 6.37 | -22.98 | 13.4 |
| | 5.52 | 11_814343 | 11 | 814343 | C | T | 6.37 | -22.98 | 13.4 |
| | 5.52 | 11_1123733 | 11 | 1123733 | C | T | 6.81 | -24.31 | 13.3 |
| | 5.52 | 11_1683052 | 11 | 1683052 | C | T | 5.71 | -20.72 | 13.0 |
| | 5.52 | 11_2065906 | 11 | 2065906 | A | G | 6.52 | -20.08 | 14.8 |
| | 5.52 | 11_2068637 | 11 | 2068637 | C | G | 6.18 | -20.91 | 12.9 |
| | 5.52 | 11_3751177 | 11 | 3751177 | A | G | 5.93 | -23.41 | 9.1 |
| | 5.52 | 11_4473431 | 11 | 4473431 | C | G | 5.93 | -23.41 | 9.1 |
| | 5.52 | 11_4535534 | 11 | 4535534 | A | T | 5.87 | -22.28 | 9.4 |
| | 5.52 | 11_4604936 | 11 | 4604936 | A | T | 5.93 | -23.41 | 9.0 |
| | 5.52 | 11_4742648 | 11 | 4742648 | A | G | 8.37 | -25.12 | 8.8 |

*Phenotypic variance explained

## 2.5 Superior resistance to *Phytophthora infestans* in new pre-breeding clones under different nitrogen fertilisation regimes

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Eingereicht bei „Biological Agriculture & Horticulture”

**Superior resistance to *Phytophthora infestans* in new pre-breeding clones under different nitrogen fertilisation regimes**


Abstract

Late blight caused by *Phytophthora infestans* is the most devastating disease for cultivated potatoes and causes annually considerable costs due to yield losses and fungicide applications. Especially in organic farming, strong limitations on fungicide applications make research necessary to investigate, which factors influence disease severity. Therefore, effects of organic nitrogen fertilisation rates on leaf and tuber blight in potato cultivars and pre-breeding clones were analysed in the present study. It was found that the foliage of the pre-breeding clones was little or not at all affected by *P. infestans*, irrespectively of the nitrogen level, while the cultivars reacted differently with mild to strong late blight symptoms. In some clones and cultivars, the tubers were mostly affected at higher nitrogen application, but most showed no differences between N levels. We conclude from the present study that in the future, the use of resistant cultivars will be a suitable way in particular for organic farming, in order to still achieve high yields with varying nitrogen contents and a few control options against *P. infestans*.


Introduction

Potato cultivation is still affected by high yield losses due to late blight, caused by the oomycete *Phytophthora infestans*. This is a major problem, especially for organic farming, as the European Union only allows active substance copper compounds as control agents (Implementing Regulation (EU) 2018/1981). Copper accumulates in the soil and can become harmful to soil organisms in high concentrations (Rajput et al. 2020). In addition to the use of copper, also other agronomic measures can limit or prevent *P. infestans* infestation. These include, for example, crop rotations with a minimum three-year break in potato cultivation (Bødker et al. 2006; Hannukkala et al. 2007; Van Bruggen et al. 2015), the use of non-infected potato tubers (Ghorbani et al. 2004) or pre-sprouting, so that the plants have a head start on *P. infestans* (Waschl and Hein 2010). Strip intercropping with cereals and a grass-clover mix could also reduce infestation (Bouws & Finckh 2008). The use of microorganisms and plant extracts has so far proved to be less effective than copper (Ghorbani et al. 2005; Dorn et al. 2007). However, this area is still in research and full of potentials.

The amount of fertiliser can also influence the infestation. With regard to nitrogen, however, there are many studies that came to different results. Juárez et al. (2000) studied two cultivars and three different nitrogen applications. They concluded that higher nitrogen levels led to a more severe course of disease. Greenhouse trials with one cultivar and two nitrogen levels by Mittelstraß et al. (2006) also saw a higher susceptibility in the plants growing in the high nitrogen level. This was also the conclusion of Ros et al. (2008), who investigated four cultivars and two levels under greenhouse conditions, and also of Bangemann (2010), using two cultivars but four nitrogen levels. Jensen and Nielsen concluded in 2015 that there is a tendency that more nitrogen can lead to more infestation. Sunita et al. (2011) came to the opposite conclusion, and Cicore et al. (2012) found no difference between the levels, although only two Argentine cultivars were used. Agu (2004) came to the same conclusion, but with additional phosphorus application, a stronger infestation was found in the high nitrogen levels. However, he only examined one cultivar. In Jin et al. (2014) and Jha et al. (2019), the lowest infestation of *P. infestans* was detected at medium nitrogen levels (Table 1).

Table 1 Current literature on the influence of nitrogen levels on infestation with *P. infestans* in potatoes

| Reference | Amount of Genotypes | Nitrogen fertilizer levels | Conclusion |
|---|---|---|---|
| Bangemann 2010[a] | 2 | 4 rates (0-240 kg N/ha) | + N → + infestation |
| Jensen & Nielsen 2015[a] | 1 | 3 rates (60-180 kg N/ha) | Tendency<br>+ N → + infestation |
| Juárez et al. 2000[a] | 2 | 3 rates (0-320 kg N/ha) | + N → + infestation |
| Ros et al. 2008[b] | 4 | 2 rates (27-36 kg N/ha and 175-185 kg N/ha) | + N → + infestation |
| Mittelstraß et al. 2006[b] | 1 | 2 rates | + N → + infestation |
| Agu 2004[a] | 1 | 3 rates (0-138 kg N/ha) | + N in combination with + P → + infestation |
| Jha et a. 2019[a] | 1 | 6 rates (0-250 kg N/ha) | Medium N → lowest infestation |
| Jin et al. 2014[b] | 1 | 4 rates (45-180 kg N/ha) | Medium N → lowest infestation |

| | | | |
|---|---|---|---|
| Cicore et al. 2012[c] | 2 | 2 rates (70 kg N/ha and 50+80 kg N/ha) | No influence |
| Sunita et a. 2011[a] | 1 | 3 rates (150-250 kg N/ha) | + N → - infestation |

[a]Field experiments

[b]Glasshouse experiments

[c]Field and glasshouse experiments

In the evaluation of data from several farmers by Möller et al. (2006 and 2007), it was entirely in doubt with regard to organic farming whether nitrogen has any influence at all on *P. infestans* infestation. The aim of this study was to clarify whether the amount of nitrogen can influence late blight infestation on both foliage and tubers. To our knowledge, no previous study has combined field and laboratory tests and most studies used four or less genotypes in their investigations, which makes it difficult to generalise results. The studies also mainly focused on foliage blight. Furthermore, with one exception (Möller et al. 2006 and 2007), only inorganic nitrogen fertiliser was used in past publications. Since nowadays organic farming is increasing strongly, the focus in this article is placed on organic fertilisation in addition to an increased number of genotypes that was tested. Another special aspect of the present article is that the influence was not only analysed by using released cultivars, but also resistant pre-breeding clones.

## Materials and Methods

### Plant materials and experimental design

The trials were set up in 2020 and 2021 on the experimental field of the Julius Kuehn Institute in Groß Lüsewitz, Germany in a randomised block design with the three nitrogen fertiliser levels 50 (N1), 100 (N2) and 200 (N3) kg N $ha^{-1}$ and three replicates. Each plot consisted of ten plants. The ware cultivars Adretta, Jelly, Krone (susceptible controls) and Otolia (moderately resistant control) were included in the trial, as well as 20 pre-breeding clones that had proven resistant in previous studies and were developed together with the Bavarian State Research Centre for Agriculture (LfL) in a previous project. The organic N-fertiliser 'Diaglutin N pellet' (Biofa, Münsingen), which consists mainly of heated feather meal, was applied two weeks after planting at the beginning of May before the final ridge shaping.

Assessment of late blight infestation

Foliage blight infestation was determined both directly in the field and with a detached leaf assay. Tuber blight infestation was determined with a tuber slice test. At the end of flowering of the cultivar 'Adretta', one plant per experimental plot was inoculated with 5 ml of a *P. infestans* suspension of common field isolates, a composition which was supplemented each year with newly collected pathogen material ($1.2 \times 10^4$ sporangia $ml^{-1}$, Darsow 2008). The pathogen spectrum was analysed by the James Hutton Institute using FTA cards. For 2020, mainly the genotypes EU_41_A2 and EU_13_A2 were detected. In 2021, mainly the genotype EU_37_A2 was identified. The infestation was assessed as the percentage of the infested foliage area of each plot, excluding the inoculated plant, every three to four days until an infestation of 100 % was reached, or until the respective clone had matured. Based on these assessments, relative Area Under Disease Progress Curve (rAUDPC) values were calculated (Fry 1978; Colon 1994). Since late blight resistance is often associated with late maturity, the rAUDPC values were additionally maturity-corrected according to Truberg et al. (2009) and presented as ΔrAUDPC values.

For the detached leaf assay, five leaves of different plants per plot were taken shortly before inoculation in the field trial and 20 µl drops of the *P. infestans* suspension were applied onto the underside of each leaf in the laboratory. After 24 h, the leaves were turned and incubated for another five days at 16 °C, 95 % relative humidity (RH) and 150 Lux. Scoring was based on the necrotic leaf area and mycelium formation on the underside of the leaf with scores from 1 (no infestation) to 9 (full infestation). The tuber slice test was performed on four tubers per plot. One slice from each tuber was inoculated with 20 µl of a low (1,900 sporangia $ml^{-1}$) and a high (15,000 sporangia $ml^{-1}$) concentrated *P. infestans* suspension. After 24 h, the slices were rotated and then incubated for another five days at 16°C, 95 % RH. Scoring was based on mycelium formation, rotting and browning with scores from 1 (no infestation) to 9 (full infestation) for both concentrations. The mean value was used for evaluation.

Statistical analysis

The statistical evaluation was carried out by an analysis of variance (ANOVA) using the program R version 3.6.3. Fixed effect was the genotype and the N level and random effects were the year and the replicates. The differences between the fertiliser levels were then determined with the Tukey test after verifying the normal distribution of residuals (Shapiro-Wilk test). Means were considered to be statistically significant at $p < 0.05$.

Results

The effect of the N fertiliser was confirmed by the significantly different yields of the three levels (N1 10,028 kg plot$^{-1}$, N2 12,098 kg, plot$^{-1}$, N3 13,200 kg, plot$^{-1}$. ANOVA revealed for all traits that besides the N level the year, the genotype and their interactions (fertiliser x genotype, fertiliser x year and genotype x year) had an influence on the infestation (Tab 2).

Table 2 P-values of ANOVA for all traits

| Trait | Genotype (G) | N level (N) | Year (Y) | G x N | G x Y | N x Y |
|---|---|---|---|---|---|---|
| rADUPC | 2.2e-16 | 0.001727 | 2.2e-16 | 4.045e-10 | 2.2e-16 | 0.062053 |
| ΔrAUDPC | 2.2e-16 | 9.672e-07 | 2.2e-16 | 1.240e-09 | 2.2e-16 | 0.002041 |
| Detached leaf assay | 2.2e-16 | 0.0095458 | 2.2e-16 | 0.0033142 | 2.2e-16 | 0.1500146 |
| Tuber slice test | 2.2e-16 | 1.231e-12 | 2.2e-16 | 0.1284666 | 2.726e-11 | 0.0002023 |

Therefore years and genotypes were analysed individually. The results of the various tests are summarised below and are presented in detail in Supplementary Table 1. The figures show the four cultivars and two clones as an example.

Field test

Overall, the susceptible cultivars were clearly more susceptible to *P. infestans* than the clones in both years, with ‘Otolia’ showing the lowest infestation in the cultivar comparison (Figure 1).

