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Breeding Late Blight Resistant Potatoes for Organic Farming—a Collaborative Model of Participatory Plant Breeding: the Bioimpuls Project

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Abstract
In organic potato production, the need for varieties with durable late blight resistance developed through classical breeding programmes is urgent. Besides late blight resistance, other variety characteristics needed in organic potato production are early canopy closure for weed suppression and good tuber dormancy to eliminate the need for (chemical) sprouting inhibition during storage, amongst others. This paper is a unique example of collaboration between researchers, farmers and professional breeders of both large, medium and small breeding companies. The aim of the resulting breeding project, Bioimpuls, was to provide a substantial impulse to both the organic and conventional potato breeding sector by enlarging the access to various sources of late blight resistance. The Bioimpuls activities include providing true seed populations for variety selection with five available sources of *R*-genes against *Phytophthora infestans*, early and advanced introgression breeding with six new *R*-genes, and education and communication. The results achieved over the 11-year period (2009–2019) are analysed. Many true seed populations containing multiple resistance genes are produced and selected, and a constant flow of breeding clones is entering the evaluation and positioning trials of companies. However, it will still take a considerable amount of time before varieties with stacked resistance genes will replace the new resistant single gene varieties entering the market in the next few years. Five out of six new sources of *R*-genes need more years of backcrossing before they are ready for commercial use. Bioimpuls successfully introduced a training course for farmer breeders, and published a manual for potato breeding.

Keywords Durable resistance · Organic farming · Participatory plant breeding · *Phytophthora infestans* · Pre-breeding

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Introduction

The Dutch Organic Potato Production

The agricultural area under organic management in the Netherlands is gradually increasing (3.1% of the total in 2017, moving up to 3.8% in 2019), but is still well below the average organic area in the EU-28, i.e. 7.7% in 2019 (Bionext 2019; Eurostat 2019). Although the Netherlands is a leading country in producing and exporting seed potatoes (Haverkort et al. 2008, 2016), the development of Dutch organic potato production was, for a long time, struggling and had dropped down from approx. 1500 to some 1200 ha of seed and ware potato production in 2007 (Lammerts van Bueren et al. 2008). Late blight caused by the oomycete *Phytophthora infestans* is the major problem for organic potato production throughout Europe (Tamm et al. 2004). The resistance against late blight (based on genes from *Solanum demissum*) of the varieties that performed well in organic farming back in the 1980s, such as 'Escort' and 'Santé', has already been broken. In addition, the aggressiveness of the *P. infestans* population has increased during the 1980s by the arrival and spread of the A2 mating type in the Netherlands. The co-existence of both mating types enabled sexual reproduction of the oomycete and enhanced the occurrence of physiological races that contain new patterns of virulence (Rausher 2001; McDonald and Linde 2002; Fry 2008; Li et al. 2012).

In organic farming, no measures against late blight are economically effective to reduce losses, except for spraying copper sulphate (Finckh et al. 2006). Spraying copper sulphate is allowed according to EU organic regulations (EC 834/2007 2007) and is common practice in many member states. However, the Dutch government banned the use of copper as a fungicide for both non-organic and organic agriculture. Therefore, in the Netherlands and for decades, organic potato production is very difficult as not only late blight resistant varieties are lacking but also effective permitted 'organic' fungicides for late blight management are not available (Finckh et al. 2006; Tiemens-Hulscher et al. 2007). In addition, in order to control late blight outbreaks, the Dutch government has required a set of hygiene measures such as destroying the potato haulm at 7% leaf infestation for both organic and non-organic potato production (HPA 2003; NVWA 2017). In this context, an early outbreak of late blight can cause severe yield losses in organic potato production. The only measure for organic growers to prevent a complete harvest failure was advancing tuber bulking through chitting (pre-sprouting of seed tubers before planting) which enables an acceptable yield at the time the haulm has to be destroyed (Struik and Wiersema 1999; Finckh et al. 2006; Hospers-Brands et al. 2008). However, this measure is not widely applied by organic growers as it requires extra labour and facilities and does not provide an economic advantage in all years.

Until 2007, the organic sector had to rely on varieties from non-organic breeding programmes that were the least sensitive to late blight or very early bulking to escape from late blight infection. In 2007, after several nation-wide dramatic late blight years with harvest failures in organic farming, the Dutch organic potato sector concluded that breeding with a diversity of late blight resistance genes would be the only way out.

Breeding for Late Blight Resistance

The year 2006 saw the start of the research project Durable Resistance against Phytophthora (DuRPh, 2006–2016), aimed to deliver a proof of principle for cis-genesis as a novel breeding technique in potato. However, it would not provide a solution for the organic sector as such 'novel breeding techniques' are not compatible with the organic values (Lammerts van Bueren et al. 2008; Haverkort et al. 2016; Nuijten et al. 2017). Therefore, there was an urgent need for varieties with durable late blight resistance for the organic sector developed through classical breeding programmes.

In order to protect potato crops for a more prolonged period, stacking of multiple resistance genes within one potato variety is a promising way forward (Tan et al. 2010; Vleeshouwers et al. 2011; Jo et al. 2014; Ghislain et al. 2019; Rakosy-Tican et al. 2020). Moreover, Rodewald and Trognitz (2013) argued that combining resistance genes with a different mode of action would make it less probable that *P. infestans* can overcome these new stacks of resistance genes with one single mutation in its virulence spectrum, extending the time period in which these resistance stacks are expected to be effective in commercial (organic) potato production. To realise a breeding programme for durable late blight resistance, access to a diversity of resistance genes is the key. Late blight resistance genes must be derived from *Solanum* species other than *S. tuberosum*. However, identifying new late blight resistance genes amongst wild and primitive crop relatives and their subsequent introgression into advanced breeding material requires specific knowledge and approximately 12–16 years or sometimes even longer (Hermsen and Ramanna 1973; Bradshaw 2017). To get rid of undesired wild characteristics without losing the desired resistance traits, several generations of backcrossing (BC) with advanced breeding clones and/or varieties are needed to arrive at an acceptable agronomic level in order to release the resistance genes for commercial breeding programmes. Medium and small breeding companies lack financial capacity to invest in facilities and knowledge to bridge the gap between the identification of resistance sources and the actual use of this plant material in commercial breeding. And although large breeding companies can allocate capacity to invest in a pre-breeding programme of their own, at the time they were not eager to work with wild or primitive plant material with various ploidy levels and/or long-term introgression programmes. For that reason, many Dutch potato breeding companies were willing to collaborate in a (classical) pre-breeding project if public funding would be made available.

The project, called Bioimpuls, intended to facilitate a constant supply of new suitable and resistant potato varieties for the organic sector, by not only focusing on short-term success, but also on a continuous flow of improved varieties with sustainable resistances for the medium- and long-term through an organic breeding project. Right from the start, a spill-over of these varieties into non-organic potato production was intended. The expectation was that with the availability of a broad set of breeding clones with different resistance genes, breeding companies would put more effort into dedicated variety development for the organic sector. To ensure that the Bioimpuls project would generate varieties well adapted to organic growing and storage conditions, the project included organically managed seed production, selection and trial fields.

In this paper, we will describe how the Dutch organic sector set up an organic breeding project for late blight resistance as a collaboration between researchers, farmers and potato breeding companies. We will first describe the traits of priority for organic potato production and the participatory approach of the Bioimpuls project. The Bioimpuls activities are described in four work-packages (WP): WP1 providing true seed populations for variety selection, WP2 advanced introgression breeding, WP3 early introgression breeding, and WP4 education and communication activities. The results achieved in the various work packages over the 11-year period (2009–2019) will be analysed. Finally, we discuss the outcomes of the project (e.g. in terms of material processed and developed), the spin-off and impact (e.g. a well-established training course for Dutch potato breeders), and the perspectives (such as shifting focus in Dutch commercial potato breeding and national economic benefits in relation to public money invested).

