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Special Report

e-**X**tra*

The Impact of Management Strategies on the Development and Status of Potato Cyst Nematode Populations in Switzerland: An Overview from 1958 to Present

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Abstract

Globodera rostochiensis and *G. pallida* are some of the most successful and highly specialized plant parasitic nematodes and among the most regulated quarantine pests globally. In Switzerland, they have been monitored by annual surveys since their first detection in Swiss soil in 1958. The dataset created was reviewed to produce an overview of the development and actual status of potato cyst nematodes (PCNs) in Switzerland. Positive fields represent 0.2% of all the samples analyzed, and their distribution is limited to central-west and western Switzerland, suggesting that new introduction of PCNs and the spread of the initial introduced PCN populations did not occur. In this way, the integrated management used in Switzerland appears to be effective. However, the increasing availability of potato varieties with resistance to *G. rostochiensis* and the limited availability of varieties with resistance to *G. pallida*, together with other biotic and abiotic factors, have promoted changes in the dominance of either species. Consequently, an extended monitoring program is of interest to Swiss farmers, to avoid favoring virulent traits that could be present in Swiss *Globodera* populations.

Keywords: *Globodera pallida*, *Globodera rostochiensis*, history, monitoring, phytosanitary measures, quarantine, Switzerland

Globodera rostochiensis (Skarbilovich, 1959; Wollenweber, 1923) and *G. pallida* (Stone, 1973) are responsible for major yield losses in the production of industrial, seed, and staple potatoes (Schenk et al. 1999; Turner and Subbotin 2013; Varypatakis et al. 2019) and together with *G. ellingtonae* (Handoo et al. 2012) are known as potato cyst nematodes (PCNs). The distribution of *G. ellingtonae* is restricted to the Americas (Handoo et al. 2012; Lax et al. 2014; Skantar et al. 2011), whereas *G. rostochiensis* and *G. pallida* are reported to be present on all continents where potato is grown (CABI 2020). PCNs are host-specific, obligate sedentary endoparasites suggested to have coevolved with wild potato species (*Solanum* L. section Petota Dumort.) in South America (Grenier et al. 2010; Hockland et al. 2012; Plantard et al. 2008; Spooner and Hijmans 2001; Stone 1979; Thevenoux et al. 2020). Among the most specialized and successful plant parasitic nematodes, PCNs are of great scientific and economic importance (Jones et al. 2013), having as restricted hosts plants of the Solanaceae family. Potato (*Solanum tuberosum*), tomato (*S. lycopersicum*), eggplant (*S. melongena*), and >90 other *Solanum* spp. including some weed species and hybrids have been described as hosts (CABI 2020; Blacket et al. 2019; van Riel and Mulder 1998). However, potato is the most important staple crop affected.

In 2018, >368 million metric tons of potatoes were produced globally (Food and Agriculture Organization of the United Nations 2020), with a market value of $140.5 billion, and because of the growing global demand for food, the potato market is expected to continue to grow in the coming decades. Switzerland contributes a small share of world potato production (447,600 tons). However, potatoes are the third most important arable crop in Switzerland, with a planted surface area of 11,107 ha, yield of 403 kg/ha (Swisspatat Statistische Angaben 2019), and a self-supply of 90%, greater than any other planted crop (Lüthi et al. 2018).

Since the introduction of the potato before the end of the 16th century in Europe (Ames and Spooner 2008), it has become one of the main crops, with a very important role in the global food supply chain. Alongside potato tubers, PCNs were introduced to Europe, presumably in the mid-19th century, and in many countries they went unnoticed until nematode damage was observed (Jones 1970). In Switzerland, PCNs were first observed in imported seed potatoes in 1955, and later, in 1958, they were detected on Swiss soils.