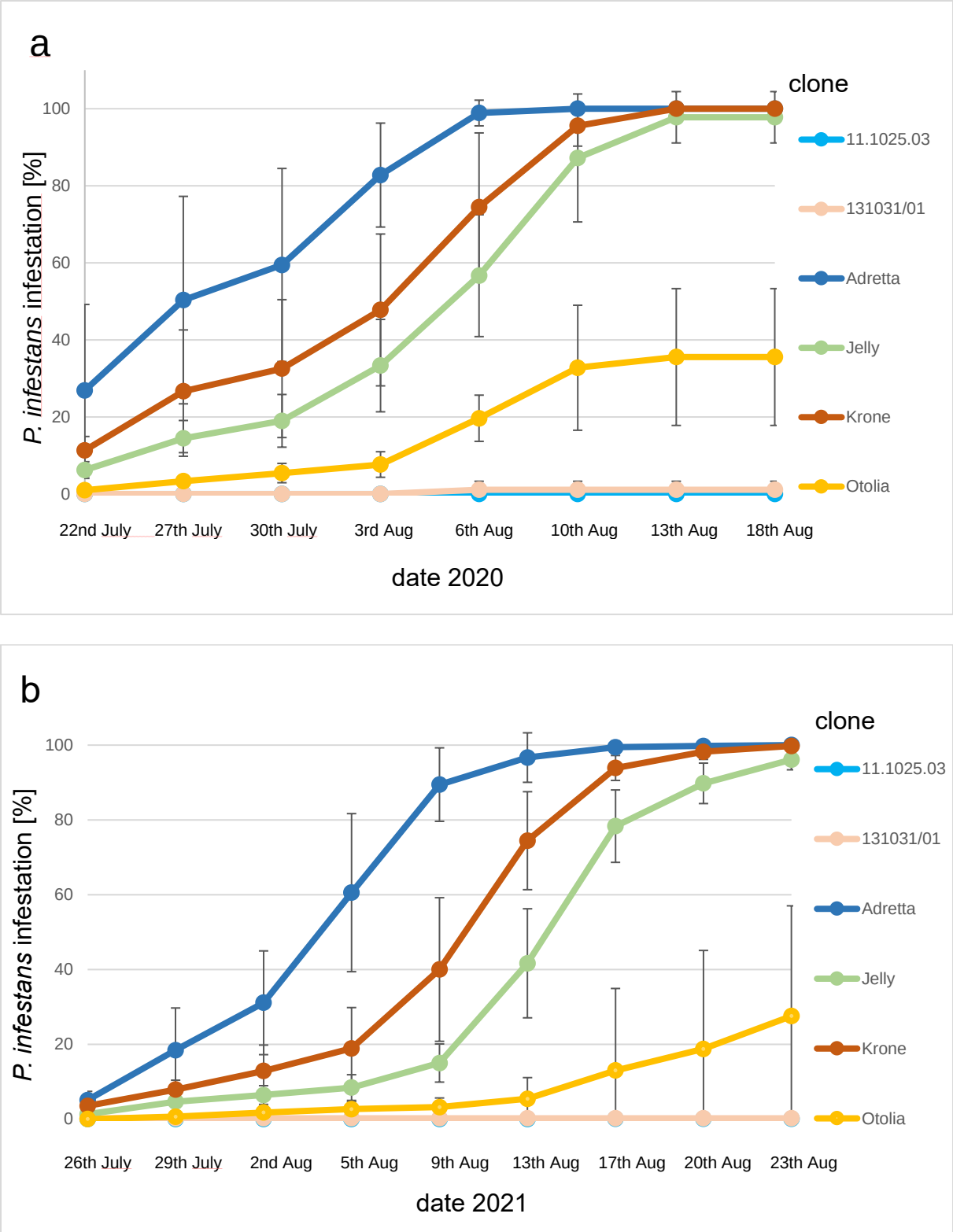
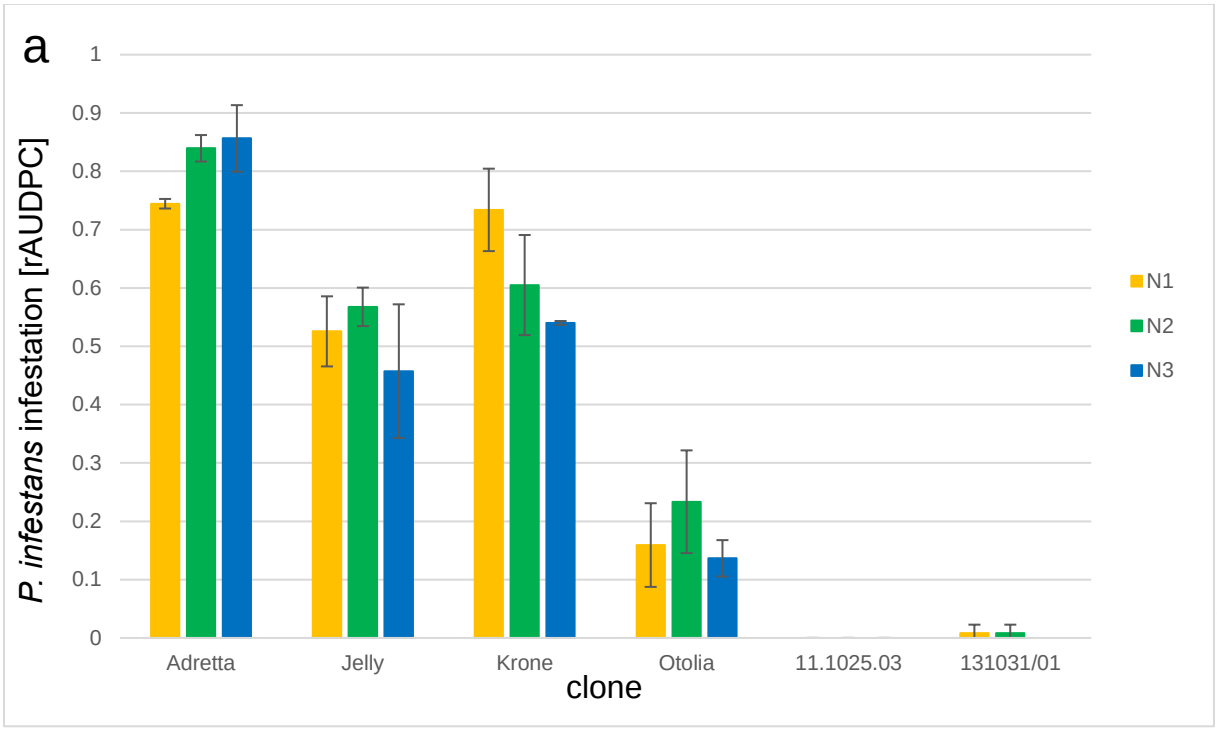



Figure 1 Development of *P. infestans* infestation of four potato cultivars and two pre-breeding clones in 2020 (a) and 2021 (b)

Within the 20 pre-breeding clones, no significant influence of the nitrogen level on the infestation (ΔrAUDPC values) was found in 18 clones in 2020 (Supplementary Table 1). In only two clones the infestation was significantly increased at higher nitrogen doses. Of the

cultivars, ‘Krone’ showed a significantly lower incidence with higher N application. The rAUDPC values were significantly higher with more N application for ‘Adretta’ and lower for ‘Krone’ (Figure 2a). The rAUDPC values of all pre-breeding clones remained unaffected by the nitrogen level. For 2021 one clone and ‘Adretta’ had significantly higher ΔrAUDPC values with higher N application. The rAUDPC values remained unaffected by the N level (Figure 2b).




a

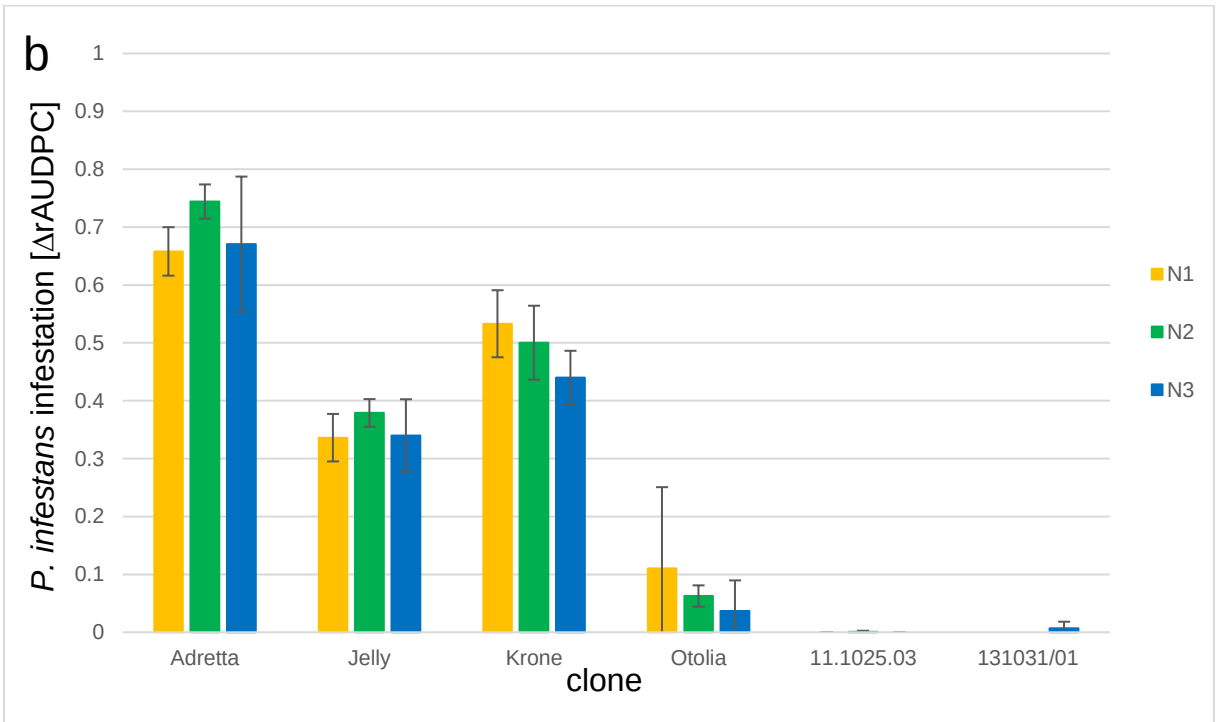


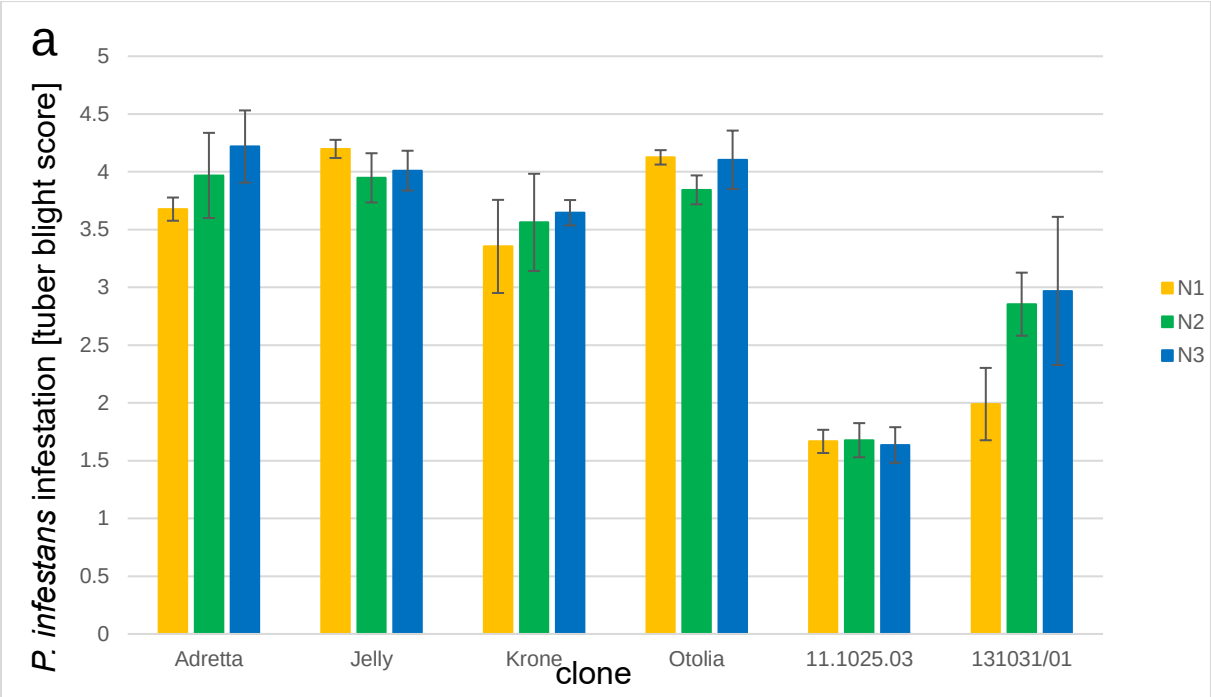
Figure 2 *P. infestans* (foliage blight) rAUDPC values of four potato cultivars and two pre-breeding clones in 2020 (a) and 2021 (b)

Detached leaf assay

In 2020, one clone and 'Adretta' were significantly more affected at higher N levels. The opposite was the case with one clone. 'Otolia' showed significantly less infestation with higher N doses in 2021. The rest of the clones and cultivars showed no significant differences between the N levels.

Tuber slice test

In 2020, no influence of the N level on the infestation of the tuber slices was determined (Figure 3a). In 2021 the infestation of two clones and 'Krone' were significantly affected by N dosage (Figure 3b).



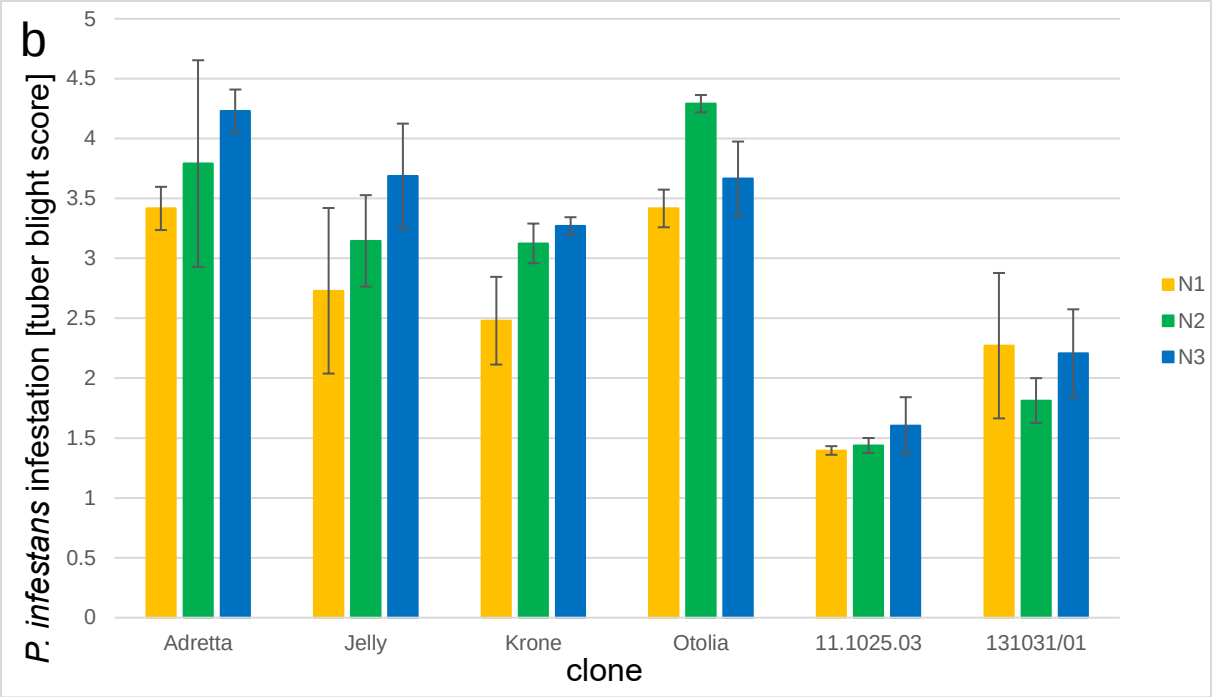



Figure 3 *P. infestans* (tuber blight) infection scores of four potato cultivars and two pre-breeding clones in 2020 (a) and 2021 (b)