Variety Improvement for Organic Potato

To stimulate organic potato production in the Netherlands, the Bioimpuls project aimed not only at making new late blight resistance genes available but also at focusing on a broader range of traits (Table 1). The concept of organic farming is based

Table 1 Required traits with high priority for organic ware and seed potato production in light of climate change (adapted after Finckh et al. 2006; Lammerts van Bueren et al. 2008; Tiemens-Hulscher et al. 2012)

Above ground	• Resistance in foliage and tubers to *Phytophthora infestans* based on a diversity of *R* genes not linked to late maturity • Resistance/tolerance to *Alternaria spp.* • Early canopy closure under low N for good weed suppression
Below ground	• Early to mid-early tuber setting and tuber bulking to be less exposed to late blight season • High N-efficiency and adaptability to varying N levels • Well established root system for efficient nutrient uptake • Resilience to irregular water availability: not sensitive to secondary growth nor growth cracks • Reduced susceptibility to black scurf (*Rhizoctonia solani*), silver scurf (*Helminthosporium solani)* and common scab (*Streptomyces scabies*)
After harvest	• Late sprouting for good storability • Reduced susceptibility to *Fusarium* spp.
Seed potato	• Low sensitivity to viruses and *Rhizoctonia solani*
Quality	• Good skin appearance • Good flavour • Good cooking and/or frying characteristics • After 90 days after planting an under-water-weight of at least 320 for table stock and 380 for frying and chipping

on long term improvement of the resilience of the agro-ecosystem, for example by enhancing biodiversity above and below ground, but lacks measures to interfere directly during crop growth when conditions are adverse or sub-optimal. Therefore, variety characteristics for more robustness as described below have a higher priority for organic growers than for non-organic, high-external input farming systems.

With respect to yield, Dutch organic potato growers indicated that with organic market prices a yield level of 35–40 t ha^{-1} in 90–100 days after planting is acceptable, and does not need to reach the level of 50–60 t ha^{-1} at which Dutch non-organic ware growers usually aim (Tiemens-Hulscher et al. 2012). From a resistance management point of view late maturity is unwanted, as that would prolong the field period in which *P. infestans* could overcome the resistance (Pacilly et al. 2018).

In addition to a high priority for late blight resistance, organic potato growers also identified other high priorities with regard to disease resistance (e.g. Rhizoctonia and Alternaria) and adaptation to low-input nutrient conditions and mechanical weed management (Table 1). To reduce the chance of weed infestation and the amount of labour for weed management, an early closing canopy is required.

Nitrogen plasticity as the ability to maintain performance under low and/or irregular nitrogen availability is required as there is a shortage of organic (stable) manure. Also, for environmental reasons, organic growers want to limit the amount of nitrogen input to approx. 150 kg N/ha, whereas some non-organic growers go up to 300 kg N/ha (Tiemens-Hulscher et al. 2014; Ospina et al. 2014). Moreover, most nitrogen available for the organic potato crop stems from mineralization of organic fertilisers by soil micro-organism activity, which can be retarded due to cold weather in spring or dry soil conditions.

To be better adapted to changing climate conditions with weather patterns becoming more irregular, selection for types that are less sensitive to secondary growth and growth cracks would be beneficial (Ewing and Struik 1992; Schaap et al. 2011). The refraining from use of synthetic-chemical crop protectants also includes sprouting inhibitors which instead requires long dormancy types for good storability.

Approach of the Bioimpuls Breeding Project

Collaboration in a Participatory Model

At the time (2007) the Bioimpuls breeding project was designed, several Dutch seed potato trading companies were involved in serving the organic market with organically produced seed and ware potatoes next to their conventional, non-organic market (Lammerts van Bueren et al. 2006). As in the Netherlands the size of the organic sector was and still is limited, potato trading and/or breeding companies do not consider a (complete) separate breeding programme for merely organic potato varieties economically feasible. Therefore, it is necessary that varieties suitable for organic farming systems also serve an additional market in non-organic or low-input production areas (export).

In this context, Bioimpuls was designed to make use of the existing Dutch potato breeding system in which potato breeding companies collaborate with affiliated and/or independent farmer breeders (Almekinders et al. 2014). These farmer breeders receive and/or process some 300–3000 potato true seeds or seedling tubers on a yearly basis to perform on-farm selection in the early generations, usually up to the third or fourth field generation. The selected clones are handed over to the trading/breeding companies for further selection up to registration and marketing of the selected varieties. When a clone is finally selected for market introduction, it will be registered for intellectual property rights of both involved farmer breeder and company. This participatory model is based on a 'no-cure, no pay' system; only when a clone enters the market is the farmer breeder remunerated with a percentage of the royalties and/or trading value of the volume of seed potatoes sold. The idea behind this system is that the farmer breeders enlarge the capacity of the breeding companies by selecting in the first clonal generations and discard most (approx. 95–99%) of the non-promising clones. The companies are equipped to perform the further selection under multiple environments and to add laboratory or targeted field tests for disease resistance screening, and culinary and processing quality tests. At the time the Bioimpuls project started, there were about 150 farmer breeders involved in the Dutch potato breeding sector of which only two were organic farmers. Bioimpuls adopted this collaborative approach to enlarge capacity for organic potato breeding (Lammerts van Bueren et al. 2014; 2016; Almekinders et al. 2016). One of the goals of the Bioimpuls project was to increase the number of farmer breeders involved within the organic sector.

The participatory approach of Bioimpuls matched the funding method of the Dutch Ministry of Agriculture as 40% of the total required budget for this project needed to be covered by in-kind contributions from partners to the Bioimpuls breeding project. The funding under the Green Breeding programme (2010–2019) was altogether approved for 11 years including a preparation year (2009).

Partners in the Project

The partners of the Bioimpuls project consisted of two research institutes, six commercial breeding companies and several farmer breeders. The Plant Breeding Department of Wageningen University & Research (WUR) provided the necessary (pre-)breeding knowledge and incorporated their ongoing pre-breeding programme with various wild relatives as a basis for Bioimpuls. Louis Bolk Institute (LBI) coordinated the overall project, provided necessary knowledge of organic agriculture, and took care of education and communication with the organic sector and the wider public.

When the project was in the design phase, already six breeding companies, varying in size from small (less than 50,000 seedlings per year) to large (more than 100,000 seedlings per year), expressed their willingness to join and contribute in-kind with breeding activities. In the first 6 years (2009–2014) the commercial partners were: Agrico, Den Hartigh, Fobek, HZPC, Meijer Potato and Van Rijn (later under the name of KWS Potatoes).

For the second 5-year period (2015–2019), two companies withdrew: KWS changed its focus from clonal to true potato seed (TPS) breeding and handed over its involvement in Bioimpuls to HZPC, while Agrico, being the largest potato breeding company in the Netherlands, wanted to continue independently with their own organic breeding programme. This change in partners made it possible for other companies to join, resulting in (once again) six potato breeding companies: Den Hartigh, Fobek, HZPC, Meijer Potato, Plantera, and TPC (Fig. 1).

In this set-up, the central Bioimpuls breeding programme is conducted by the research institutes and aimed to yearly provide true potato seed populations from crosses involving at least one major late blight resistance gene/source for early generation selection by either the central breeding programme, farmer breeders or breeding companies involved in the project (Fig. 1). WUR arranged common yield and resistance trials for resistance screening and the selection of next generation breeding parents, while commercial testing, variety registration and market introduction were done by the breeding companies.

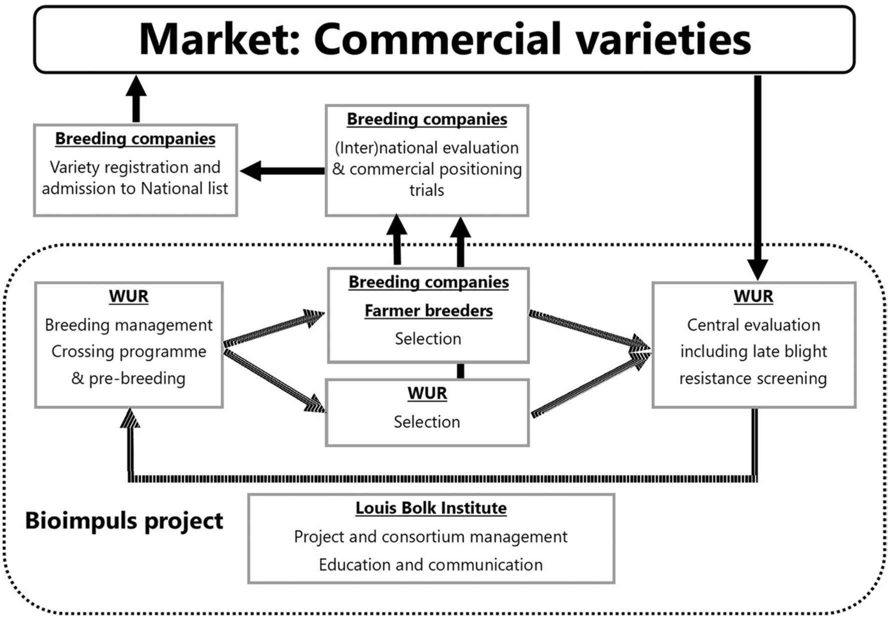

Fig. 1 The organisation structure of Bioimpuls in which the two research institutes Wageningen University & Research (WUR) and Louis Bolk Institute took care of the central (pre-)breeding programme and distributed yearly true seeds (and some advanced clones) to the partner breeding companies and farmer breeders to perform selection for marketable varieties and breeding clones. Selections were centrally evaluated and tested for late blight resistance to be used as new parents in the crossing programme. Promising selections from farmer breeders and WUR were transferred to one of the breeding companies to be, together with their own Bioimpuls selections, internationally evaluated and in case market potential was expected submitted for official variety registration and National listing