Because of a combination of dormancy systems, diapause and quiescence (Antoniou 1989; Devine and Jones 2003), and the protection that the hard-walled cyst provides to the nematode eggs, PCNs can persist for many years in soil, even in the absence of a suitable host. Hatching of second-stage juveniles (J2) from encysted eggs occurs primarily in response to a stimulus from host plant root leachate, which usually contains multiple hatching factors (Devine et al. 1996). Both species can be classified into different pathotypes based on their virulence or avirulence reactions in potato genotypes containing varying resistance to PCNs. *G. rostochiensis* currently has five pathotypes, Ro1 to Ro5, whereas *G. pallida* has three, Pa1 to Pa3 (Dandurand et al. 2019; Gartner et al. 2021; Kort et al. 1977). In addition, new *Globodera* species and pathotypes are still being discovered and may pose new threats to global potato production (Knoetze et al. 2013; Mwangi et al. 2019; Niere et al. 2014; Subbotin et al. 2010).

Current management of PCNs relies on nematicides, resistant potato cultivars, and long crop rotations. However, under current European Union legislation (EC) no. 1107/2009, several nematicides have been banned. In Switzerland, no nematicides are available or registered for PCN control, and farmers rely on the use of certified seeds, resistant cultivars, and long crop rotation cycles of ≥4 years.

To monitor the distribution of PCNs, contain the spread, promote correct management, and prevent loss of food and economic resources, annual surveys have been conducted by the Swiss center of excellence for agricultural research, Agroscope, since the detection of PCNs on Swiss soil. Thus, the aim of this study is to provide an

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overview of the development and status of PCNs over time in Switzerland and to provide an update on available management strategies. These findings will support the understanding of the use in tracking plant pathogens over time and show the importance of resistant cultivars and their development for the future.

Regulation of PCNs in Switzerland

The Plant Protection Ordinance (PSV SR 916.20) has determined that *G. rostochiensis* and *G. pallida* are quarantine organisms in Switzerland, and any suspected infestation must be immediately reported to the administrative division, which is the cantonal (member state of the Swiss Confederation) plant protection service.

Before the detection of the first PCN on Swiss soil in 1958, PCNs were regulated as an import measure for seed potatoes (Bundesratsbeschluss, November 1956). In 1962, the federal council implemented a decision to combat PCNs on Swiss soil (Bundesratsbeschluss, March 1962). The scope included the definition of host plants, control zones where PCNs were located with their infestation center and protection zone, and the regulation of seed potato production with a 3-year crop rotation free of host plants, with the narrow range of PCN hosts used as an advantage. Furthermore, potato growers were subject to control of potential infestations, and infected areas were under strict regulation. For host plant production, weakly infected fields were blocked for 4 years, and severely infected fields were blocked for 8 years (however, the degree of infection is not described in the legislation and is subjective for the current officer). The cultivation of resistant potato varieties was also regulated by this Federal Council determination. Fifty years later, in 2012, the Federal Office of Agriculture's Directive no. 1 (https://www.blw.admin.ch/blw/de/home/nachhaltige-produktion/Pflanzengesundheit/schaedlingeundkrankheiten/quarantaeneorganismen.html) replaced the 1962 directive and began to regulate the monitoring and management of PCNs. This new legislation mandated the testing of all seed potato fields and 0.5% of other intended potato production areas for the presence of PCNs before planting. In the case of seed potato fields, if positive samples are detected, the infected field is blocked for 6 years, before an official request for approval can be attempted at the cantonal level. In general, farmers can still circumvent the restriction and use the fields for potato production, except for seed potatoes, if the PCN pathotype is determined and a resistant variety is available (https://www.blw.admin.ch/blw/de/home/nachhaltige-produktion/Pflanzengesundheit/schaedlingeundkrankheiten/quarantaeneorganismen.html).

Annual surveys began in 1959, and until 1965 only fields with characteristic PCN infestation symptoms were sampled. Initially, the Agroscope station in Changins and later in Reckenholz were responsible for data collection. The survey was expanded, and from 1966 to 2011, of the 1,800 Swiss growers registered for seed potato production, only fields intended for the production of seed potatoes were checked (Högger 1984). In 2012, it became the responsibility of the nematology group of Agroscope Wädenswil to analyze soil samples from seed potato and staple potato fields. Currently 3,500 to 4,000 samples are analyzed per year (depending on needs and the availability of fields after the minimum required 4-year crop rotation cycle), with a MEKU automated soil sample extractor (modified Seinhorst-can; Germany, www.meku-pollaehne.de), as described in European and Mediterranean Plant Protection Organization (EPPO) Bulletin PM 7/119 (Hallmann and Viaene 2013). Positive PCN samples detected by morphological features are confirmed via the multiplex PCR test of Bulman and Marshall (1997) described in the EPPO Bulletin for diagnosis of *G. rostochiensis* and *G. pallida* to identify the respective *Globodera* spp. (EPPO 2017).