## Discussion

The literature shows different results of the effects of N fertilisation levels on *P. infestans* (Tab 1). Thus, common theories, such as that of Herms and Mattson (1992), which states that a low C/N ratio leads to lower defence mechanisms and thus to more infestation, or that of Snoeijers et al. (2000), according to which a better nutrient supply of the plant also creates a better environment for pathogens, could only be partially confirmed. The results of 4 cultivars and 20 pre-breeding clones of the present study show that the genotype is most likely responsible for whether the amount of nitrogen can influence late blight infestation: Resistant clones, for example, are hardly or not at all infested with late blight regardless of the nitrogen supply. In 2020, 11 and in 2021, 19 of the 20 clones tested were only up to 10 % infected with late blight until complete maturity. The cultivars showed infestation at every nitrogen level, but an increase or decrease in infestation with a change in the amount of fertiliser depended both on the respective cultivar and, to a considerable extent, on the year of the trial. Overall, it must therefore be said that the results indicate that the influence of the amount of nitrogen is not decisive for the level of infestation with *P. infestans* and that the sporadically significant results are possibly based on chance or cultivar specific effects, which, however, were not reproducible in the present study. Besides N fertilisation, other nutrients can also influence the infestation. It

was shown, that higher potassium applications led to a lower infestation (Bista & Bhandari 2019; Kowalska & Drożdżyński 2018). Dey and Chakraborty (2016) obtained similar results, but in combination with phosphorus application. These interactions could be investigated in further experiments together with the application of nitrogen.

## Conclusion

Overall, it can be said that N fertilisation has only a minor influence on the occurrence of late blight and that it is much more relevant to grow a resistant cultivar. This is especially important for organic farming because of the low disease control possibilities. For this purpose, the pre-breeding clones investigated here should be included in breeding programmes in the future.

## References


Agu, C. M. (2004). Effect of nitrogen and phosphorus combination on late blight disease and potato yield. *Tropical Science, 44*(4), 163-165. https://doi.org/10.1002/ts.159

Bangemann, L. W. (2010). Pathogen-Nährstoff-Interaktionen in der Kartoffel: Am Beispiel der Kraut-und Knollenfäule und der Stickstoffversorgung im ökologischen Anbau. 53. Jahrestagung der Gesellschaft für Pflanzenbauwissenschaften, 31-44.

Bista, B., & Bhandari, D. (2019). Potassium fertilization in potato. *International Journal of Applied Science and Biotechnology, 7*, 153-160. https://doi.org/10.3126/ijasbt.v7i2.24636

Bødker, L., Pedersen, H., Kristensen, K., Møller, L., Lehtinen, A., Hannukkala, A. (2006). Influence of crop history of potato on early occurrence and disease severity of potato late blight caused by *Phytophthora infestans*. *PPO-Special Report, no. 11*, 53.

Bouws, H., & Finckh, M. R. (2008). Effects of strip intercropping of potatoes with non-hosts on late blight severity and tuber yield in organic production. *Plant Pathology, 57*(5), 916-927. https://doi.org/10.1111/j.1365-3059.2008.01860.x

Bruggen, van A. H., Gamliel, A., Finckh, M. R. (2016). Plant disease management in organic farming systems. *Pest Management Science, 72*(1), 30-44. https://doi.org/10.1002/ps.4145

Cicore, P. L., Andreu, A. B., Huarte, M. A. (2012). Reaction to late blight in response to nitrogen management in Argentine potato cultivars. *Crop Protection, 42*, 69-73. https://doi.org/10.1016/j.cropro.2012.07.016

Colon, L. (1994). Resistance to *Phytophthora infestans* in *Solanum tuberosum* and wild *Solanum* species. Wageningen University and Research.

Darsow, U. (2008). Pre-breeding for quantitative resistance of potato to late blight at the Institute of Agricultural Crops Gross Lüsewitz in the departmental research of BMELV-state of research and breeding. Mitteilungen aus dem Julius Kühn-Institut, 415.

Dey, S., & Chakraborty, A. (2016). Influence of agronomic practices on severity of late blight of potato (*Phytophthora infestans*). *Journal of Applied and Natural Science, 8*(3), 1302-1305. https://doi.org/10.31018/jans.v8i3.957

Dorn, B., Musa, T., Krebs, H., Fried, P. M., Forrer, H. R. (2007). Control of late blight in organic potato production: evaluation of copper-free preparations under field, growth chamber and laboratory conditions. *European Journal of Plant Pathology, 119*(2), 217-240. https://doi.org/10.1007/s10658-007-9166-0

Fry, W. E. (1978). Quantification of general resistance of potato cultivars and fungicide effects for integrated control of potato late blight. *Phytopathology, 68*(11), 1650-1655.

Ghorbani, R., Wilcockson, S. J., Giotis, C., Leifert, C. (2004). Potato late blight management in organic agriculture. *Outlooks on Pest Management, 15*(4), 176-180. https://doi.org/10.1564/15aug12

Ghorbani, R., Wilcockson, S., Leifert, C. (2005). Alternative treatments for late blight control in organic potato: Antagonistic micro-organisms and compost extracts for activity against *Phytophthora infestans*. *Potato Research, 48*(3), 181-189. https://doi.org/10.1007/BF02742375

Hannukkala, A. O., Kaukoranta, T., Lehtinen, A., Rahkonen, A. (2007). Late-blight epidemics on potato in Finland, 1933–2002; increased and earlier occurrence of epidemics associated with climate change and lack of rotation. *Plant Pathology, 56*(1), 167-176. https://doi.org/10.1111/j.1365-3059.2006.01451.x

Herms, D. A., & Mattson, W. J. (1992). The dilemma of plants: to grow or defend. *The Quarterly Review of Biology, 67*(3), 283-335. https://doi.org/10.1086/417659

Implementing Regulation (EU) 2018/1981 der Kommission vom 13. Dezember 2018 zur Erneuerung der Genehmigung für die Wirkstoffe Kupferverbindungen als Substitutionskandidaten gemäß der Verordnung (EG) Nr. 1107/2009 des Europäischen Parlaments und des Rates über das Inverkehrbringen von Pflanzenschutzmitteln und zur Änderung des Anhangs der Durchführungsverordnung (EU) Nr. 540/2011 der Kommission (Text von Bedeutung für den EWR.) https://op.europa.eu/de/publication-detail/-/publication/c5ac184b-ff4b-11e8-a96d-01aa75ed71a1

Jensen, P. K., & Nielsen, B. J. (2015). Development of potato late blight (*Phytophthora infestans*) in differently developed potato crops and the potential to graduate the fungicide dose according to crop biomass. *Acta Agriculturae Scandinavia – Section B Soil and Plant Science, 65*(7), 667-672. https://doi.org/10.1080/09064710.2015.1043334

Jha, S., Khalko, S., Abhijith, M., Bhattacharya, P. M., Roy, A. (2019). Study of effect of different regimes of nitrogen on late blight of potato. *Journal of Entomology and Zoology Studies, 7*, 918-921.

Jin, X., Hao, N., Jiao, F., Yang, Y., Wang, D., Xu, C., Zhai, R. (2014). The effect of nitrogen supply on potato yield, tuber size and pathogen resistance in *Solanum tuberosum* exposed to *Phytophthora infestans*. *African Journal of Agricltural Research, 9*(35), 2657-2663. https://doi.org/10.5897/AJAR2013.7550

Juárez, H. S., Amaro, J. R., Rivera, M. D., Párraga, A., Hijmans, R. J. (2000). The effect of nitrogen fertilization on potato late blight in the field. CIP program report 69-76.

Kowalska, J., & Drożdżyński, D. (2018). Effects of potassium fertilisation on potato late blight and yield – short communication. *Plant Protection Science, 54*(2), 87–91. https://doi.org/10.17221/79/2017-PPS

Mittelstraß, K., Treutter, D., Pleßl, M., Heller, W., Elstner, E. F., Heiser, I. (2006). Modification of primary and secondary metabolism of potato plants by nitrogen application differentially affects resistance to *Phytophthora infestans* and *Alternaria solani*. *Plant Biology, 8*(5), 653-661. https://doi.org/10.1055/s-2006-924085

Möller, K., Habermeyer, J., Zinkernagel, V., Reents, H. J. (2006). Impact and interaction of nitrogen and *Phytophthora infestans* as yield-limiting and yield-reducing factors in organic potato (*Solanum tuberosum* L.) crops. *Potato Research, 49*(4), 281-301. https://doi.org/10.1007/s11540-007-9024-7

Möller, K., & Reents, H. J. (2007). Impact of agronomic strategies (seed tuber pre-sprouting, cultivar choice) to control late blight (*Phytophthora infestans*) on tuber growth and yield in organic potato (*Solanum tuberosum* L.) crops. *Potato Research, 50*(1), 15-29. https://doi.org/10.1007/s11540-007-9026-5

Rajput, V., Minkina, T., Sushkova, S., Behal, A., Maksimov, A., Blicharska, E., Ghazaryan, K., Movsesyan, H., Barsova, N. (2020). ZnO and CuO nanoparticles: a threat to soil organisms, plants, and human health. *Environmental Geochemistry Health, 42*(1), 147–158. https://doi.org/10.1007/s10653-019-00317-3

Ros, B., Mohler, V., Wenzel, G., Thümmler, F. (2008). *Phytophthora infestans*-triggered response of growth-and defense-related genes in potato cultivars with different levels of resistance under the influence of nitrogen availability. *Physiologia Plantarum, 133*(2), 386-396. https://doi.org/10.1111/j.1399-3054.2008.01048.x

Snoeijers, S. S., Pérez-García, A., Joosten, M. H., De Wit, P. J. (2000). The effect of nitrogen on disease development and gene expression in bacterial and fungal plant pathogens. *European Journal of Plant Pathology, 106*(6), 493-506. https://doi.org/10.1023/A:1008720704105

Sunita, M., Zubair, A., Ayana, C., Srikanta, D. (2011). Effects of different levels of nitrogen against foliar diseases of potato under different fertility gradient soil on field condition. *Journal of Mycopathological Research, 49*(2), 273-278.

Truberg, B., Hammann, T., Darsow, U., Piepho, H. P. (2009). Empirischer Vergleich verschiedener Methoden zur Reifekorrektur von Daten zum Befall mit Krautfaule (*Phytophthora infestans* (Mont.) de Bary) in Selektionsexperimenten bei der Kartoffel (*Solanum tuberosum subsp. tuberosum*). Journal für Kulturpflanzen-*Journal of Cultivated Plants, 61*, 77-81.

Waschl, H., & Hein, W. (2010). Möglichkeiten der alternativen Bekämpfung von Krautfäule (*Phytophthora infestans*) im biologischen Kartoffelanbau. Control of potato late blight (*Phytophthora infestans*) with alternative treat-ments in organic farming. ALVA Jahrestagung 2010, Vom Lebensmittel zum Genussmittel–was essen wir morgen? 273-275.

Supplementary Table 1 ΔrAUDPC values, rAUDPC values, scores of the detached leaf assay and scores of the tuber slice test of 4 cultivars and 20 pre-breeding clones of three N levels in 2020 and 2021. Significance is based on results of ANOVA and Tukey test