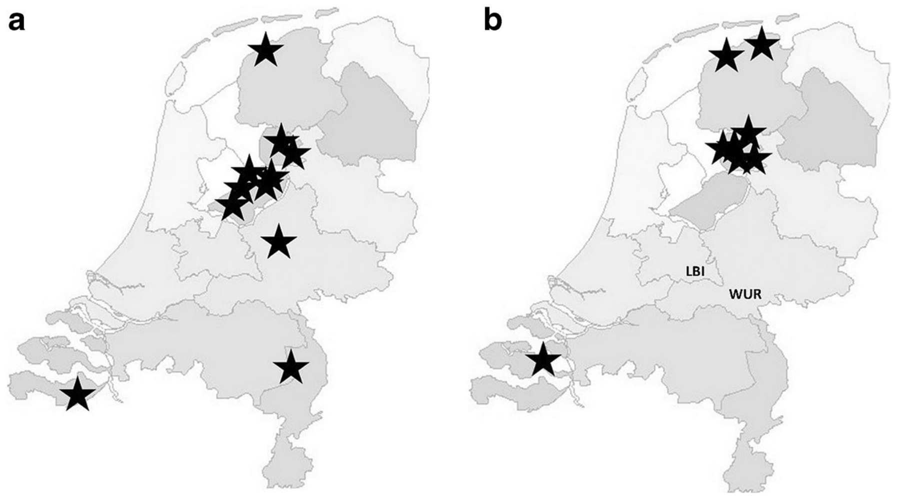

Fig. 2 Location of 14 farmer breeders (left hand panel) and all 8 Dutch potato breeding companies plus Wageningen University & Research (WUR) and Louis Bolk Instituut (LBI) (right hand panel) involved in Bioimpuls over the years 2009-2019

Locations

The potato breeding facilities of WUR in Wageningen included a crossing greenhouse with evaporative cooling, screenhouses for virus free potato maintenance and the production of seedling tubers, cold stores for storage of seed potatoes and potato trial samples, equipment to conduct quality assessment (e.g. cooking and frying), and a molecular marker laboratory. Yearly, Bioimpuls made use of a trial field in Wageningen under non-organic management inoculated with the *P. infestans* IPO-C isolate, carrying virulence for *R1-R7*, *R10* and *R11*, for field assessment of late blight resistance. Most of the true seedlings, first and second year breeding clones, and seed potatoes of the central breeding program were grown at an organic farmer field in Kraggenburg (province of Flevoland, silty-clay soil). Over time, organic yield trials were conducted in Kraggenburg, Randwijk (close to Wageningen, clay soil), Wageningen (sandy soil), and at a non-organically managed field in Wageningen (heavy clay soil).

The involved breeding companies and farmer breeders used their own trial fields for evaluation and selection (Fig. 2), and/or collaborated with organic farmers to acquire the obligatory organic selection conditions.

Genetic Resources

At the start of the project (2009), available sources of late blight resistance were divided into three groups: one group called 'Ready for commercial crossing', which consisted of *R8* (Jo et al. 2011) (derived from *S. demissum,* e.g. present in variety Sarpo Mira*)* and *Rpi-blb2* (Van der Vossen et al. 2005; derived from *S.*

bulbocastanum, e.g. present in variety Bionica) containing varieties and advanced breeding clones. The other two groups contained sources of resistance that still required several rounds of backcrossing: 'Introgression group 1' containing *R9* (from *S. demissum*) (Jo et al. 2015) and *Rpi-edn2* (from *S. edinense*) (Verzaux 2010) breeding clones which required 1 or 2 rounds of backcrossing, and 'Introgression group 2' containing late blight resistant material derived of *S. brachycarpum*, *S. bukasovii*, *S. iopetalum*, *S. multi-interruptum* and *S. sucrense* requiring 3 to 5 rounds of backcrossing. The sources representing 'Introgression group 2' originated from a large survey for late blight resistance amongst wild *Solanum* species (Vleeshouwers et al. 2011), and sources/accessions were furthermore chosen because of their ploidy level and crossability with tetraploid *S. tuberosum* genotypes.

As Bioimpuls moved on in time, several new potato varieties containing late blight resistance reached the market. Most of them were released by Agrico, a company that already had a long time focus on breeding for late blight resistance and the production of seed potatoes for the organic market. Although late blight resistance in most of these new varieties was based on the presence of *R8*, additional sources of late blight resistance were found homologous to *Rpi-cap1* (*S. capsibaccatum*) (Verzaux et al. 2012), *Rpi-chc1* (*S. chacoense*) (Vossen et al. 2011) and Rpi-vnt1 (*S. venturii*) (Pel et al. 2009).

Molecular Markers, Identification of Resistance Genes

To be able to identify which resistance genes are present and whether selected clones are resistant due to one or more resistance genes, marker assisted selection (MAS) is needed. As a diagnostic tool molecular markers are permitted and applied in organic breeding programmes (Lammerts van Bueren et al. 2010). The Bioimpuls project over the years gained access to molecular markers derived from various projects within WUR Plant Breeding, especially from the Durable Resistance against Phytophthora project (DuRPh) (Haverkort et al. 2016). During the project PCR (Polymerase Chain Reaction) based markers became available to detect (homologues of) *R8*, *R9*, *Rpi-blb1* (Van der Vossen et al. 2003), *Rpi-blb2*, *Rpi-chc1 and Rpi-vnt1*. Before markers became available, field testing was the only option to screen potato genotypes for absence/presence of resistance genes. After markers became available, field testing was still applied to validate the ongoing development of molecular markers and to check functionality under field conditions of the resistance genes present.

Intellectual Property Rights

In this project, there were no patents involved; the breeders' rights and royalties derived from later seed potato sales were described in contracts between Bioimpuls and the breeding companies, between Bioimpuls and the farmer breeders, and between the breeding companies and the farmer breeders. The commercial rights of new varieties, based on material of the central Bioimpuls programme, reside with the farmer breeder or breeding company/institute processing the seedlings. There is no royalty obligation back to the Bioimpuls project. Farmer breeders and the institutes were obliged to offer their selected breeding clones for commercial testing, and eventually variety registration and market introduction to one of the participating breeding companies. With that, we ensured that the breeding companies involved in Bioimpuls reaped the commercial benefits of their in-kind contribution within the project.

Work Packages

The various activities within the Bioimpuls project were grouped into four work packages (WP1, WP2, WP3, WP4), summarised in Table 2.

Work Package 1: True Seed Populations for Commercial Variety Selection

The objective of WP1 was to increase the short-term overall selection capacity for the breeding of potato varieties suitable for organic cultivation, by yearly providing true seed populations from advanced crosses containing at least one major resistance gene for late blight resistance, from the central Bioimpuls crossing programme as starting material in commercial selection pipelines of breeding companies/institutes and farmer breeders. All project partners participated in the selection of WP1 generated breeding material.

For WP1, crossing parents were selected amongst varieties and advanced breeding clones which could improve sustainability of potato production and/or contain late blight resistance. Each year, approximately 250 potato varieties and advanced breeding clones were tested under both organic and non-organic management to get an impression of their performance and yield potential under organic and non-organic growing conditions to evaluate their suitability as parental clones for the Bioimpuls breeding programme.

Each year, true seed populations were distributed to all partners according to their capacity and preference. All partners had to raise the true seedlings themselves in either greenhouse, screenhouse or field facilities. All partners were obligated to grow/select the next three to four field generations (partly) under organic field management to create appropriate selection conditions to select late blight resistant clones suitable for organic cultivation and seed production.