Historical Data on PCNs in Switzerland

In an attempt to promote Swiss agriculture, seed potatoes were imported in 1950, particularly from the Netherlands, Denmark, and Germany (Bundesblatt 1950).

From the data collected in the annual surveys (1959 to 2019), we could produce an overview of the development, spread, and status of PCN distribution in Switzerland. Positive PCN fields represent 0.2% of all samples over the years. PCN with infestation in Switzerland occurred mainly between 1965 and 1970 and between 1980 and 1995, indicating that the introduction or spread of PCNs occurred over many years or even decades, as suggested by Högger (1984). After that, a sharp decline in the number of PCN-positive fields could be observed (Fig. 1).

To provide an overview of whether PCN infestations were locally restricted or spread across Switzerland, the total numbers of PCN-positive fields and samples were analyzed by canton over time (Fig. 2). PCNs were first detected in Vaud (VD) in 1959, and the next year in the neighboring canton of Fribourg (FR) (Fig. 2). In 1963, PCNs were detected in Valais (VS), Graubünden (Grisons, GR), and Ticino (TI), all located in southern Switzerland. Between 1983 and 1990, PCN, were widespread in Switzerland, detected in 17 of the 26 cantons, including the territory of Lichtenstein (FL) (Fig. 2). Bern (BE), FR, GR, St. Gallen (SG), VS, and VD were the cantons with the highest numbers of PCN-positive fields (Supplementary Fig. S1). The cantons of GR and VS (Supplementary Fig. S1C and F) discontinued seed potato production in 2000, contributing to the decrease in the total number of fields positive for PCN (Fig. 1). Together, BE, FR, and VD are the main potato-producing regions in Switzerland, accounting for 66% of Swiss potato production (Swisspatat Statistische Angaben 2019) and are the only cantons where PCN-positive fields have been detected between 2015 and 2019 (Supplementary Fig. S1A, B, and E). In this sense, the distribution of PCNs is currently limited to central-west and western Switzerland (Fig. 2).

To assess the dynamics of *Globodera* species in Switzerland over half a century, we reviewed the dataset and retrieved the identified species (Fig. 3). Excluding data in which PCN species were not identified, 77% of positive fields were infested with *G. rostochiensis*, 9% with *G. pallida*, and 14% with mixed populations. *G. rostochiensis* was first detected on Swiss soil in 1959 and *G. pallida* a year later. A gradual increase in *G. rostochiensis*-positive fields was observed from 1959 until 1978, whereas *G. pallida*-positive fields remained constant. After the introduction of the first potato variety with resistance to *G. rostochiensis* in 1968, a gradual decrease in *G. rostochiensis* and an increase in *G. pallida* could be observed from 1979 to 1998. During this period, the planted area (Fig. 4) and the number of potato varieties resistant to *G. rostochiensis* (Supplementary Tables S1 to S3) increased, leading to an increase in the prevalence of *G. pallida* over *G. rostochiensis*, from 1999 to 2019. Furthermore, 4% of the PCN-positive fields where *G. rostochiensis* or both PCN species were detected previously showed a shift toward *G. pallida.* The shift in the prevalence of PCN species took an average of 10 years and occurred from 1971 to 1994, when 13 potato varieties with resistance to *G. rostochiensis* were cultivated in Switzerland (Supplementary Tables S1 and S2).