| | **mean ΔrAUDPC 2020** | | |
|---|---|---|---|
| **Clone/Cultivar** | **N1** | **N2** | **N3** |
| 11.1025.03 | -0.141±0.001 | -0.137±0.005 | -0.134±0.002 |
| 131031/01 | -0.129±0.014 | -0.128±0.015 | -0.133±0.009 |
| 14.1022/07 | -0.102±0.024 | -0.118±0.005 | -0.124±0.011 |
| 14.1081/01 | -0.146±0.002 | -0.127±0.011 | -0.131±0.002 |
| 14442/04 | -0.137±0.014 | -0.143±0.001 | -0.117±0.033 |
| 14442/06 | -0.166±0.008 a | -0.126±0.025 ab | -0.087±0.040 b |
| 15176/01HC | -0.137±0.017 | -0.121±0.009 | -0.119±0.013 |
| 15207/01 | -0.117±0.003 | -0.120±0.009 | -0.120±0.013 |
| 15703/06 | -0.155±0.017 a | -0.120±0.016 ab | -0.090±0.022 b |
| 16186/02 | -0.164±0.019 | -0.160±0.009 | -0.134±0.013 |
| 16186/03 | -0.150±0.005 | -0.150±0.007 | -0.126±0.021 |
| 16282/01 | -0.119±0.020 | -0.101±0.010 | -0.100±0.012 |
| 16588/03 | -0.117±0.023 | -0.100±0.014 | -0.093±0.019 |
| 16650/16 | -0.117±0.008 | -0.113±0.009 | -0.127±0.004 |
| 16742/01 | -0.128±0.003 | -0.128±0.003 | -0.121±0.004 |
| 14.1077/02 | 0.088±0.071 | 0.050±0.041 | 0.025±0.079 |
| 16.1056/02HC | 0.232±0.079 | 0.600±0.180 | 0.454±0.184 |
| 16.1089/01 | -0.062±0.037 | 0.015±0.167 | -0.030±0.030 |
| 16.1061/01HC | -0.025±0.045 | -0.003±0.002 | -0.087±0.033 |
| 15176/05 | -0.102±0.038 | -0.043±0.026 | -0.088±0.011 |
| Adretta | 0.654±0.066 | 0.647±0.041 | 0.675±0.044 |
| Jelly | 0.400±0.058 | 0.442±0.033 | 0.333±0.116 |
| Krone | 0.572±0.093 b | 0.464±0.072 ab | 0.410±0.003 a |
| Otolia | 0.020±0.070 | 0.100±0.085 | 0.006±0.030 |
| | **mean rAUDPC 2020** | | |
| | **N1** | **N2** | **N3** |
| 11.1025.03 | 0.000±0.000 | 0.000±0.000 | 0.000±0.000 |
| 131031/01 | 0.008±0.014 | 0.008±0.014 | 0.000±0.000 |
| 14.1022/07 | 0.040±0.026 | 0.023±0.004 | 0.015±0.013 |
| 14.1081/01 | 0.000±0.000 | 0.012±0.013 | 0.000±0.000 |
| 14442/04 | 0.008±0.014 | 0.000±0.000 | 0.019±0.033 |
| 14442/06 | 0.000±0.000 | 0.025±0.025 | 0.055±0.040 |
| 15176/01HC | 0.010±0.017 | 0.020±0.009 | 0.017±0.144 |
| 15207/01 | 0.023±0.004 | 0.016±0.012 | 0.008±0.014 |
| 15703/06 | 0.008±0.014 | 0.023±0.015 | 0.043±0.023 |
| 16186/02 | 0.008±0.014 | 0.000±0.000 | 0.000±0.000 |
| 16186/03 | 0.000±0.000 | 0.003±0.006 | 0.013±0.023 |
| 16282/01 | 0.018±0.018 | 0.037±0.013 | 0.029±0.006 |
| 16588/03 | 0.024±0.022 | 0.042±0.014 | 0.047±0.014 |
| 16650/16 | 0.012±0.011 | 0.012±0.011 | 0.000±0.000 |

| | | | |
|---|---|---|---|
| 16742/01 | 0.002±0.003 | 0.000±0.000 | 0.000±0.000 |
| 14.1077/02 | 0.024±0.084 | 0.190±0.044 | 0.163±0.081 |
| 16.1056/02HC | 0.381±0.075 | 0.746±0.180 | 0.591±0.182 |
| 16.1089/01 | 0.090±0.052 | 0.163±0.163 | 0.110±0.026 |
| 16.1061/01HC | 0.117±0.046 | 0.135±0.003 | 0.045±0.043 |
| 15176/05 | 0.042±0.039 | 0.100±0.027 | 0.049±0.012 |
| Adretta | 0.744±0.008 a | 0.840±0.023 b | 0.857±0.057 b |
| Jelly | 0.526±0.060 | 0.568±0.033 | 0.457±0.115 |
| Krone | 0.734±0.071 | 0.605±0.086 | 0.540±0.003 |
| Otolia | 0.159±0.072 | 0.234±0.088 | 0.137±0.031 |
| | **mean score 2020 (detached leaf assay)** | | |
| | **N1** | **N2** | **N3** |
| 11.1025.03 | 1.100±0.173 | 1.000±0.000 | 1.000±0.000 |
| 131031/01 | 1.000±0.000 | 1.000±0.000 | 1.000±0.000 |
| 14.1022/07 | 1.133±0.231 | 1.000±0.000 | 1.133±0.153 |
| 14.1081/01 | 1.100±0.173 | 1.000±0.000 | 1.033±0.058 |
| 14442/04 | 1.200±0.200 | 1.100±0.100 | 1.000±0.000 |
| 14442/06 | 1.067±0.115 | 1.000±0.000 | 1.000±0.000 |
| 15176/01HC | 1.033±0.058 | 1.000±0.000 | 1.100±0.173 |
| 15207/01 | 1.100±0.153 | 1.100±0.100 | 1.100±0.173 |
| 15703/06 | 1.000±0.000 | 1.000±0.000 | 1.000±0.000 |
| 16186/02 | 1.033±0.058 | 1.000±0.000 | 1.000±0.000 |
| 16186/03 | 1.000±0.000 | 1.000±0.000 | 1.000±0.000 |
| 16282/01 | 1.500±0.700 | 1.433±0.321 | 1.200±0.173 |
| 16588/03 | 1.033±0.058 | 1.133±0.231 | 1.000±0.000 |
| 16650/16 | 1.533±0.462 | 1.500±0.458 | 1.533±0.924 |
| 16742/01 | 1.133±0.153 | 1.100±0.173 | 1.167±0.289 |
| 14.1077/02 | 1.300±0.361 | 1.333±0.351 | 1.700±1.044 |
| 16.1056/02HC | 4.067±0.757 | 2.700±0.346 | 3.667±1.050 |
| 16.1089/01 | 2.767±1.097 | 2.700±0.300 | 2.133±0.416 |
| 16.1061/01HC | 1.333±0.289 | 1.500±0.400 | 1.333±0.351 |
| 15176/05 | 1.567±0.289 b | 1.133±0.231 ab | 1.000±0.000 a |
| Adretta | 4.800±0.265 a | 5.233±0.208 a | 6.600±0.557 b |
| Jelly | 3.833±2.250 | 3.033±0.666 | 3.600±0.721 |
| Krone | 4.700±0.529 b | 3.533±0.289 ab | 2.733±1.172 a |
| Otolia | 3.267±0.462 | 3.733±1.563 | 3.700±0.265 |
| | **mean score 2020 (tuber slice test)** | | |
| | **N1** | **N2** | **N3** |
| 11.1025.03 | 1.667±0.100 | 1.677±0.148 | 1.635±0.154 |
| 131031/01 | 1.990±0.313 | 2.854±0.273 | 2.969±0.641 |
| 14.1022/07 | 2.344±0.360 | 2.396±0.036 | 2.583±0.319 |
| 14.1081/01 | 2.302±0.361 | 2.156±0.108 | 2.427±0.230 |
| 14442/04 | 1.990±0.203 | 2.271±0.160 | 2.208±0.048 |
| 14442/06 | 3.813±0.054 | 3.760±0.470 | 3.323±0.110 |
| 15176/01HC | 4.490±0.144 | 4.000±0.706 | 3.750±0.136 |
| 15207/01 | 2.927±0.398 | 3.063±0.225 | 3.208±0.253 |
| 15703/06 | 2.875±0.094 | 3.104±0.396 | 3.010±0.095 |

| | | | |
|---|---|---|---|
| 16186/02 | 2.646±0.663 | 2.615±0.280 | 3.379±0.115 |
| 16186/03 | 1.507±0.033 | 1.500±0.054 | 1.750±0.545 |
| 16282/01 | 1.969±0.298 | 1.792±0.048 | 2.063±0.143 |
| 16588/03 | 3.302±0.474 | 3.115±0.308 | 3.094±0.281 |
| 16650/16 | 1.417±0.036 | 1.531±0.063 | 1.552±0.065 |
| 16742/01 | 2.750±0.108 | 2.854±0.300 | 2.900±0.563 |
| 14.1077/02 | 3.688±0.094 | 3.208±0.203 | 4.021±0.398 |
| 16.1056/02HC | 2.500±0.344 | 2.906±0.434 | 2.938±0.308 |
| 16.1089/01 | 2.896±0.048 | 3.000±0.136 | 2.896±0.455 |
| 16.1061/01HC | 2.792±0.126 | 2.625±0.467 | 2.927±0.090 |
| 15176/05 | 3.271±0.203 | 3.104±0.144 | 3.208±0.402 |
| Adretta | 3.677±0.100 | 3.969±0.368 | 4.219±0.313 |
| Jelly | 4.198±0.079 | 3.948±0.213 | 4.010±0.172 |
| Krone | 3.354±0.403 | 3.563±0.420 | 3.646±0.110 |
| Otolia | 4.125±0.063 | 3.844±0.125 | 4.104±0.253 |
| | **mean ΔrAUDPC 2021** | | |
| | **N1** | **N2** | **N3** |
| 11.1025.03 | -0.226±0.000 | -0.229±0.007 | -0.215±0.019 |
| 131031/01 | -0.255±0.012 | -0.233±0.012 | -0.234±0.047 |
| 14.1022/07 | -0.217±0.018 | -0.230±0.022 | -0.212±0.012 |
| 14.1081/01 | -0.220±0.027 | -0.215±0.019 | -0.212±0.012 |
| 14442/04 | -0.234±0.021 | -0.244±0.016 | -0.230±0.006 |
| 14442/06 | -0.245±0.021 | -0.255±0.033 | -0.192±0.043 |
| 15176/01HC | -0.263±0.017 a | -0.212±0.012 ab | -0.208±0.027 b |
| 15207/01 | -0.278±0.093 | -0.218±0.012 | -0.199±0.095 |
| 15703/06 | -0.240±0.016 | -0.240±0.006 | -0.230±0.006 |
| 16186/02 | -0.283±0.054 | -0.227±0.010 | -0.223±0.017 |
| 16186/03 | -0.237±0.011 | -0.244±0.006 | -0.209±0.007 |
| 16282/01 | -0.253±0.040 | -0.234±0.026 | -0.240±0.016 |
| 16588/03 | -0.266±0.025 | -0.247±0.019 | -0.240±0.016 |
| 16650/16 | -0.244±0.016 | -0.212±0.053 | -0.233±0.016 |
| 16742/01 | -0.148±0.027 | -0.162±0.037 | -0.123±0.080 |
| 14.1077/02 | -0.234±0.035 | -0.230±0.006 | -0.187±0.036 |
| 16.1056/02HC | 0.164±0.065 | 0.295±0.047 | 0.303±0.082 |
| 16.1089/01 | -0.236±0.014 | -0.202±0.018 | -0.202±0.039 |
| 16.1061/01HC | -0.222±0.007 | -0.234±0.004 | -0.222±0.012 |
| 15176/05 | -0.301±0.060 | -0.240±0.016 | -0.233±0.012 |
| Adretta | 0.133±0.042 a | 0.337±0.157 ab | 0.502±0.146 b |
| Jelly | 0.153±0.051 | 0.231±0.050 | 0.210±0.047 |
| Krone | 0.286±0.109 | 0.317±0.064 | 0.289±0.047 |
| Otolia | -0.098±0.144 | -0.139±0.025 | -0.150±0.050 |
| | **mean rAUDPC 2021** | | |
| | **N1** | **N2** | **N3** |
| 11.1025.03 | 0.000±0.000 | 0.001±0.002 | 0.000±0.000 |
| 131031/01 | 0.000±0.000 | 0.000±0.000 | 0.007±0.012 |
| 14.1022/07 | 0.005±0.005 | 0.000±0.000 | 0.000±0.000 |
| 14.1081/01 | 0.002±0.004 | 0.000±0.000 | 0.000±0.000 |

| | | | |
|---|---|---|---|
| 14442/04 | 0.003±0.005 | 0.000±0.000 | 0.000±0.000 |
| 14442/06 | 0.006±0.010 | 0.000±0.000 | 0.006±0.005 |
| 15176/01HC | 0.005±0.005 | 0.000±0.000 | 0.000±0.000 |
| 15207/01 | 0.001±0.002 | 0.001±0.001 | 0.002±0.004 |
| 15703/06 | 0.000±0.000 | 0.000±0.000 | 0.000±0.000 |
| 16186/02 | 0.000±0.000 | 0.013±0.015 | 0.003±0.005 |
| 16186/03 | 0.000±0.000 | 0.000±0.000 | 0.003±0.005 |
| 16282/01 | 0.005±0.009 | 0.003±0.005 | 0.000±0.000 |
| 16588/03 | 0.006±0.010 | 0.000±0.000 | 0.000±0.000 |
| 16650/16 | 0.000±0.000 | 0.000±0.000 | 0.000±0.000 |
| 16742/01 | 0.000±0.000 | 0.000±0.000 | 0.000±0.000 |
| 14.1077/02 | 0.013±0.004 | 0.003±0.005 | 0.010±0.010 |
| 16.1056/02HC | 0.454±0.093 | 0.525±0.041 | 0.529±0.063 |
| 16.1089/01 | 0.004±0.003 | 0.006±0.010 | 0.013±0.014 |
| 16.1061/01HC | 0.011±0.011 | 0.002±0.004 | 0.011±0.001 |
| 15176/05 | 0.000±0.000 | 0.000±0.000 | 0.000±0.000 |
| Adretta | 0.658±0.042 | 0.744±0.030 | 0.671±0.117 |
| Jelly | 0.336±0.041 | 0.379±0.024 | 0.340±0.063 |
| Krone | 0.533±0.058 | 0.500±0.064 | 0.440±0.047 |
| Otolia | 0.100±0.140 | 0.063±0.018 | 0.037±0.053 |
| | **mean score 2021 (detached leaf assay)** | | |
| | **N1** | **N2** | **N3** |
| 11.1025.03 | 1.033±0.058 | 1.000±0.000 | 1.000±0.000 |
| 131031/01 | 1.000±0.000 | 1.000±0.000 | 1.000±0.000 |
| 14.1022/07 | 1.000±0.000 | 1.000±0.000 | 1.000±0.000 |
| 14.1081/01 | 1.033±0.058 | 1.033±0.058 | 1.000±0.000 |
| 14442/04 | 1.000±0.000 | 1.000±0.000 | 1.000±0.000 |
| 14442/06 | 1.367±0.635 | 1.000±0.000 | 1.000±0.000 |
| 15176/01HC | 1.000±0.000 | 1.000±0.000 | 1.000±0.000 |
| 15207/01 | 1.467±0.404 | 1.000±0.000 | 1.033±0.058 |
| 15703/06 | 1.033±0.058 | 1.000±0.000 | 1.000±0.000 |
| 16186/02 | 1.033±0.058 | 1.000±0.000 | 1.000±0.000 |
| 16186/03 | 1.000±0.000 | 1.000±0.000 | 1.067±0.115 |
| 16282/01 | 1.100±0.100 | 1.000±0.000 | 1.133±0.115 |
| 16588/03 | 1.067±0.115 | 1.000±0.000 | 1.000±0.000 |
| 16650/16 | 1.000±0.000 | 1.000±0.000 | 1.000±0.000 |
| 16742/01 | 1.000±0.000 | 2.367±2.281 | 1.000±0.000 |
| 14.1077/02 | 5.200±0.346 | 4.333±1.102 | 3.533±1.361 |
| 16.1056/02HC | 5.300±0.529 | 5.433±0.252 | 5.100±0.100 |
| 16.1089/01 | 2.000±0.346 | 1.775±0.426 | 1.633±0.513 |
| 16.1061/01HC | 1.167±0.153 | 1.267±0.379 | 1.100±0.100 |
| 15176/05 | 1.767±0.666 | 1.733±0.493 | 2.233±1.201 |
| Adretta | 6.433±0.666 | 7.433±0.551 | 6.567±0.751 |
| Jelly | 6.467±0.252 | 6.100±1.000 | 5.867±1.002 |
| Krone | 7.600±0.265 | 5.167±2.003 | 6.767±0.643 |
| Otolia | 5.975±0.663 b | 4.900±1.179 ab | 2.833±1.504 a |
| | **mean score 2021 (tuber slice test)** | | |