In the central Bioimpuls breeding programme, most seedlings were grown in the field at the organic site near Kraggenburg. Natural late blight infection was used to select against late blight susceptible seedlings. From all selected seedlings, one tuber was harvested to raise first year clones in the next year. During the first (1 plant) and second (6 plants) seed tuber generations, clones were visually selected on important traits such as plant type, tuber appearance, re-growth, dormancy, grading, yield and the occurrence of common or powdery scab. In the second seed tuber generation, molecular markers were employed (if applicable) to ascertain the presence of late blight resistance genes, and to identify which (combination of) genes were involved.

Table 2 Overview of activities of the Bioimpuls breeding programme, 2009–2019

	Work package 1 (short-term) Providing true seed populations for variety selection	Work package 2 (medium-term) Advanced introgression breeding 'Introgression group 1'	Work package 3 (long-term) Early introgression breeding 'Introgression group 2'	Work package 4 Education and communication
Activities	Evaluation of varieties and breeding clones under organic and conventional conditions to select crossing parents Making crosses to provide true seed populations to all partners for the selection of commercial varieties, commercial testing, and eventually variety registration and market introduction	Evaluation of breeding clones to select late blight resistant crossing parents Conduct crosses to provide true seed populations to the central program and breeding companies for selection of breeding clones	Evaluation of breeding clones to select late blight resistant crossing parents Conduct crosses to provide true seed populations to the central breeding program for selection of breeding clones	Developing a breeding course to enlarge the group of organic farmer breeders Developing a manual for potato breeding Organising yearly field visits for feedback and knowledge exchange Communication to a general public

In the third tuber generation, apart from further seed multiplication for next season, the remaining clones were tested for yield and agronomic parameters both under organic and non-organic field conditions and tested for late blight resistance on a spray-inoculated screening field.

Farmer breeders and breeding companies conducted their selection according to their facilities, breeding/selection scheme and capacity. Selected fourth year tuber generation material of farmer breeders and breeding companies was tested alongside the third-year tuber generation of the central breeding programme in yield trials and the late blight trial field of the central programme. Molecular markers for late blight resistance genes were employed on all the material. Evaluations in yield trial material included maturity type, skin colour, tuber shape, eye-depth, flesh colour, general impression, yield, under-water-weight (as indication for starch content or specific gravity), cooking and processing quality, and remarks for specific defects or diseases found within or on the surface of the tubers. Finally, container tests were conducted to screen for the presence of potato cyst nematode resistance type A (*Globodera rostochiensis* pathotype 1) and type E (*Globodera pallida* pathotype 3).

Late blight resistance was assessed in an additional field trial applying artificial inoculation with *P. infestans* isolate IPO-C (virulent against late blight resistance genes *R1* to *R7*, *R10* and *R11*) and sprinkler irrigation.

The most promising breeding clones from these pooled trials entered the Bioimpuls crossing programme. This way, the crossing programme became truly cyclic in a sense that the most promising breeding clones out of each year (re-)entered the central crossing programme.

At the onset, the ambition of WP1 was set at developing a crossing programme based on approximately 300 cross combinations per year and to yearly issue some 20,000 true potato seeds to the partners. The central breeding programme at Wageningen aimed to select yearly in 20,000–25,000 seedlings. Furthermore, the goal of the central breeding programme for this work package was set at yearly sending approximately ten potential varieties to the companies affiliated with Bioimpuls for further evaluation and commercial positioning. Parallel to this, farmer breeders could send their selected fourth year tuber generation clones to the affiliated companies for further evaluation and commercial positioning or postpone that for another year to wait for the central evaluation first.

At the start of Bioimpuls in 2009, only two late blight resistance genes (*Rpi-blb2* and *R8*) were available for commercial crosses (i.e. potentially leading to a commercial variety). During the years, newly released varieties added (homologues of) resistance genes *Rpi-cap1*, *Rpi-chc1 and Rpi-vnt1* to the commercial gene pool.

Given the intent to make the resistance barrier in potato against late blight as durable as possible, stacking of different resistance genes was an important goal of the Bioimpuls project. We ensured that before making crosses intended to stack genes, the individual sources containing different resistance genes should each have reached an acceptable agronomic level to avoid getting stuck in offspring containing only agronomically poor potato clones. Another reason not to conduct stacking from the beginning was the inability to identify stackings: we had to wait until proper molecular markers were available. For those reasons, at the start of Bioimpuls just stacking of *R8* with *Rpi-blb2* was attempted. Gradually the number of different late blight resistance genes brought in by the parents in a single cross combination has grown to six (*R8*, *R9*, *Rpi-blb2*, *Rpi-cap1*, *Rpi-chc1*, *Rpi-edn2*) (Fig. 3).

The initial aim to annually produce some 300 cross combinations totalling some 60,000 true seeds, was reached in 2010 and that number was well maintained right through 2019. The number of seeds distributed to the breeding companies increased steadily up to around 25,000; the number of true seeds that farmer breeders received varied yearly from 5000 to 25,000 (Fig. 4).

The central Wageningen breeding programme increased initially up to 25,000 true potato seeds in 2013, but was reduced in later years to some 18,000 per year as the work load arising from yield and late blight trials, and marker analysis of selected clones, increased. For the pre-breeding programme on average some 2500 true seeds were sown up to a maximum of 5000. In 2019, numbers sown within the central programme were further reduced due to uncertainty about prolonged funding of the project beyond 2019.

The collaborative nature of the project, as designed at the onset, can be demonstrated by the relative portion of true seeds sown by the breeding companies and farmer breeders per year, which increased over the years from an initial 47% in 2009 to 74% in 2019 (Fig. 5).

The number of selected clones kept in each field generation of the various annual series within WP1 by the breeding companies, the farmer breeders and the central Bioimpuls breeding pipeline are shown in Table 3.

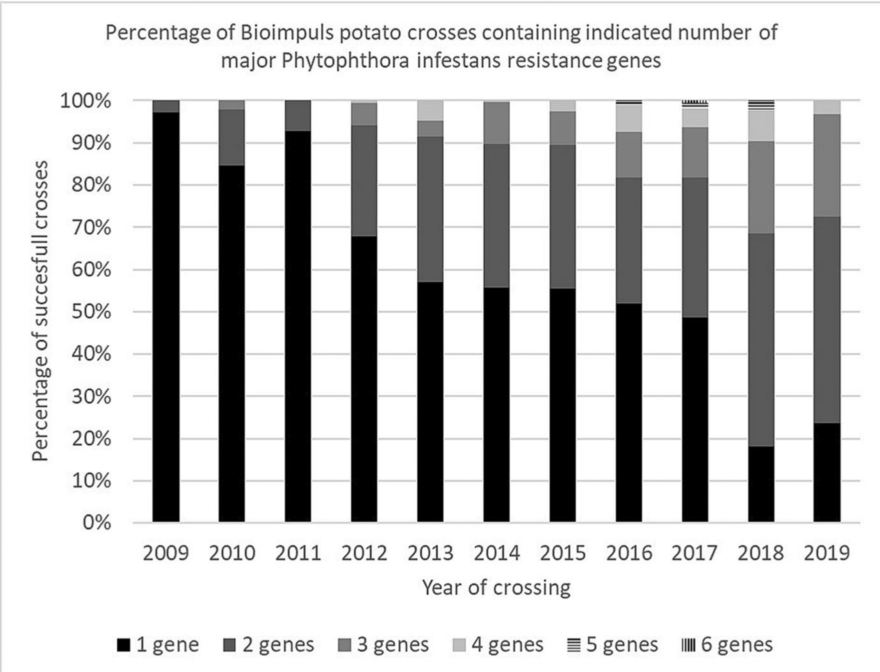

Fig. 3 Percentage of true seed yielding potato crosses within the Bioimpuls programme with indicated number of major *R* genes against *Phytophthora infestans* brought together in a single cross combination