| | N1 | N2 | N3 |
|---|---|---|---|
| 11.1025.03 | 1.396±0.036 | 1.438±0.063 | 1.604±0.237 |
| 131031/01 | 2.271±0.607 | 1.813±0.188 | 2.208±0.366 |
| 14.1022/07 | 1.604±0.237 | 1.896±0.282 | 1.979±0.219 |
| 14.1081/01 | 2.281±0.094 | 2.344±0.156 | 2.719±0.281 |
| 14442/04 | 1.708±0.130 | 1.646±0.072 | 2.021±0.315 |
| 14442/06 | 2.167±0.315 | 2.271±0.796 | 2.667±0.564 |
| 15176/01HC | 3.438±0.217 | 3.465±0.558 | 4.146±0.157 |
| 15207/01 | 2.417±0.237 | 2.521±0.443 | 2.833±0.180 |
| 15703/06 | 2.583±0.832 | 2.521±0.473 | 2.208±0.282 |
| 16186/02 | 2.000±0.488 | 2.250±0.390 | 2.396±0.564 |
| 16186/03 | 1.375±0.063 | 1.396±0.130 | 1.604±0.072 |
| 16282/01 | 1.646±0.144 | 1.958±0.407 | 2.146±0.201 |
| 16588/03 | 2.708±0.191 | 2.771±0.629 | 3.271±0.377 |
| 16650/16 | 1.333±0.072 | 1.479±0.095 | 1.521±0.095 |
| 16742/01 | 2.208±0.201 a | 2.854±0.686 ab | 3.708±0.477 b |
| 14.1077/02 | 3.417±0.469 | 3.167±0.377 | 3.333±0.289 |
| 16.1056/02HC | 2.292±0.219 a | 3.042±0.308 ab | 3.646±0.567 b |
| 16.1089/01 | 2.708±0.201 | 3.500±0.798 | 3.521±0.157 |
| 16.1061/01HC | 2.479±0.295 | 2.542±0.509 | 2.792±0.315 |
| 15176/05 | 2.625±0.125 | 2.750±0.534 | 2.958±0.407 |
| Adretta | 3.417±0.180 | 3.792±0.862 | 4.229±0.377 |
| Jelly | 4.000±0.691 | 3.146±0.382 | 3.688±0.438 |
| Krone | 2.479±0.366 a | 3.125±0.165 b | 3.271±0.072 b |
| Otolia | 3.417±0.157 | 4.292±0.072 | 3.667±0.308 |

significant higher scores with higher N level

significant lower scores with higher N level

## 3. Diskussion

In der vorliegenden Arbeit wurde das *Phytophthora infestans* Resistenzpotential wilder Kartoffelverwandter dargestellt und die Möglichkeiten erläutert, dieses Potential für die Kartoffelzüchtung zugänglich zu machen (Kapitel 2.1). Anschließend wurde der Kartoffelgenpool des JKI auf das Vorhandensein verschiedener R-Gene gegen *P. infestans* aus eingekreuzten Wildarten untersucht (Kapitel 2.2) und es wurden genomweite Assoziationsstudien durchgeführt (Kapitel 2.3 und 2.4). Abschließend wurde untersucht, ob verschieden hohe Stickstoffgaben das Befallsniveau mit *P. infestans* bei herkömmlichen Sorten und Zuchtstämmen beeinflussen (Kapitel 2.5).

### 3.1 Resistenzpotential wilder Verwandter

Die Züchtung *P. infestans* resistenter Sorten ist bis heute von enormer Bedeutung für den Kartoffelanbau, da die Krautfäule Verluste in Milliardenhöhe verursacht (Haas et al. 2009; Haverkort et al. 2009; USABlight 2021). Ein erster Schritt zu deren Bekämpfung besteht darin, Resistenzquellen in Wildmaterial ausfindig zu machen.

Bei der Zusammenstellung von 74 Studien, die sich mit der *P. infestans* Resistenz bei wilden Verwandten der Kulturkartoffel beschäftigten, zeigte sich ein großes Potential bisher ungenutzter Resistenzquellen. So wurden seit dem letzten Review von Tiwari et al. (2013) insgesamt 25 weitere Wildarten mit Resistenzen entdeckt. Zudem zeigte sich, dass neben diesen 25 Arten 30 weitere als Resistenzquellen beschrieben, die Resistenzen aber nicht näher untersucht wurden. Insgesamt konnte in 85 Wildarten eine Resistenz gefunden werden. Da nicht einmal bei der Hälfte dieser Arten entsprechende R-Gene oder QTL detektiert worden sind, besteht noch ein erheblicher Forschungsbedarf, um weitere potentielle Resistenzquellen züchterisch nutzbar zu machen.

### 3.2 Möglichkeiten für eine zukünftige Kartoffelzüchtung

Die heutige Kartoffelzüchtung ist überwiegend auf klassische Methoden fokussiert. Tetraploide Zuchtstämme und Sorten werden gekreuzt und die anschließende heterozygote F1 Generation über mehrere Jahre auf viele verschiedene Merkmale wie Knollenform, Schalenfarbe, Speiseeignung oder das Resistenzniveau gegenüber verschiedenen Schaderregern hin bonitiert und selektiert. Dieses Vorgehen ist langwierig und dauert bis zur Entstehung einer neuen Sorte etwa 14 Jahre (Jansky & Spooner 2018).

Eine Möglichkeit für eine schnellere und weniger umfangreiche Züchtung wäre die diploide Züchtung, die sich bereits bei einigen Kartoffelzuchtunternehmen in einer Testphase befindet.

In diploiden Zuchtstämmen kann aufgrund der Mendelschen Regeln schneller auf rezessive Allele selektiert werden und ungewünschte Allele können einfacher entfernt werden (Jansky et al. 2016). Langfristiges Ziel für die Zuchtunternehmen wäre das Erstellen von Inzuchtlinien, bei denen zudem die Vermehrung über true potato seeds (TPS) kostengünstiger ist und die Samen das Risiko minimieren, Krankheiten in die nächste Generation zu überführen (Jansky et al. 2016; Lindhout et al. 2016). Bei der diploiden Züchtung wäre es auch deutlich einfacher, Resistenzen einzukreuzen (Su et al. 2020). So könnte mit einem Großteil der in Kapitel 2.1 aufgezeigten Wildarten mit Krautfäuleresistenz direkt gekreuzt werden.

Neben der diploiden Züchtung stellt die genetische Modifikation eine weitere Möglichkeit dar, um die Züchtung schneller und einfacher zu gestalten. Zum Beispiel konnte in Bezug auf eine *P. infestans* Resistenz mithilfe der Cisgenesis Methode die Sorte „Fortuna“ entwickelt werden, die die beiden R-Gene *Rpi-blb1* und *Rpi-blb2* trägt (Storck et al. 2011). Da diesen Methoden aber gerade in der EU aufgrund strenger Regularien und geringer Verbraucherakzeptanz wenig Bedeutung zukommt (Eckerstorfer et al. 2019; McComas et al. 2014), sollte angesichts der vielen Vorteile dieser Methoden über eine neue Regulierung nachgedacht werden (Waters et al. 2021).

### 3.3 R-Gene und QTL für eine *P. infestans* Resistenz im JKI Kartoffelgenpool

Der Kartoffelgenpool des JKI wird seit den 1950iger Jahren in einem Langzeitzuchtprogramm fortgeführt. Während anfänglich Kreuzungen zwischen Sorten und *P. infestans* Resistenzträgern durchgeführt wurden, steht zum jetzigen Zeitpunkt das Einbringen agronomischer Eigenschaften durch Sorteneinkreuzungen im Vordergrund. Mittlerweile befinden sich die Zuchtstämme in der Rückkreuzungsgeneration sieben und höher. In der vorliegenden Arbeit wurde mittels eines Screenings ein Umfang von 52 Zuchtklonen auf das Vorhandensein verschiedener R-Gene untersucht (Kapitel 2.2). Dabei zeigte sich zum einen, dass in einzelnen Zuchtstämmen bis zu vier R-Gene nachweisbar waren, zum anderen konnte aber auch festgestellt werden, dass einige Zuchtstämme ein hohes Resistenzniveau aufwiesen, obwohl kein R-Gen detektiert wurde. Um diesem weiter nachzugehen, wurden zwei genomweite Assoziationsstudien durchgeführt. Bei der ersten wurden anhand von 265 pre-breeding Stämmen und 102 Sorten insgesamt fünf QTL für eine *P infestans* Resistenz auf den Chromosomen 1, 7, 10 und 11 gefunden (Kapitel 2.3). Darüber hinaus wurde zwischen 2018 und 2021 eine weitere Assoziationsstudie mit 161 pre-breeding Stämmen und 39 Sorten durchgeführt (Kapitel 2.4). Dabei zeigten sich für die Krautfäuleresistenz zwei Marker-Merkmalsassoziationen auf Chromosom 9 und 11. Für die in dieser Studie auch untersuchte

Knollenfäuleresistenz wurde keine Marker-Merkmalsassoziation detektiert. Kraut- und Knollenfäule werden vermutlich unabhängig voneinander vererbt (Douches et al. 2002; Mayton et al. 2010; Platt & Tai 1998). Die Zuchtstämme hatten bei der Krautfäuleprüfung deutlich niedrigere Boniturnoten als bei der Knollenfäuleprüfung (Kapitel 2.4, Supplementary Table 1), sodass die Resistenz des JKI Genpools möglicherweise vor allem auf Krautfäuleresistenz basiert.

Diese neueren Ergebnisse zeigen, dass sich der JKI Genpool durch jährliche Kreuzungsarbeiten auch bezogen auf seine Krautfäuleresistenz stetig weiterentwickelt. Auf Chromosom 9 befinden sich auf dem Arm, auf dem die Marker-Merkmalsassoziation liegt, einige R-Gene, unter anderem *R8* und *R9a*, die möglicherweise durch Kreuzungen mit *S. demissum* in den Genpool gelangten. Sie sind aber zu weit entfernt, als dass sie Ursache der Marker-Merkmalsassoziation sein können (Jo et al. 2011 und 2015; Jiang et al. 2018). Von einer anderen Arbeitsgruppe wurde dagegen ein QTL gefunden, der nur 0.28 Mb von dem hier beschriebenen entfernt liegt (Lindqvist-Kreuze et al. 2014).

In beiden Studien wurden Marker-Merkmalsassoziationen auf Chromosom 11 gefunden, dabei ist die aus der ersten Studie ca. 0.5 Mb von den Marker-Merkmalsassoziationen aus der zweiten Studie entfernt. Dies dürfte darauf zurückzuführen sein, dass Zuchtstämme aus der ersten Studien teilweise als Eltern für Zuchtstämme der zweiten Studie eingesetzt worden sind. Die Genotypisierung erfolgte bei der ersten Studie mittels Diversity Arrays Technology (DArT Array), während für die zweite Studie Genotyping-by-sequencing (GBS) verwendet wurde. Aufgrund dieser unterschiedlichen Methoden ist ein genauerer Vergleich der Ergebnisse nicht möglich.

Auf Chromosom 11 befinden sich außerdem fünf NBS-LLR Gene im Bereich signifikanter Marker. Diese Resistenz auf Chromosom 11 könnte auch aus der häufig eingekreuzten Art *S. phureja* oder aus der ebenfalls für viele Kreuzungen verwendeten Sorte *S. tuberosum* cv. „Sarpo Mira“ stammen. Im Fall von „Sapro Mira“ sind allerdings noch weitere Untersuchungen notwendig, denn einerseits befindet sich das Gen *Rpi-Smira1* auf Chromosom 11 in Nähe von *R3a* aus *S. demissum* (Rietman et al. 2012) und somit nicht in der Nähe der Marker-Merkmalsassoziation, andererseits wurde das resistenztragende Allel aber auch bei „Sarpo Mira“ nachgewiesen. Weiterführenden Studien, die diese Resistenz näher untersuchen, gehören zum möglichen Aufgabenpotential zukünftiger Forschungen am JKI.

Bei der Betrachtung aller Ergebnisse aus den Kapitel 2.2 bis 2.4 kann über den Genpool zusammengefasst werden, dass er sowohl R-Genen, als auch QTL bzw. Marker-

Merkmalsassoziationen gegen *P infestans* trägt. Dabei bestätigte Kapitel 2.2, dass einzelne R-Gene wie beispielsweise *R3a* oder *R3b* alleine nicht für die Resistenz verantwortlich sein können, da diese auch bei anfälligen Zuchtstämmen nachweisbar waren. Gerade aus *S. demissum* sind viele R-Gene allein vorkommend schon lange gebrochen worden (Wastie 1991). In Kombination mit R-Genen aus anderen Arten dagegen konnte gezeigt werden, dass sie an einer langfristigen Resistenz beteiligt sind (Zhu et al. 2012; Ghislain et al. 2019; Stefańczyk et al. 2020). Auch das spiegelte sich in Zuchtstämmen wieder, bei denen zusätzliche Gene wie beispielsweise *Rpi-blb1*, welches eine Resistenz gegen ein breites Erregerspektrum trägt (Van der Vossen et al. 2003), detektiert wurden. Manche der Zuchtstämme zeigten aber auch ohne das Auffinden von R-Genen ein hohes Resistenzniveau, welches somit auf den QTL und Marker-Merkmalsassoziationen aus den Kapitel 2.3 und 2.4 begründet sein kann.

Die eingangs genannten Hypothesen über das Vorhandensein von R-Genen und QTL im JKI Genpool konnten somit in Teilen bestätigt werden. Wenngleich der Genpool somit schon heute ein Potential für die zukünftige Züchtung birgt, bleibt längerfristig das Ziel, diesen sowohl durch eine quantitative Resistenz, die bisher kaum im Genpool vorhanden ist, als auch durch weitere monogene Resistenzen in Form einer Pyramidisierung einzelner R-Gene in seinen Resistenzeigenschaften zu optimieren.

So haben die Auswertungen aus Kapitel 2.1 gezeigt, dass es noch wesentlich mehr Resistenzen in Wildmaterial gibt, das als eine Option für die Zukunft in den Genpool eingekreuzt werden könnte. In Kapitel 1.5 wurden verschiedene Studien vorgestellt, die QTL für eine *P. infestans* Resistenz detektierten. Beispielsweise wurden bei Mosquera et al. (2016) 27 QTL gefunden. Es wäre demnach eine weitere Möglichkeit, das Zuchtmaterial dieser verschiedenen Studien mit in den JKI Kartoffelgenpool einzukreuzen. Parallel dazu sollte auch das Pyramidisieren von R-Gene oder QTL in einzelnen Zuchtstämmen weiter im Fokus stehen, um die Gefahr eines Durchbrechens der *P. infestans* Resistenz zu minimieren.

### 3.4 Einfluss von Stickstoff auf den Befall mit *P. infestans*

In einem zweijährigen Versuch mit drei Stickstoffdüngestufen und 24 Prüfgliedern zeigte sich, dass der Krankheitsbefall mit *P. infestans* durch die eingesetzte Menge an Stickstoff wenig beeinflusst wurde. Entscheidend ist hierbei viel mehr die Sortenwahl. Allgemein erwiesen sich die zugelassenen Sorten in allen Düngestufen ähnlich anfällig für *P. infestans*, während die hochresistenten Zuchtstämme des JKI unabhängig von der Stickstoffdüngung kaum bis gar nicht befallen wurden. Besonders für den ökologischen Landbau, für den die Möglichkeiten der *P. infestans* Bekämpfung sehr begrenzt sind, sollten diese Zuchtstämme des JKI zukünftig

verstärkt in Zuchtprogrammen Verwendung finden. Die eingangs genannte Hypothese, dass organischer Stickstoff in hohen Gaben den Krankheitsbefall mit *P. infestans* bei herkömmlichen Sorten, nicht aber bei den resistenten JKI Zuchtstämmen erhöht, konnte somit nicht bestätigt werden. Anders als Stickstoff können andere Nährstoffe wie Phosphor oder Kalium den Befall deutlich beeinflussen. So konnte beispielsweise für Kalium gezeigt werden, dass hohe Gaben den Befall verringern (Kowalska & Drożdżyński 2018; Bista & Bhandari 2019). Auch hinsichtlich diese Nährstoffe besteht weiterführender Forschungsbedarf.

## 3.5 Ausblick

Mit dieser Arbeit wurde aufgezeigt, dass eine große Anzahl wilder Verwandter der Kulturkartoffel noch viele in der Züchtung bisher ungenutzte Resistenzquellen bieten. Überdies wurden Möglichkeiten erläutert, mit denen diese Resistenzen in Zuchtprogramme eingebaut werden können. Dazu zählt neben der klassischen Züchtung vor allem die diploide Züchtung, aber auch die Gentechnik könnte dafür eingesetzt werden. Des Weiteren wurde in dieser Arbeit der Kartoffelgenpool des JKI auf seine *P. infestans* Resistenz hin untersucht. Dabei wurden einige bekannte R-Gene aus Wildarten sowie zusätzliche QTL bzw. Marker-Merkmalsassoziationen gefunden. Zum Abschluss wurde der Zusammenhang zwischen Stickstoffdüngung und *P. infestans* Befall untersucht, bei dem sich zeigte, dass sich Stickstoff kaum auf den Befall auswirkt und einzig hochresistente Zuchtstämme wie die des JKI kaum befallen werden und somit von großem Nutzen gerade für den ökologischen Landbau mit seinen begrenzten Bekämpfungsmöglichkeiten sein können. Für die Zukunft der Kartoffelzüchtung sollte in Hinblick auf eine langfristige *P. infestans* Resistenz zunächst das Charakterisieren der noch wenig untersuchten Resistenzen aus Wildmaterial im Vordergrund stehen. Ein nächster Schritt bestünde im Einkreuzen dieser Resistenzen, möglicherweise auch über die diploide Züchtung oder auch über genetische Modifikation. Wichtig dabei wäre es, zum einen mehrere R-Gene in einzelnen Stämmen zu pyramidisieren aber auch durch QTL bedingte quantitative Resistenzen mit einzubringen, um die Stämme bzw. Sorten möglichst langfristig resistent zu machen.

# 4 Literaturverzeichnis Kapitel 1 und 3


Agu, C. M. (2004). Effect of nitrogen and phosphorus combination on late blight disease and potato yield. *Tropical Science*, *44*(4), 163-165. https://doi.org/10.1002/ts.159

Arora, R. K., Sharma, S., & Singh, B. P. (2014). Late blight disease of potato and its management. *Potato Journal*, *41*(1), 16-40.

Bangemann, L. W. (2010). Pathogen-Nährstoff-Interaktionen in der Kartoffel: Am Beispiel der Kraut-und Knollenfäule und der Stickstoffversorgung im ökologischen Anbau. Mitt. Ges. Pflanzenbauwiss. 22, 31-34.

Birch, P. R., Bryan, G., Fenton, B., Gilroy, E. M., Hein, I., Jones, J. T., Prashar, A., Taylor, M. A., Torrance, L., & Toth, I. K. (2012). Crops that feed the world 8: potato: are the trends of increased global production sustainable?. *Food Security*, *4*(4), 477-508. https://doi.org/10.1007/s12571-012-0220-1

Bista, B., & Bhandari, D. (2019). Potassium fertilization in potato. *International Journal of Applied Sciences and Biotechnology*, *7*(2), 153-160. https://doi.org/10.3126/ijasbt.v7i2.24636

Black, W., Mastenbroek, C., Mills, W. R., & Peterson, L. C. (1953). A proposal for an international nomenclature of races of *Phytophthora infestans* and of genes controlling immunity in *Solanum demissum* derivatives. *Euphytica*, *2*(3), 173-179. https://doi.org/10.1007/BF00053724

Bradshaw, J. E., Bryan, G. J., Lees, A. K., McLean, K., & Solomon-Blackburn, R. M. (2006). Mapping the *R10* and *R11* genes for resistance to late blight (*Phytophthora infestans*) present in the potato (*Solanum tuberosum*) R-gene differentials of Black. *Theoretical and Applied Genetics*, *112*(4), 744-751. https://doi.org/10.1007/s00122-005-0179-9

Bradshaw, J. E. (2007). Potato-breeding strategy. *Potato biology and biotechnology* , 157-177, Elsevier Science BV.

Bruggen, A. H. C. van, Gamliel, A., & Finckh, M. R. (2016). Plant disease management in organic farming systems. *Pest Management Science*, *72*(1), 30-44. https://doi.org/10.1002/ps.4145

Bormann, C. A., Rickert, A. M., Castillo Ruiz, R. A., Paal, J., Lübeck, J., Strahwald, J., Buhr, K. & Gebhardt, C. (2004). Tagging quantitative trait loci for maturity-corrected late blight resistance in tetraploid potato with PCR-based candidate gene markers. *Molecular plant-microbe interactions*, *17*(10), 1126-1138. https://doi.org/10.1094/MPMI.2004.17.10.1126

Burton, W. G. (1989). *The potato* (No. Ed. 3). Longman Group Limited, Harlow, Essex, United Kingdom.

Cicore, P. L., Andreu, A. B., & Huarte, M. A. (2012). Reaction to late blight in response to nitrogen management in Argentine potato cultivars. *Crop protection*, *42*, 69-73. https://doi.org/10.1016/j.cropro.2012.07.016

Cooke, D. E. L., Young, V., Birch, P. R. J., Toth, R., Gourlay, F., Day, J. P., Carnegie, S. F., & Duncan, J. M. (2003). Phenotypic and genotypic diversity of *Phytophthora infestans* populations in Scotland (1995–97). *Plant Pathology*, *52*(2), 181-192. https://doi.org/10.1046/j.1365-3059.2003.00817.x

Danan, S., Veyrieras, J. B., & Lefebvre, V. (2011). Construction of a potato consensus map and QTL meta-analysis offer new insights into the genetic architecture of late blight resistance and plant maturity traits. *BMC Plant Biology*, *11*(1), 1-17. https://doi.org/10.1186/1471-2229-11-16

De Ferrière le Vayer, M. (2017). The potato: A long history to fit our contemporary world. *Potato Research*, *60*(3), 223-235. https://doi.org/10.1007/s11540-018-9352-9

De Jong, H. (2016). Impact of the potato on society. American journal of potato research, 93(5), 415-429. https://doi.org/10.1007/s12230-016-9529-1

Douches, D. S., Kirk, W. W., Bertram, M. A., Coombs, J. J., & Niemira, B. A. (2002). Foliar and tuber assessment of late blight (*Phytophthora infestans* (Mont.) de Bary) reaction in cultivated potato (*Solanum tuberosum* L.). *Potato Research*, *45*(2), 215-224. https://doi.org/10.1007/BF02736116

Drenth, A., Tas, I. C., & Govers, F. (1994). DNA fingerprinting uncovers a new sexually reproducing population of *Phytophthora infestans* in the Netherlands. *European Journal of Plant Pathology*, *100*(2), 97-107. https://doi.org/10.1007/BF01876244

Drenth, A., Janssen, E. M., & Govers, F. (1995). Formation and survival of oospores *of Phytophthora infestans* under natural conditions. *Plant pathology*, *44*(1), 86-94. https://doi.org/10.1111/j.1365-3059.1995.tb02719.x

Durchführungsverordnung (EU) 2018/1981 der Kommission vom 13. Dezember 2018 zur Erneuerung der Genehmigung für die Wirkstoffe Kupferverbindungen als Substitutionskandidaten gemäß der Verordnung (EG) Nr. 1107/2009 des Europäischen Parlaments und des Rates über das Inverkehrbringen von Pflanzenschutzmitteln und zur Änderung des Anhangs der Durchführungsverordnung (EU) Nr. 540/2011 der Kommission (Text von Bedeutung für den EWR.) https://op.europa.eu/de/publication-detail/-/publication/c5ac184b-ff4b-11e8-a96d-01aa75ed71a1

Eckerstorfer, M. F., Engelhard, M., Heissenberger, A., Simon, S., & Teichmann, H. (2019). Plants developed by new genetic modification techniques - comparison of existing regulatory frameworks in the EU and non-EU countries. *Frontiers in Bioengineering and Biotechnology*, *7*, 26. https://doi.org/10.3389/fbioe.2019.00026

Engel, F. (1970). Exploration of the Chilca canyon, Peru. *Current Anthropology*, *11*(1), 55-58. https://doi.org/10.1086/201093

FAO (2021). World Food and Agriculture - Statistical Yearbook 2021. Rome. https://doi.org/10.4060/cb4477en

FAOSTAT (2022). Top Countries in Potatoes Production – Source FAO. https://www.nationmaster.com/nmx/ranking/potatoes-production-fao

Fry, E., Goodwin, S., Dyer, A., Matusralt, M., Drenth, A., Cohen, A., & Spielman, L. (1993). Historical and recent migrations of *Phytophthora infestans*: chronology, pathways, and implications. *Plant disease*, *77*, 653-661.