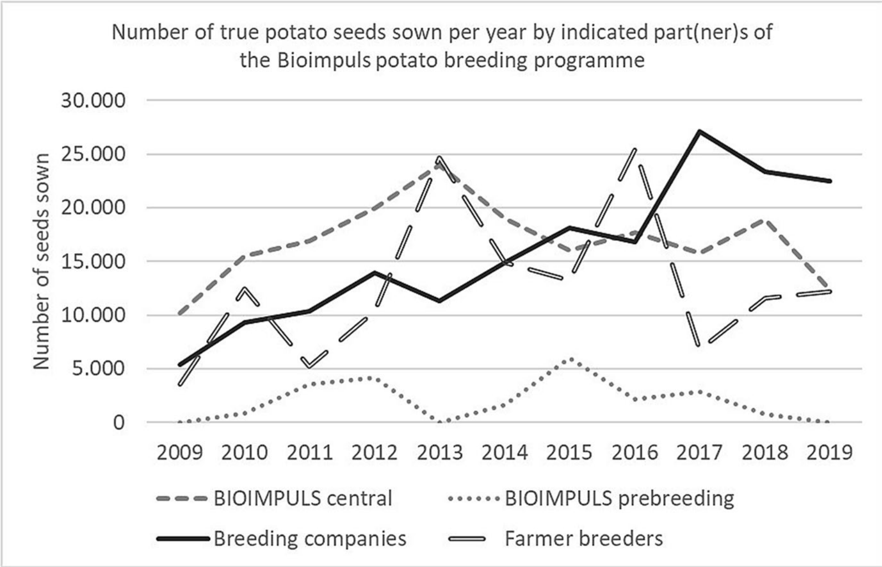

Fig. 4 Distribution within the Bioimpuls programme of true seeds over partnering breeding companies, farmer breeders and the central Wageningen breeding programme

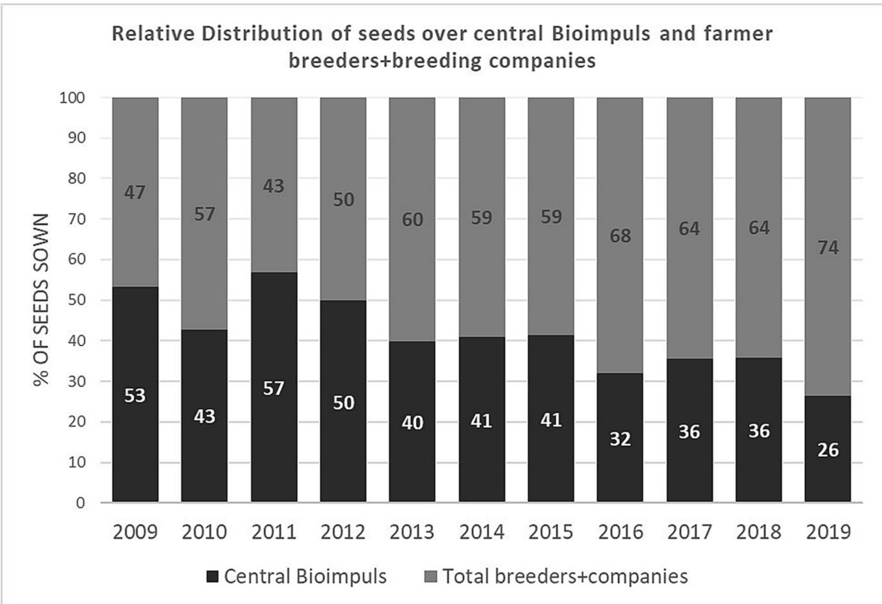

Fig. 5 Relative amounts of true potato seeds sown in the participative breeding programme Bioimpuls by either the central breeding programme at Wageningen University & Research or by the farmer breeders and breeding companies

Table 3 Selection results per annual series of sowing true seeds and subsequent seedlings (FG-0), first field generation, etc. of Bioimpuls material processed by the WUR selection pipeline and by the breeding companies and farmer breeders in WP1

Annual series		Selection results: number of clones selected										
year of sowing	Number of seeds sown	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019
2009	**11.062**	511	58	31	14	9	6	3	1	1	1	1
2010	**13.726**		4.602	326	87	43	27	16	10	8	6	6
2011	**11.058**			2.420	247	56	13	10	4	2	2	2
2012	**17.528**				4.704	491	132	51	25	11	8	7
2013	**17.975**					2.486	255	84	33	13	9	5
2014	**16.448**						3.469	301	72	30	12	6
2015	**12.457**							2.450	221	60	17	10
2016	**12.602**								3.022	312	98	31
2017	**7.570**									1.556	256	49
2018	**11.587**										1.456	330
2019	**10.537**											5.205

According to plan, potato clones selected by the breeding companies and farmer breeders entered the central Bioimpuls yield and late blight trials.

In 2012, the first clones from the breeders were evaluated in the central trials (Fig. 6). Between 2009 and 2019, in total, some 480 clones were submitted by the

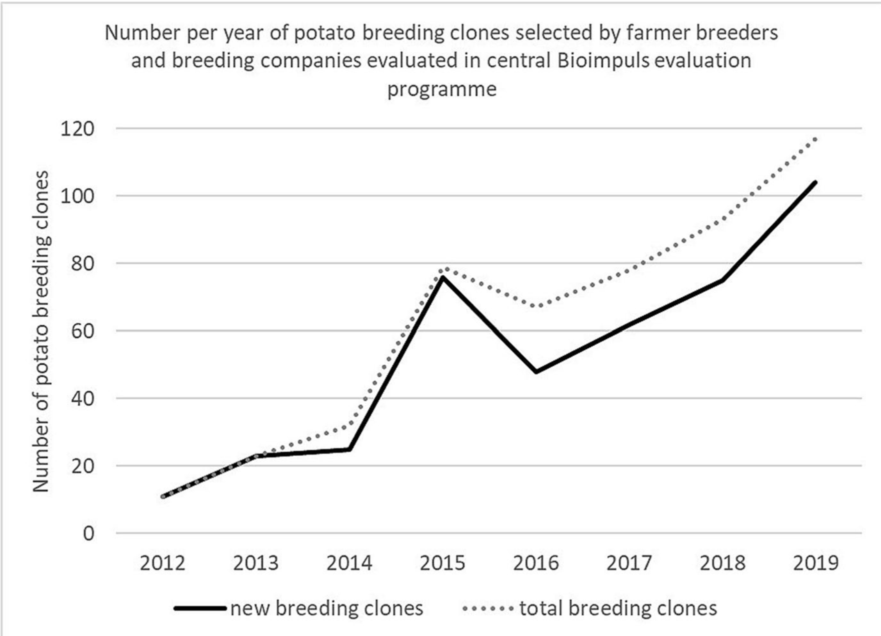

Fig. 6 Number of selected clones out of Bioimpuls crosses made by Bioimpuls partners (farmer breeders and breeding companies) brought back into the central Bioimpuls breeding programme to be tested for their value as potential breeding parents for a new round of crossings within Bioimpuls. 'New breeding clones' indicating the number of selected clones entering the central yield and late blight trials for the first time, and 'total breeding clones' indicating the total number of selected clones evaluated

partners for central evaluation as potential breeding parent, on top of the selected clones derived from the central Wageningen breeding programme.

As planned, each year at least ten late blight resistant breeding clones out of the central Bioimpuls breeding programme were chosen by the involved breeding companies to be taken up in their selection and commercial positioning pipelines (Fig. 7).

As shown in Fig. 7, the number of breeding clones entering the commercial selection pipelines of the partnering breeding companies varied between companies and between years, depending on the number of commercially interesting breeding clones available and on whether the available breeding clones matched the market focus of the companies involved.

In 2018, four breeding clones selected by breeding companies from seeds from Bioimpuls crosses were shown at three different commercial potato exhibitions of partnering breeding companies (Photo 1). In November 2019, another breeding clone YPB13-1044, selected from Bioimpuls true seed population BIM13-676 ('Mariola' × 'Athlete'), was submitted for official Dutch registration and National List trials in 2020 and 2021. In 2020, this late blight resistant breeding clone was named 'Nola', and is expected to be officially released early 2022.

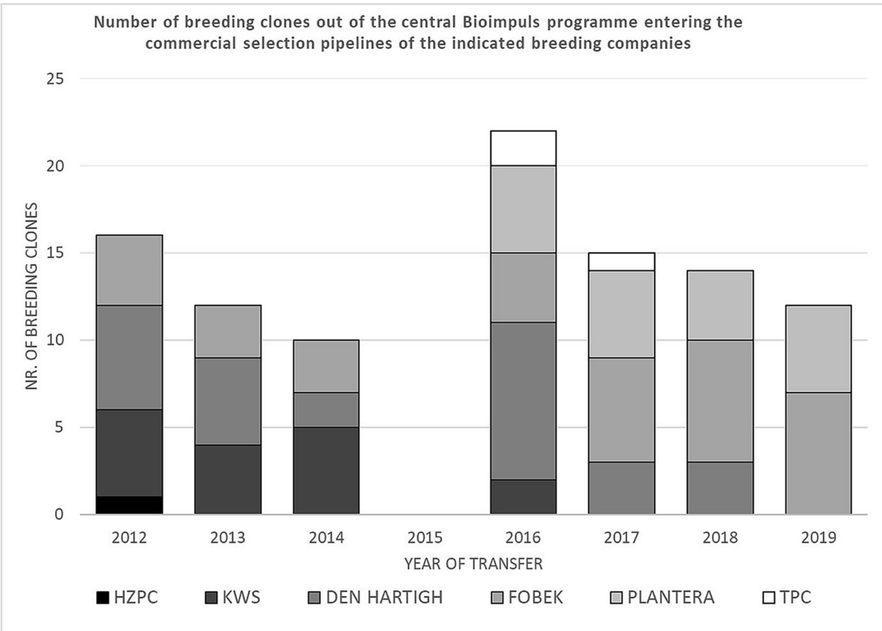

Fig. 7 Number of yearly new Bioimpuls breeding clones derived from the Bioimpuls central breeding programme entering the commercial selection pipelines of the partnering breeding companies for further evaluation and commercial positioning. KWS left Bioimpuls in 2016, while Plantera and TPC joined Bioimpuls in 2015. In 2015, transfer of Bioimpuls breeding clones was postponed to 2016 due to temporary quarantine restrictions. Breeding clones are assigned to a single company

Photo 1 Four advanced Bioimpuls breeding clones under evaluation and commercial positioning by from left to right: Den Hartigh (BIM12-414), Plantera (BIM12-439-04 and BIM13-678-1) and Stet Holland/HZPC (BIM10-4). The 2 breeding clones at Plantera are derived from the WUR Bioimpuls selection programme, the other 2 originate from Bioimpuls true seed populations sown at and selected by the companies

Although Bioimpuls aimed for resistant varieties containing stacks of late blight resistance genes and the amount of sown true seed populations containing multiple late blight resistance genes is strongly rising since 2011 (Fig. 3), the number of stacked breeding clones commercially evaluated by the breeding companies is still limited.

Work Package 2: Medium-Term Process—Advanced Introgression Breeding (Introgression Group 1)

The objective of Work package 2 was to upgrade available resistant genotypes containing *Rpi-edn2* or *R9* into suitable breeding clones through one or two cycles of backcrossing. In this way, the sources of resistance of this so-called Introgression group 1 would become available for commercial crosses in due course of the project. As time proceeded and markers were developed it became clear that *R9* and *Rpi-edn2* are homologues and contain totally identical coding sequences (Personal communication by Jack Vossen, WUR Plant Breeding 2020). So, although we stick to using both gene names (to indicate the original source of resistance *S. demissum* vs *S. edinense*), their interaction with all isolates of *P. infestans* is assumed to be identical.

For the introgression of resistance genes into commercially interesting breeding material, *S. tuberosum* backcross parents containing traits which are important to improve sustainability of potato production are selected. Successive cycles of backcrossing are always conducted in the Wageningen central breeding programme with different varieties or breeding clones to avoid inbreeding.

Crosses involving resistance genes *R9* and *Rpi-edn2* of Introgression group 1 were first sown in 2010 (Table 4). Some breeding clones containing *R9* or *Rpi-edn2*, or even containing a combination of one of these two genes with a resistance gene from WP1, have entered the commercial trials.

Table 4 Number of true seeds sown and selection results per annual series of sowing true seeds and subsequent seedlings, first field generation, etc. for WP2 in which potato crosses were made with major resistance genes *R9* or *Rpi-edn2*

Annual series		Selection results: number of clones selected										
year of sowing	Number of seeds sown	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019
2009	**-**	-	-	-	-	-	-	-	-	-	-	-
2010	**3.511**		1.209	108	19	10	5	3	3	-	-	-
2011	**5.834**			2.364	244	62	25	14	9	6	5	5
2012	**2.422**				610	55	16	4	2	-	-	-
2013	**5.992**					1.030	114	31	16	8	2	2
2014	**2.532**						698	79	11	6	3	1
2015	**3.611**							1.145	83	18	5	1
2016	**5.089**								1.744	214	82	24
2017	**8.219**									2.180	300	57
2018	**5.785**										668	173
2019	**1.850**											920

Work Package 3: Long Term Process—Early Introgression Breeding (Introgression Group 2)

The objective of WP3 was to make new wild sources of resistance available for breeding of late blight resistant varieties, by means of repeated backcrosses to *S. tuberosum* varieties or breeding clones and subsequent selection.

For WP3, five wild species were used: *S. brachycarpum* (*bcp*), *S. bukasovii* (*buk*), *S. iopetalum* (*iop*), *S. multi-interruptum* (*mtp*) and *S. sucrense* (*scr*). From each source, just a single clone was selected to start introgression breeding. These selected founders were respectively *BCP 326–3*, *BUK 510–2*, *IOP 273–1*, *MTP 364–1* and *SCR 849–6*. In 2009, true seed populations of first or second backcross generations of these sources were produced, and together this material made up Introgression group 2. The breeding activities for WP3 were carried out only by the Wageningen central breeding programme.

The further agronomic improvement of this Introgression group 2 material takes a more specialized approach because F1 hybrids between *S. tuberosum* and wild *Solanum* species and their first backcross generations often have a poor tuber set under long-day field conditions and the presence of long stolons makes it difficult to retrieve tubers in the field and to identify which tubers belong to which breeding clone. The best way to overcome these 'wild' characteristics as soon as possible in the introgression process is to use early maturing varieties or breeding clones to produce hybrid and first backcross generations. As male fertility of wild species genotypes, F1 and BC1 hybrids was not investigated, mostly good male fertile early maturing varieties, as for example 'Anosta', 'Fresco', 'Frieslander' and 'Miranda', were used in early back-cross generation crossings.

The work on Introgression group 2 started in 2009 with crossing hybrid (F1) or selecting first backcross (BC1) generation breeding clones. True seed populations from crosses 2009 were sown in 2010 as annual series '2010' (Table 5).

Backcross cycles of crossing (year 1), raising true seedlings (year 2), followed by at least three tuber generations including resistance testing in the field (as molecular markers are not available for these genes) and agronomic evaluation (years 3–5), take a minimum period of 5 years.

Table 5 Number of true seeds sown and selection results per annual series of sowing true seeds and subsequent seedlings, first tuber generation, etc. for Bioimpuls WP3 in which potato crosses were made with sources of resistance against *Phytophthora infestans* from Introgression group 2 (*Solanum brachycarpum*, *S. bukasovii*, *S. iopetalum*, *S. multiinterruptum* and *S. sucrense*)

Annual series		Selection results: number of clones selected										
year of sowing	Number of seeds sown	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019
2009	**-**	-	-	-	-	-	-	-	-	-	-	-
2010	**838**		130	42	11	5	5	5	2	2	2	2
2011	**3.528**			388	79	30	22	16	6	5	4	4
2012	**4.176**				886	85	26	15	10	7	4	3
2013	**-**	-	-	-	-	-	-	-	-	-	-	-
2014	**1.604**						78	14	6	1	1	1
2015	**6.010**							867	79	32	13	9
2016	**2.174**								434	42	26	12
2017	**2.892**									838	85	21
2018	**1.187**										187	33
2019	**-**	-	-	-	-	-	-	-	-	-	-	-

The five sources of resistance which made up Introgression group 2 mostly entered the Bioimpuls breeding programme as BC1 breeding population. Being a BC1, the wild species has been crossed twice with early maturing *S. tuberosum* varieties or breeding clones. As can be seen in Fig. 8, we expect some resistance sources need