Fry, W. (2008). *Phytophthora infestans*: the plant (and R gene) destroyer. *Molecular plant pathology*, *9*(3), 385-402. https://doi.org/10.1111/j.1364-3703.2007.00465.x

Ghislain, M., Byarugaba, A. A., Magembe, E., Njoroge, A., Rivera, C., Román, M. L., Tovar, J. C., Gamboa, S., Forbes, G. A., Kreuze, J. F., Barekye, A., & Kiggundu, A. (2019). Stacking three late blight resistance genes from wild species directly into African highland potato varieties confers complete field resistance to local blight races. *Plant Biotechnology Journal*, *17*(6), 1119-1129. https://doi.org/10.1111/pbi.13042

Goss, E. M., Tabima, J. F., Cooke, D. E., Restrepo, S., Fry, W. E., Forbes, G. A., Fieland V. J., Cardenas, M., & Grünwald, N. J. (2014). The Irish potato famine pathogen *Phytophthora infestans* originated in central Mexico rather than the Andes. *Proceedings of the National Academy of Sciences*, *111*(24), 8791-8796. https://doi.org/10.1073/pnas.1401884111

Haas, B. J., Kamoun, S., Zody, M. C., Jiang, R. H. Y., Handsaker, R. E., Cano, L. M., Grabherr, M., Kodira C. D., Raffaele, S., Torto-Alalibo, T., Bozkurt, T. O., Ah-Fong, A. M. V., Alvarado L., Anderson, V. L., Armstrong, M. R., Avrova, A., Baxter, L., Beynon, J., Boevink, P. C., Bollmann, S. R., Bos, J. I. B., Bulone, V., Cai, G., Cakir, C., Carrington, J. C., Chawner, M., Conti, L., Costanzo, S., Ewan, R., Fahlgren N., Fischbach, M. A., Fugelstad, J., Gilroy, E. M., Gnerre, S., Green, P. J., Grenville-Briggs, L. J., Griffith, J., Grünwald, N. J., Horn, K., Horner, N. R., Hu, C.-H., Huitema, E., Jeong, D.-H., Jones, A. M. E.,. Jones, J. D. G., Jones, R. W., Karlsson, E. K., Kunjeti, S. G., Lamour, K., Liu, Z., Ma, L., MacLean, D., Chibucos, M. C., McDonald, H., McWalters, J., Meijer, H. J. G., Morgan, W., Morris, P. F., Munro, C. A., O'Neill, K., Ospina-Giraldo, M., Pinzón, A., Pritchard, L., Ramsahoye, B., Ren, Q., Restrepo, S., Roy, S., Sadanandom, A., Savidor, A., Schornack, S., Schwartz, D. C., Schumann, U. D., Schwessinger, B., Seyer, L., Sharpe, T., Silvar, C., Song, J., Studholme, D. J., Sykes, S., Thines, M., van de Vondervoort, P. J. I., Phuntumart, V., Wawra, S., Weide, R., Win, J., Young, C., Zhou, S., Fry, W., Meyers, B. C., van West, P., Ristaino, J., Govers, F., Birch, P. R. J., Whisson, S. C., Judelson, H. S., & Nusbaum, C. (2009). Genome sequence and analysis of the Irish potato famine pathogen *Phytophthora infestans*. *Nature*, *461*(7262), 393-398. https://doi.org/10.1038/nature08358

Haverkort, A. J., Struik, P. C., Visser, R. G. F., & Jacobsen, E. J. P. R. (2009). Applied biotechnology to combat late blight in potato caused by *Phytophthora infestans*. *Potato Research*, *52*(3), 249-264. https://doi.org/10.1007/s11540-009-9136-3

Haverkort, A. J., Boonekamp, P. M., Hutten, R., Jacobsen, E., Lotz, L. A. P., Kessel, G. J. T., Vossen, J. H., & Visser, R. G. F. (2016). Durable late blight resistance in potato through dynamic varieties obtained by cisgenesis: scientific and societal advances in the DuRPh project. *Potato Research*, *59*(1), 35-66. https://doi.org/10.1007/s11540-015-9312-6

Hawkes, J. G. (1990). The potato: evolution, biodiversity and genetic resources. Washington, D. C. Smithsonian Institution Press.

Hein, I., Birch, P. R., Danan, S., Lefebvre, V., Achieng Odeny, D., Gebhardt, C., Trognitz, F., & Bryan, G. J. (2009). Progress in mapping and cloning qualitative and quantitative resistance against *Phytophthora infestans* in potato and its wild relatives. *Potato Research*, *52*(3), 215-227. https://doi.org/10.1007/s11540-009-9129-2

Jansky, S.H., Charkowski, A. O., Douches, D. S., Gusmini, G., Richael, C., Bethke, P. C., Spooner, D. M., Novy, R. G., De Jong, H., De Jong, W. S., Bamberg, J. B., Thompson, A. L., Bizimungu, B., Holm, D. G., Brown, C. R., Haynes, K. G., Sathuvalli, V. R., Veilleux, R. E., Miller, J. C., Bradeen, J. M. & Jiang, J. (2016). Reinventing potato as a diploid inbred line-based crop. *Crop Science*, *56*(4), 1412–1422. https://doi.org/10.2135/cropsci2015.12.0740

Jansky, S. H., & Spooner, D. M. (2018). The evolution of potato breeding. *Plant breeding reviews*, *41*, 169-214. https://doi.org/10.1002/9781119414735.ch4

Jensen, P. K., & Nielsen, B. J. (2015). Development of potato late blight (*Phytophthora infestans*) in differently developed potato crops and the potential to graduate the fungicide dose according to crop biomass. *Acta Agriculturae Scandinavica, Section B—Soil & Plant Science*, *65*(7), 667-672. https://doi.org/10.1080/09064710.2015.1043334

Jha, S., Khalko, S., Abhijith, M., Bhattacharya, P. M., & Roy, A. (2019). Study of effect of different regimes of nitrogen on late blight of potato. *Journal of Entomology and Zoology Studies*, *7*, 918-921.

Jiang, R., Li, J., Tian, Z., Du, J., Armstrong, M., Baker, K., Lim, J. T.-Y., Vossen, J. H., He, Portal, L., Zhou, J., Bonierbale, M., Hein, I., Lindqvist-Kreuze, H., & Xie, C. (2018). Potato late blight field resistance from QTL dPI09c is conferred by the NB-LRR gene *R8*. *Journal of experimental botany*, *69*(7), 1545-1555. https://doi.org/10.1093/jxb/ery021

Jin, K., Hao, N., Jiao, F., Yang, Y., Wang, D., Xu, C., & Zhai, R. (2014). The effect of nitrogen supply on potato yield, tuber size and pathogen resistance in *Solanum tuberosum* exposed to *Phytophthora infestans*. *African Journal of Agricultural Research*, *9*(35), 2657-2663. https://doi.org/10.5897/AJAR2013.7550

Jo, K.-R., Arens, M., Kim, T.-J., Jongsma, M. A., Visser, R. G. F., Jacobsen, E., & Vossen, J. H. (2011). Mapping of the *S. demissum* late blight resistance gene *R8* to a new locus on chromosome IX. *Theoretical and Applied Genetics*, *123*(8), 1331–1340. https://doi.org/10.1007/s00122-011-1670-0

Jo, K.-R., Visser, R. G., Jacobsen, E., & Vossen, J. H. (2015). Characterisation of the late blight resistance in potato differential MaR9 reveals a qualitative resistance gene, *R9a*, residing in a cluster of Tm-22 homologs on chromosome IX. *Theoretical and Applied Genetics 128*(5), 931–941. https://doi.org/10.1007/s00122-015-2480-6

Juárez, H. S., Amaro, J. R., Rivera, M.D., Párraga, A., & Hijmans, R. J. (2000). The effect of nitrogen fertilization on potato late blight in the field. CIP program report 69-76.

Keijbets, M. J. H. (2008). Potato processing for the consumer: developments and future challenges. *Potato Research*, *51*(3), 271-281. https://doi.org/10.1007/s11540-008-9104-3

Knight, T. A. (1814). On raising new and early varieties of the potato (*Solanum tuberosum*). The Belfast Monthly Magazine, 12(67), 137-138.

Korte, A., & Farlow, A. (2013). The advantages and limitations of trait analysis with GWAS: a review. *Plant methods*, *9*(1), 1-9. https://doi.org/10.1186/1746-4811-9-29

Kowalska, J., & Drożdżyński, D. (2018) Effects of potassium fertilisation on potato late blight and yield – short communication. *Plant Protect Science, 54*, 87–91. https://doi.org/10.17221/79/2017-PPS

Kraak, A. (1992). Industrial applications of potato starch products. *Industrial Crops and Products*, *1*(2-4), 107-112. https://doi.org/10.1016/0926-6690(92)90007-I

La Torre, A., Righi, L., Iovino, V., & Battaglia, V. (2019). Control of late blight in organic farming with low copper dosages or natural products as alternatives to copper. *European Journal of Plant Pathology*, *155*(3), 769-778. https://doi.org/10.1007/s10658-019-01804-0

Li, G., Huang, S., Guo, X., Li, Y., Yang, Y., Guo, Z., Kuang, H., Rietman, H., Bergervoet, M., Vleeshouwers, V. G. G. A., van der Vossen, E. A. G., Qu, D., Visser, R. F. G., Jacobsen, E., & Vossen, J. H. (2011). Cloning and characterization of *R3b*; Members of the *R3* superfamily of late blight resistance genes show sequence and functional divergence. *Molecular Plant-Microbe Interactions*, *24*(10), 1132–1142. https://doi.org/10.1094/MPMI-11-10-0276

Lindhout, P., Vries, M. De, Maat, M., Ying, S., Viquez-Zamora, M., & Heusden, S. A. W. Van. (2016). Hybrid potato breeding for improved varieties. *Achieving sustainable cultivation of potatoes*, *1*, 1–24. https://doi.org/10.19103/AS.2016.0016.04

Lindqvist-Kreuze, H., Gastelo, M., Perez, W., Forbes, G. A., de Koeyer, D., & Bonierbale, M. (2014). Phenotypic stability and genome-wide association study of late blight resistance in potato genotypes adapted to the tropical highlands. *Phytopathology*, *104*(6), 624-633. https://doi.org/10.1094/PHYTO-10-13-0270-R

Lindqvist-Kreuze, H., De Boeck, B., Unger, P., Gemenet, D., Li, X., Pan, Z., Sui, Q., Qin, J., Woldegjorgis, G., Negash, K., Seid, I., Hirut, B., Gastelo, M., Vega, J. De, & Bonierbale, M. (2021). Global multi-environment resistance QTL for foliar late blight resistance in tetraploid potato with tropical adaptation. *G3*, *11*(11), https://doi.org/10.1093/g3journal/jkab251

LTZ (Hrsg.) (2007). Strategien zur Krautfäule- und Alternariabekämpfung, Landwirtschaftliches Technologiezentrum Augustenberg, Karlsruhe, Baden-Württemberg.

Malcolmson, J. F., & Black, W. (1966). New R genes in *Solanum demissum* Lindl. and their complementary races of *Phytophthora infestans* (Mont.) de Bary. *Euphytica*, *15*(2), 199-203. https://doi.org/10.1007/BF00022324

Malcolmson, J. F. (1969). Races of *Phytophthora infestans* occurring in Great Britain. *Transactions of the British Mycological Society*, *53*(3), 417-423. https://doi.org/10.1016/S0007-1536(69)80099-9

Massa, A. N., Manrique-Carpintero, N. C., Coombs, J. J., Zarka, D. G., Boone, A. E., Kirk, W. W., Hackett, C. A., Bryan, G. J., & Douches, D. S. (2015). Genetic linkage mapping of economically important traits in cultivated tetraploid potato (*Solanum tuberosum* L.). *G3: Genes, Genomes, Genetics*, *5*(11), 2357-2364. https://doi.org/10.1534/g3.115.019646

Mayton, H., Griffiths, H., Simko, I., Cheng, S., Lorenzen, J., De Jong, W., & Fry, W. E. (2010). Foliar and tuber late blight resistance in a *Solanum tuberosum* breeding population. *Plant breeding*, *129*(2), 197-201. https://doi.org/10.1111/j.1439-0523.2009.01671.x

McComas, K. A., Besley, J. C., & Steinhardt, J. (2014). Factors influencing U.S . consumer support for genetic modification to prevent crop disease. Appetite, 78, 8–14. https://doi.org/10.1016/j.appet.2014.02.006

Meade, F., Hutten, R., Wagener, S., Prigge, V., Dalton, E., Kirk, H. G., Griffin, D., & Milbourne, D. (2020). Detection of novel QTLs for late blight resistance derived from the wild potato species *Solanum microdontum* and *Solanum pampasense*. *Genes*, *11*(7), 1–18. https://doi.org/10.3390/genes11070732

Mittelstraß, K., Treutter, D., Pleßl, M., Heller, W., Elstner, E. F., & Heiser, I. (2006). Modification of primary and secondary metabolism of potato plants by nitrogen application differentially affects resistance to

*Phytophthora infestans* and *Alternaria solani. Plant Biology*, *8*(05), 653-661. https://doi.org/10.1055/s-2006-924085

Mizubuti, E. S., & Fry, W. E. (2006). Potato late blight. In The epidemiology of plant disease. 445-471, Springer, Dordrecht.