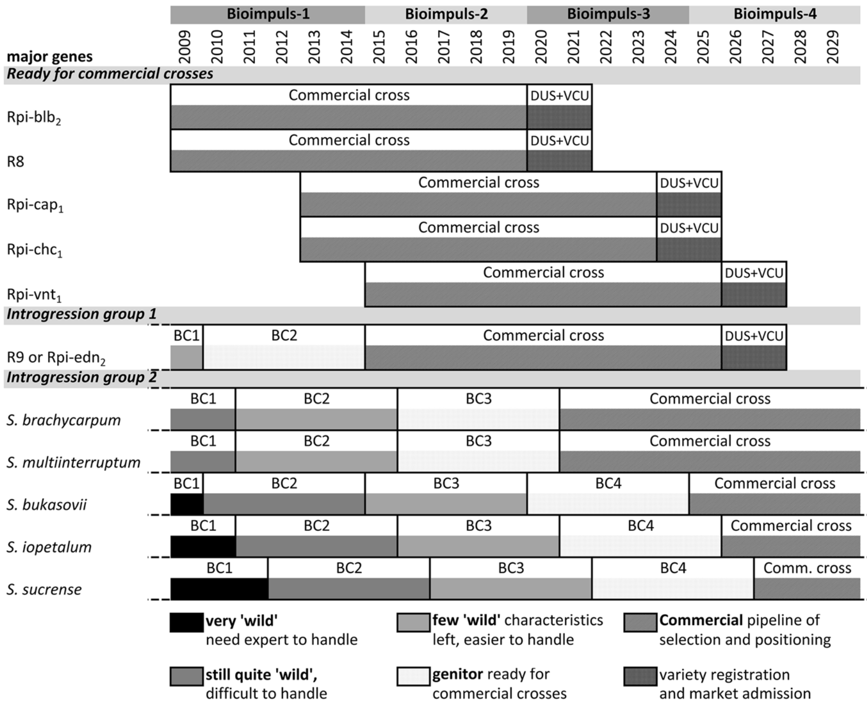

Fig. 8 Bioimpuls flowchart of resistance sources introgressed in commercial *S. tuberosum* backgrounds to produce new *Phytophthora infestans* resistant varieties. The project ran for two stages, 2009–2014 and 2015–2019, and is to be prolonged as of 2020 for another 10 years to process all resistance sources up to a commercially acceptable level

another two generations of backcrossing to reach acceptable levels for the wide range of essential agronomic and quality traits to become available for commercial crosses (*S. brachycarpum* and *S. multiinterruptum*), whereas other sources need three additional generations of backcrossing (*S. bukasovii*, *S. iopetalum* and *S. sucrense*).

Work Package 4: Education and Communication

The objective of WP4 was to train and support farmer breeders, continuously encourage knowledge exchange amongst researchers, farmer breeders and breeding companies, and to encourage communication to a general audience through popular and (semi-)scientific publications.

Every December, breeders/researchers from the central programme presented the progress made in the project and further steps were discussed amongst the partnering farmer breeders and breeding companies. During these winter meetings, a selection of breeding clones and varieties assessed in the central evaluation trials including all crossing parents used in newly offered true seed populations were showcased for the partnering farmer breeders and breeding companies. This offered the partners a more educated view on the choice of crosses they would like to receive true seed populations for the next season.

Most summers, a field visit was organised to the central late blight trial site where partners could see and discuss the performance of the resistance genes/sources incorporated in breeding material when challenged by artificial infection with late blight isolate IPO-C.

To further facilitate the knowledge exchange, feedback and (social) interaction between all participants, the breeders/researchers of the central programme regularly visited the farmer breeders at their potato fields during summer or in their potato storage during winter for personal reflection and to discuss Bioimpuls material under evaluation. The breeding companies were visited every few years on one of their trial fields, and every year at their annual trade show in November to discuss progress in their commercial positioning trials and developments within the organic market segments in general.

The Bioimpuls breeding project also aimed to enlarge the efforts for organic/sustainable potato variety selection. To this end, one goal was to enlarge the group of (organic) farmer breeders by introducing a breeding course named 'Potato breeding course for small breeders' (*in Dutch*).

Before 2008, there was no potato breeding course in the sector to train farmer breeders. Many farmers first wanted to know what on-farm potato breeding entailed in order to come to a well-considered decision whether or not to participate in the Dutch potato farmer-breeding system on which Bioimpuls expected to build. For that reason, a first introductory course was initiated in 2008. Jan van Loon, an experienced potato breeder with teaching ability compiled the content. In the first years, the course consisted of two theory lessons in winter and two practical field excursions in the potato growing season. After some years the need for more background arose and the course was extended as a more in-depth course to four theory sessions of four hours each, in addition to the two field excursions. Although the course started within the context of Bioimpuls to recruit organic farmer breeders for the project, also current breeders from both the non-organic and organic sector joined the course to refresh and deepen their knowledge. And increasingly, potato breeding companies have sent their young staff or affiliated breeders to join, and also other people involved in the potato sector (e.g. from the potato processing industry, trade or the seed certification authority) have joined the course (Table 6). The course thus became a recognized and appreciated part of the entire Dutch potato sector. This was the reason in 2013 to involve the potato sector in organizing the course. The three Dutch potato breeders' associations (Aardappel Kwekersvereniging Midden Nederland, Vereniging van Drentse en Groninger Aardappelkwekers and Fries-Groningse Aardappelkwekers Vereniging) started co-organizing the course in 2013 and took over entirely in 2019 (see http://louisbolk.org/bioimpuls/cursus/). Up to date, the course is still successfully offered on a yearly basis with some 15–20 participants per year. So far there has been sufficient interest every year as the course fills the gap between breeding practice and research.

Also, the developed training syllabus, compiled with background information on aspects of genetics, practical breeding and clonal selection, inspection, variety registration and plant breeders' rights, seemed to fill a gap for a larger audience, and a publisher got interested to officially publish the 'Potato breeding handbook' in Dutch and English, and later even in Chinese (Tiemens-Hulscher et al. 2013).

Table 6 Number of trainees of the 'Potato breeding course for small breeders' categorized as organic farmers, non-organic farmers, breeders and breeding technicians, and other interested persons

Year	Organic farmers	Nonorganic farmers	Breeders and technicians (1)	Other (2)	Total
Short introductory course					
2008	11	2	0	2	**15**
2009	6	3	0	2	**11**
2010	8	8	1	3	**20**
Full curriculum					
2011	6	5	4	4	**19**
2012	2	4	3	4	**13**
Breeders associations joined the organisation; update curriculum					
2013	3	0	10	3	**16**
2014	1	2	7	7	**17**
2015	3	5	7	4	**19**
2016	1	6	2	4	**13**
2017	4	6	5	3	**18**
2018	3	7	6	5	**21**
Breeders associations took over the organisation, full new curriculum					
2019	2	9	9	1	**21**
Total	**50**	**57**	**54**	**42**	**203**

(1)Breeding company staff, farmer breeders

(2)NAK certification inspectors, potato traders, teachers at Agricultural colleges etc.

The Bioimpuls project received much positive attention in the ongoing societal debates on GMOs and available alternatives through classical breeding. Because the Bioimpuls project for many years ran parallel to the DuRPh cisgenesis project (2006–2016) and WUR Plant Breeding was involved in both projects, on many occasions the two projects jointly presented their approach and perspectives at national and international scientific and public discussions stressing the importance of using diverse approaches, such as the non-GM, classical breeding approach and the GM cisgenesis approach, to significantly lower the economic and environmental damage caused by *Phytophthora infestans* (Bioimpuls 2013, 2015).

Discussion and Conclusions

Reflections on the Bioimpuls Goals

The Bioimpuls project aimed to set up a breeding programme that was large enough to be able to have an impact in solving the crisis in the organic potato sector due to lack of varieties adapted to organic production and resistant to late blight. The project managed to meet the initial goals with respect to the numbers of yearly produced true seed populations (300), to yearly issue these true seed populations to the farmer breeders, breeding companies, and the central breeding programme (see Fig. 4); the total amount of true seeds sown per year in the Bioimpuls project (40–50,000 true seeds/year) is comparable to a breeding programme of a middle-sized breeding company (Van Loon 2019). Also, the expectation that each year about ten selected resistant clones from breeding companies and farmer breeders would enter the centralized Wageningen evaluation trials was easily matched (Fig. 6). Another numerical goal was met from 2012 onwards, to enter about ten resistant breeding clones from the central breeding programme into the pipelines of evaluation and commercial positioning at the participating breeding companies (Fig. 7). Resistant breeding clones selected by the breeding companies and farmer breeders are also included in these pipelines.

Spinoff of the Project

In various ways, this breeding project was unique for the Netherlands. The late blight problem as the major disease in a major crop stands out in severity in both the conventional and organic sector. In the conventional potato sector, the pressure is high to solve the problem as combating this disease requires almost half of all fungicides applied in Dutch agriculture (Haverkort et al. 2016). For the organic sector the sense of urgency was also high as late blight threatened the future of the Dutch organic potato production. The fact that the Bioimpuls project under the Green Breeding Programme aimed to solve problems that occur both in the conventional and organic sector, contributed to joint efforts and making use of each other's knowledge, rather than polarising between the two sectors.

Through the project, not only the larger companies but also the smaller companies and farmer breeders got access to multiple sources of late blight resistance in order to develop and provide a diversity of cultivars to serve the various segments in the potato sector (e.g. fresh consumption, French fries and chips/crisps). This set-up of the project allowing also smaller companies to join the project was very much appreciated and reminiscent of the 1950s–1980s when the Dutch public institutes provided advanced resistant starting material against various important potato diseases (Hogen Esch 1953; Van Loon 2019).

This project also stood out as it is a unique example of participatory plant breeding operating not only with breeding researchers but also with commercial breeding companies and farmer breeders (Almekinders et al. 2014). Through this network of organic farmer breeders involved in Bioimpuls, the breeding companies could take advantage of a wide variety of organic trial conditions. Potato clones selected by these farmer breeders excelled under organic conditions, and breeding companies adapted their own evaluation system to ensure this material stood a fair chance in their further evaluation and commercial positioning pipelines.

Moreover, the overall interest of the six breeding companies involved in breeding for organic agriculture was significantly intensified, as encouraging and promising results started to emerge in their own evaluation and positioning pipelines. At the start of Bioimpuls in 2009, breeding for organic production represented a small fraction of the overall breeding programme for only one or two breeding companies. Now in 2019, breeding for organic production is a firmly established part of the breeding programmes of all breeding companies involved in Bioimpuls.

Also, within groups of farmer breeders affiliated with a breeding company, the interest for breeding for organic production has increased. Some breeding companies already were working with one or two affiliated organic farmer breeders (e.g. Agrico, Meijer Potato), but with the onset of Bioimpuls more affiliated non-organic farmer breeders joined in. As evaluation under organic conditions for at least one season is a prerequisite for participating within Bioimpuls, new organic trial sites were established by breeding companies, farmer breeders and also the largest potato breeders' association AKV-Midden-Nederland. And by doing so, Bioimpuls stimulated general interest in and debate on organic evaluation, resistance screening and perceived market opportunities for potato breeding/breeding clones with potential for organic production.

Most of the non-organic breeding companies joining Bioimpuls in 2009 reasoned that 'robust and low-input' varieties also held potential for their non-organic seed potato markets, such as most countries in the Mediterranean.

In 2017, these positive developments in breeding for organic potato varieties were supported by a full commitment of all Dutch retailers to join a covenant, formulated by the Dutch organic umbrella organisation Bionext, in which it was agreed to take a four-year period to reach the use and sales of 100% late blight resistant varieties for their organic potato segment in 2020 (see www.bionext.nl).

Future Challenges

Despite meeting the project goals in giving a substantial impulse to both the organic and conventional potato breeding sector by enlarging the access to sources of late blight resistance, the problem for the organic sector is not yet solved. As it takes at least 10 years between producing a true seed population and the market introduction of a new variety selected thereof, just now the first Bioimpuls clones are entering the registration process and subsequently the market. All late blight resistant varieties that have entered the market so far contain only one major resistance gene. As durability of single major gene-based resistance against late blight is questionable, as regional small-scale infection on solely *Rpi-blb2* and *R8* containing varieties in the Netherlands in recent years has shown, the need for varieties with late blight resistance based on multiple resistance genes is high. As shown in Fig. 3, a lot of true seed populations containing multiple resistance genes are produced by the Bioimpuls breeding programme and the first breeding clones possessing multiple resistance genes are entering the evaluation and positioning trials of companies. However, it will take a considerable amount of time before varieties with stacked genes will replace the single gene varieties. So far, no specific agronomic performance problem correlated to one of the late blight resistance sources/genes has been identified during the breeding process. Although breeding material containing sources of Introgression group 2 or containing stacked resistance genes is not yet extensively trialled, we see no insurmountable performance problems ahead.

The transition period to varieties with stacked resistance genes requires strict resistance management to prevent break down of individual resistance genes (Pacilly et al. 2018, 2019b). Many trainings in this respect have been given to the Dutch organic farmers (Pacilly et al. 2019a). Moreover, farmers can help to avoid a rapid increase of virulence towards individual resistance genes by growing varieties with different resistance genes next to each other, until new varieties with stacked resistance genes become available (Pacilly et al. 2018). The continuous monitoring of late blight populations for virulence genes present is an important informative tool for resistance management (Zwankhuizen and Zadoks 2002). It helps to choose the right resistant varieties to grow and it alerts farmers if new virulence genes are occurring during the growing season.

To meet the challenge of breeding with various combinations of resistance genes against late blight, it is important to have access to a wide diversity of resistance sources. Although there was a wide diversity of genetic sources available in this project, there is one group of genetic resources (Introgression group 2) that is still too primitive to be used in a commercial breeding programme. So, pre-breeding activities with these sources have to be prolonged. In order to be able to stack these resistance sources with the genes already present for commercial crosses, further genetic analysis of the resistance present and the development of molecular markers is indispensable.

The current breeding program was to a large extent focussed on foliage late blight resistance. However, there is also a need for more knowledge on the effect of these resistance genes in regard to tuber resistance towards *P. infestans* (Świeżyński and Zimnoch-Guzowska 2001).

Perspectives

At the start of Bioimpuls, the Dutch organic potato production area had fallen from 1440 hectares in 2000 to about 1000 in 2009, due to high disease pressure and a lack of suitable resistant varieties. With the introduction of new resistant varieties, the acreage has risen to 2045 hectares of certified organic potato production in 2020 (CBS 2020), and is expected to increase significantly further with the introduction of a broad range of new varieties resistant to late blight. Bioimpuls contributed by creating a general perception among Dutch breeders that now is the time for finally getting a grip on *P. infestans*, and secondly. Interest in late blight resistant varieties is not limited to organic potato growers. Also, non-organic potato growers worldwide exhibit a keen interest in these resistant varieties, providing additional economic advantages both in Dutch national ware production and in Dutch seed potato exports.

The total public investment of the Bioimpuls project between 2009 and 2019 was around 3 M€. Raising the average yield of organic potato production from 25 to 45 tonnes per hectare by growing resistant varieties and as a consequence no premature haulm killing nor yield losses, the increase in economic value for organic production in 2018 alone was about (1,612 ha × 20 tonnes × 250 euro) 8 M€. Besides, with resistant varieties, substantial cuts in costs on fungicides in non-organic ware and seed potato production can be achieved (approx. 300–400 euros per year per ha), impacting the overall sustainability of the potato sector.

Additionally, interest from potato growers abroad, both organic and non-organic, into varieties resistant to late blight, increases the demand for seed potatoes produced in the Netherlands from these varieties. Stimulating breeding for resistance and with that the adoption of resistant varieties in Dutch potato production easily surpasses public investment in late blight resistance breeding through Bioimpuls. Moreover, Bioimpuls strengthens the international competitiveness of a broad group of Dutch breeding companies and farmer breeders by providing them with advanced breeding material containing a broad variety of resistance genes. Bioimpuls certainly does strengthen the international competitiveness of the Dutch seed potato sector as a whole. As Dutch seed potato sales account for more than 60% of worldwide certified seed potato export, it stands to reason that Bioimpuls contributed significantly to improve sustainability of both organic and non-organic potato production worldwide.

Author Contribution All authors have been substantially involved in writing this paper:

Peter Keijzer, as first author, is the current coordinator of the Bioimpuls project and was one of the partner breeders from 2009 to 2017; he has analysed the data for this paper and wrote drafts and submitted a version of the paper together with Edith Lammerts van Bueren, and functions as submitting author.

Edith Lammerts van Bueren was the previous coordinator who was responsible for the acquisition of the funding of the project, coordinated the project, wrote the setup of the paper together with Peter Keijzer and functions as corresponding author.

Christel Engelen is the breeder of the project, designed the crossing programme and conducted all field trials, and has provided all data of the project, and commented on drafts.

Ronald Hutten is the prebreeder of this project and provided the general setup of the programme, delivered the expert knowledge on the breeding programme, and contributed substantially to the paper.

All authors have read and agreed with this manuscript version.

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Data Availability Not applicable.

Code Availability Not applicable.

Declarations

Ethics Approval and Consent to Participate Not applicable.

Consent for Publication Not applicable.

Conflict of Interest Not applicable.

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