Möller, K., Habermeyer, J., Zinkernagel, V., & Reents, H. J. (2006). Impact and interaction of nitrogen and *Phytophthora infestans* as yield-limiting and yield-reducing factors in organic potato (*Solanum tuberosum* L.) crops. *Potato Research*, *49*(4), 281-301. https://doi.org/10.1007/s11540-007-9024-7

Möller, K., & Reents, H. J. (2007). Impact of agronomic strategies (seed tuber pre-sprouting, cultivar choice) to control late blight (*Phytophthora infestans*) on tuber growth and yield in organic potato (*Solanum tuberosum* L.) crops. *Potato research*, *50*(1), 15-29. https://doi.org/10.1007/s11540-007-9026-5

Mosquera, T., Alvarez, M. F., Jiménez-Gómez, J. M., Muktar, M. S., Paulo, M. J., Steinemann, S., Li, J., Draffehn, A., Hofmann, A., Lübeck, J., Strahwald, J., Tacke, E., Hofferbert, H.-R., Walkemeier, B., & Gebhardt, C. (2016). Targeted and untargeted approaches unravel novel candidate genes and diagnostic SNPs for quantitative resistance of the potato (*Solanum tuberosum* L.) to *Phytophthora infestans* causing the late blight disease. *PLoS One*, *11*(6), e0156254. https://doi.org/10.1371/journal.pone.0156254

Muktar, M. S., Lübeck, J., Strahwald, J., & Gebhardt, C. (2015). Selection and validation of potato candidate genes for maturity corrected resistance to Phytophthora infestans based on differential expression combined with SNP association and linkage mapping. *Frontiers in Genetics*, *6*, 294. https://doi.org/10.3389/fgene.2015.00294

Navarre, D. A., Goyer, A., & Shakya, R. (2009). Nutritional value of potatoes: vitamin, phytonutrient, and mineral content. *Advances in potato chemistry and technology*. 395-424. Academic Press. https://doi.org/10.1016/B978-0-12-374349-7.00014-3

Naveed, M., Moldrup, P., Arthur, E., Holmstrup, M., Nicolaisen, M., Tuller, M., Herath, L., Hamamoto, S., Kawamoto, K., Komatsu, T., Vogel, H.-J., & Wollesen de Jonge, L. (2014). Simultaneous loss of soil biodiversity and functions along a copper contamination gradient: when soil goes to sleep. *Soil Science Society of America Journal*, *78*(4), 1239-1250. https://doi.org/10.2136/sssaj2014.02.0052

Oberhagemann, P., Chatot-Balandras, C., Schäfer-Pregl, R., Wegener, D., Palomino, C., Salamini, F., Bonnel, E., & Gebhardt, C. (1999). A genetic analysis of quantitative resistance to late blight in potato: towards marker-assisted selection. *Molecular Breeding*, *5*(5), 399-415. https://doi.org/10.1023/A:1009623212180

Platt, H. W., & Tai, G. (1998). Relationship between resistance to late blight in potato foliage and tubers of cultivars and breeding selections with different resistance levels. *American Journal of Potato Research*, *75*(4), 173-178. https://doi.org/10.1007/BF02853569

Rafalski, J. A. (2010). Association genetics in crop improvement. *Current opinion in plant biology*, *13*(2), 174-180. https://doi.org/10.1016/j.pbi.2009.12.004

Remington, D. L., Thornsberry, J. M., Matsuoka, Y., Wilson, L. M., Whitt, S. R., Doebley, J., Kresovich, S., Goodman, M. M., & Buckler IV, E. S. (2001). Structure of linkage disequilibrium and phenotypic associations in the maize genome. *Proceedings of the national academy of sciences*, *98*(20), 11479-11484. https://doi.org/10.1073/pnas.20139439

Rietman, H., Bijsterbosch, G., Cano, L. M., Lee, H. R., Vossen, J. H., Jacobsen, E., Visser, R. G. F., Kamoun, S., & Vleeshouwers, V. G. A. A. (2012). Qualitative and quantitative late blight resistance in the potato cultivar Sarpo Mira is determined by the perception of five distinct RXLR effectors. *Molecular Plant-Microbe Interactions*, *25*(7), 910–919. https://doi.org/10.1094/MPMI-01-12-0010-R

Rogozina, E. V., Beketova, M. P., Muratova, O. A., Kuznetsova, M. A., & Khavkin, E. E. (2021). Stacking resistance genes in multiparental interspecific potato hybrids to anticipate late blight outbreaks. *Agronomy*, *11*(1), 115. https://doi.org/10.3390/agronomy11010115

Rojas, D. K. J., Sedano, J. C. S., Ballvora, A., Léon, J., & Mosquera Vásquez, T. (2019). Novel organ-specific genetic factors for quantitative resistance to late blight in potato. *PloS one*, *14*(7), e0213818. https://doi.org/10.1371/journal.pone.0213818

Ros, B., Mohler, V., Wenzel, G., & Thümmler, F. (2008). *Phytophthora infestans*-triggered response of growth- and defense-related genes in potato cultivars with different levels of resistance under the influence of nitrogen availability. *Physiologia Plantarum 133*(2), 386-396. https://doi.org/10.1111/j.1399-3054.2008.01048.x

Santa, J. D., Berdugo-Cely, J., Cely-Pardo, L., Soto-Suárez, M., Mosquera, T., & Galeano M, C. H. (2018). QTL analysis reveals quantitative resistant loci for *Phytophthora infestans* and *Tecia solanivora* in tetraploid potato (*Solanum tuberosum* L.). *PLoS One*, *13*(7), e0199716. https://doi.org/10.1371/journal.pone.0199716

Schouten, H. J. (2022). The Origin of Cisgenesis, and Its Evolving Definition. In Cisgenic Crops: Potential and Prospects,1-13, Springer, Cham. DOI: 10.1007/978-3-031-06628-3_1

Selga, C., Koc, A., Chawade, A., & Ortiz, R. (2020). A bioinformatics pipeline to identify a subset of SNPs for genomics-assisted potato breeding. *Plants*, *10*(1), 30. https://doi.org/10.3390/plants10010030

Spielman, L. J., Drenth, A., Davidse, L. C., Sujkowski, L. J., Gu, W., Tooley, P. W., & Fry, W. E. (1991). A second world-wide migration and population displacement of *Phytophthora infestans*?. *Plant pathology*, *40*(3), 422-430. https://doi.org/10.1111/j.1365-3059.1991.tb02400.x

Spooner, D. M., McLean, K., Ramsay, G., Waugh, R., & Bryan, G. J. (2005). A single domestication for potato based on multilocus amplified fragment length polymorphism genotyping. *Proceedings of the National Academy of Sciences*, *102*(41), 14694-14699. https://doi.org/10.1073/pnas.0507400102

Stefańczyk, E., Plich, J., Janiszewska, M., Smyda-Dajmund, P., Sobkowiak, S., & Śliwka, J. (2020). Marker-assisted pyramiding of potato late blight resistance genes *Rpi-rzc1* and *Rpi-phu1* on di- and tetraploid levels. *Molecular Breeding*, *40*(9), 1-12. https://doi.org/10.1007/s11032-020-01169-x

Storck, T., Böhme, T., & Schultheiss, H. (2011). Fortuna et al. Status and perspectives of GM approaches to fight late blight. In Schepers, H. T. A. M. (Ed.), 45–48. St. Petersburg, Thirteenth EuroBlight workshop.

Struik, P. C. (2008). Book Review: World Catalogue of Potato Varieties 2007, Hils, U., & Pieterse, L. (eds). AgriMedia GmbH, Clenze, Germany and Allentown, PA, USA. *Potato Research*, *51*(2), 209-210. https://doi.org/10.1007/s11540-008-9101-6

Su, Y., Viquez-Zamora, M., den Uil, D., Sinnige, J., Kruyt, H., Vossen, J., Lindhout, P., & Heusden, S. van (2020). Introgression of genes for resistance against *Phytophthora infestans* in diploid potato. *American Journal of Potato Research*, *97*(1), 33-42. https://doi.org/10.1007/s12230-019-09741-8

Sunita, M., Zubair, A., Ayana, C., & Srikanta, D. (2011). Effects of different levels of nitrogen against foliar diseases of potato under different fertility gradient soil on field condition. *Journal of Mycopathological Research*, *49*(2), 273-278.

Tiwari, J. K., Siddappa, S., Singh, B. P., Kaushik, S. K., Chakrabarti, S. K., Bhardwaj, V., & Chandel, P. (2013). Molecular markers for late blight resistance breeding of potato: an update. *Plant Breeding*, *132*(3), 237-245. https://doi.org/10.1111/pbr.12053

Thornsberry, J. M., Goodman, M. M., Doebley, J., Kresovich, S., Nielsen, D., & Buckler, E. S. (2001). Dwarf8 polymorphisms associate with variation in flowering time. *Nature genetics*, *28*(3), 286-289. https://doi.org/10.1038/90135

Thurston, H. D. (1971). Relationship of general resistance: late blight of potato. *Phytopathology*, *61*, 620-626.

Turkensteen, L. J., Flier, W. G., Wanningen, R., & Mulder, A. (2000). Production, survival and infectivity of oospores of *Phytophthora infestans*. *Plant Pathology*, *49*(6), 688-696. https://doi.org/10.1046/j.1365-3059.2000.00515.x

USABlight (2021). USABlight | A National Project on Tomato & Potato Late Blight. https://usablight.org/

U.S. Department of Agriculture (2021). Potatoes, boiled, cooked in skin, flesh, without salt. https://fdc.nal.usda.gov/fdc-app.html#/food-details/170438/nutrients

Visker, M. H. P. W., Heilersig, H. J. B., Kodde, L. P., Weg, W. E. van de, Voorrips, R. E., Struik, P. C., & Colon, L. T. (2005). Genetic linkage of QTLs for late blight resistance and foliage maturity type in six related potato progenies. *Euphytica*, *143*(1), 189-199. https://doi.org/10.1007/s10681-005-3444-8

Vossen, E. van der, Sikkema, A., Hekkert, B. T. L., Gros, J., Stevens, P., Muskens, M., Wouters, D., Pereira, A., Stiekema, W., & Allefs, S. (2003). An ancient R gene from the wild potato species *Solanum bulbocastanum* confers broad-spectrum resistance to *Phytophthora infestans* in cultivated potato and tomato. *The plant journal*, *36*(6), 867-882. https://doi.org/10.1046/j.1365-313X.2003.01934.x

Wang, F., Zou, M., Zhao, L., Li, H., Xia, Z., & Wang, J. (2020). Genome-Wide Association Analysis of Late Blight Resistance Traits in Potato Germplasm Resources. *Research Square*, https://doi.org/10.21203/rs.3.rs-113697/v1

Waschl, H., & Hein, W. (2010). Möglichkeiten der alternativen Bekämpfung von Krautfäule (*Phytophthora infestans*) im biologischen Kartoffelanbau. Control of potato late blight (*Phytophthora infestans*) with alternative treat-ments in organic farming. ALVA Jahrestagung 2010, Vom Lebensmittel zum Genussmittel–was essen wir morgen? 273-275.

Wastie, R.L. (1991). Breeding for Resistance. In Ingram, D.S., & Wiliams, D.S. (eds.), *Phytophthora infestans*, the Cause of Late Blight of Potato. *Advances in Plant Pathology*, *7*, 193-224, Academic Press Ltd., London

Waters, S., Ramos, A., Culler, A. H., Hunst, P., Zeph, L., Gast, R., Mahadeo, D., Sottosanto, J., Huber, S., Shan, G., Chakravarthy, S., & & Goodwin, L. (2021). Recommendations for science-based safety assessment of genetically modified (GM) plants for food and feed uses. *Journal of Regulatory Science*, *9*(1), 16-21. https://doi.org/10.21423/jrs-v09i1waters

Widmark, A. K., Andersson, B., Cassel-Lundhagen, A., Sandström, M., & Yuen, J. E. (2007). *Phytophthora infestans* in a single field in southwest Sweden early in spring: symptoms, spatial distribution and genotypic variation. *Plant Pathology*, *56*(4), 573-579. https://doi.org/10.1111/j.1365-3059.2007.01618.x

Woodham-Smith, C. (1962). The Great Hunger. Ireland 1845-1849. Hamilton, London.

Yuen, J. (2021). Pathogens which threaten food security: *Phytophthora infestans*, the potato late blight pathogen. *Food Security*, *13*(2), 1-7. https://doi.org/10.1007/s12571-021-01141-3

Zaag, D. E. van der (1956). Overwintering en epidemiologie van *Phytophthora infestans*, tevens enige nieuwe bestrijdingsmogelijkheden, Dissertation, Veenman.

Zellner, M., Keil, S., Bangemann, L. W., Zwerger, P., Kleinhenz, B., & Tschöpe, B. (2009). Entwicklung, Überprüfung und Praxiseinführung des Prognosemodells ÖKO-SIMPHYT zur gezielten Bekämpfung der Kraut- und Knollenfäule (*P. infestans*) im ökologischen Kartoffelanbau mit dem Ziel, den Einsatz kupferhaltige Fungizide auf ein Minimum zu reduzieren. *Organic eprints*, https://orgprints.org/id/eprint/16649/

Zhu, S., Li, Y., Vossen, J. H., Visser, R. G. F., & Jacobsen, E. (2012). Functional stacking of three resistance genes against *Phytophthora infestans* in potato. *Transgenic Research*, *21*(1), 89–99. https://doi.org/10.1007/s11248-011-9510-1

**Abbildungsverzeichnis**

**Tabellenverzeichnis**

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Blossei, J., Uptmoor, R., Thieme, R., Nachtigall, M., & Hammann, T. (2021). Insights into the genetic basis of the pre-breeding potato clones developed at the Julius Kühn Institute for high and durable late blight resistance. *Plant Genetic Resources*, *19*(5), 461-464. https://doi.org/10.1017/S1479262121000447

Blossei, J., Gäbelein, R., Hammann, T., & Uptmoor, R. (2022). Late blight resistance in wild potato species - Resources for future potato (*Solanum tuberosum*) breeding. *Plant Breeding, 141*(3), 314-331. https://doi.org/10.1111/pbr.13023

Tagungsbeiträge

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Blossei, J. & Hammann, T. (2021). Genome-wide association study of resistance to late blight based on JKI pre-breeding potato clones (*Solanum tuberosum*). Young Scientists Meeting – Conference 2021, 11.-13.10.2021, Quedlinburg

Blossei, J. & Hammann, T. (2022). Influence of Nitrogen Supply on the Susceptibility of Potato Germplasm to *Phytophthora infestans* in Organic Farming. 21st EAPR Triennial Conference, 4-8 July 2022, Krakau (das Poster wurde von Thilo Hammann präsentiert.)

**Eidesstattliche Erklärung**

Hiermit erkläre ich durch eigenhändige Unterschrift, die vorliegende Dissertation selbstständig verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel verwendet zu haben. Die aus den Quellen direkt oder indirekt übernommenen Gedanken sind als solche kenntlich gemacht. Die Dissertation ist in dieser Form noch keiner anderen Prüfungsbehörde vorgelegt worden.

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