Similar changes in the predominance of *G. rostochiensis* and *G. pallida* were previously observed in British and Dutch fields in the 1960s and 1970s (Elliot et al. 2004; Hockland et al. 2012). These changes were reported after the introduction of potato cultivars with complete resistance to *G. rostochiensis* but with susceptibility to *G. pallida*. Potato cultivars bred for resistance against *G. rostochiensis* (Ro1 pathotype), the most dominant species population type in Europe, became available to European farmers in the mid-1960s (Hockland et al. 2012). Therefore, the cultivation of Ro1-resistant cultivars provided a strong selection pressure, allowing undetected individuals in a population with different genetic traits to overcome this resistance and multiply (Mwangi et al. 2019; Niere et al. 2014). The marked differences in the life cycles of *G. rostochiensis* and *G. pallida*, such as the greater level of spontaneous hatching for *G. rostochiensis* than for *G. pallida*, their selectivity in response to hatching factors (proven in vitro; e.g., Sakata et al. 2021), the optimal hatching temperatures (>20°C for *G. rostochiensis* [about 21°C] and <20°C for *G. pallida* [about 17°C]) (Byrne et al. 2001; Franco 1979; Jones et al. 2017; Kaczmarek 2014; Skelsey et al. 2018), and their differences in susceptibility to resistant potato varieties contributed to a higher rate of decline of *G. rostochiensis* populations in fields when compared with *G. pallida*. These characteristics make control of *G. pallida* less effective in integrated control strategies than that of *G. rostochiensis* (Evans and Haydock 2000). The increasing availability of potato varieties with complete resistance to *G. rostochiensis*, the limited availability of cultivars resistant to *G. pallida* (Supplementary Table S4), and the influence of other biotic and abiotic factors will probably contribute to changes in the dominance of either species in different parts of the world (Hockland et al. 2012; Holgado and Magnusson 2010).

In Switzerland, only *G. pallida* "Chavornay" pathotype Pa2/3 has been described. This strain is known as one of the most aggressive populations of *G. pallida* in Europe, and it is used as a laboratory reference for the European resistance assessment system introduced by EPPO in 2006 and for molecular analysis (Plantard et al. 2008).

The origin of the "Chavornay" population was previously analyzed by Plantard et al. (2008), who used mitochondrial haplotypes to compare European and Peruvian populations of *G. pallida.* The "Chavornay" population was grouped with nine different populations selected from the Netherlands, the United Kingdom, and France and has the Peruvian haplotype from Colca Canyon, a restricted area in southern Peru, as its sister group (Plantard et al. 2008). Consequently, this European population is assumed to have spread across Europe after its first introduction (Plantard et al. 2008; Subbotin et al. 2020).

The *G. pallida* "Chavornay" population was first detected in fields located in Chavornay (VD), Switzerland in 1960 and was last detected in 1970 in this region. However, it is possible that *G. pallida* "Chavornay" population has been spread to other potato fields in Switzerland, because Chavornay (VD) is located in the main seed potato-producing region. To confirm or exclude the presence of *G. pallida* "Chavornay" population or different populations of *G. pallida* in potato-producing fields in Switzerland, sequencing analysis still must be done, because the sequences currently available provide information only from a specific population coming from a region in western Switzerland. Likewise, no sequence information is available for the Swiss *G. rostochiensis* populations. Therefore, different populations of *Globodera* could be present in Switzerland, because the country imported the main potato varieties, and various populations of *G. pallida* are known to be present in Europe.

The genetic characterization of the PCN isolates will be of great importance, because phylogenetic information can reveal clarity of the route of entry (and whether the spread was within or into the country) and subsequent development of targeted measures to disrupt introduction and spread through intensified sampling for PCNs. In addition, analyses of multiple genetic markers or mitotypes can distinguish the PCN population and potentially indicate their virulence profiles (Eves-van den Akker et al. 2015; Subbotin et al. 2020). These findings will strengthen pathotype testing and control measures to further support growers in choosing the best resistant potato cultivars.

Management and Control of PCNs in Switzerland

Management and control of PCNs in Switzerland depend on the use of certified seeds, resistant cultivars, and long crop rotation cycles of ≥4 years, because there are no registered nematicides against PCNs in Switzerland. Other effective measures to control PCNs include

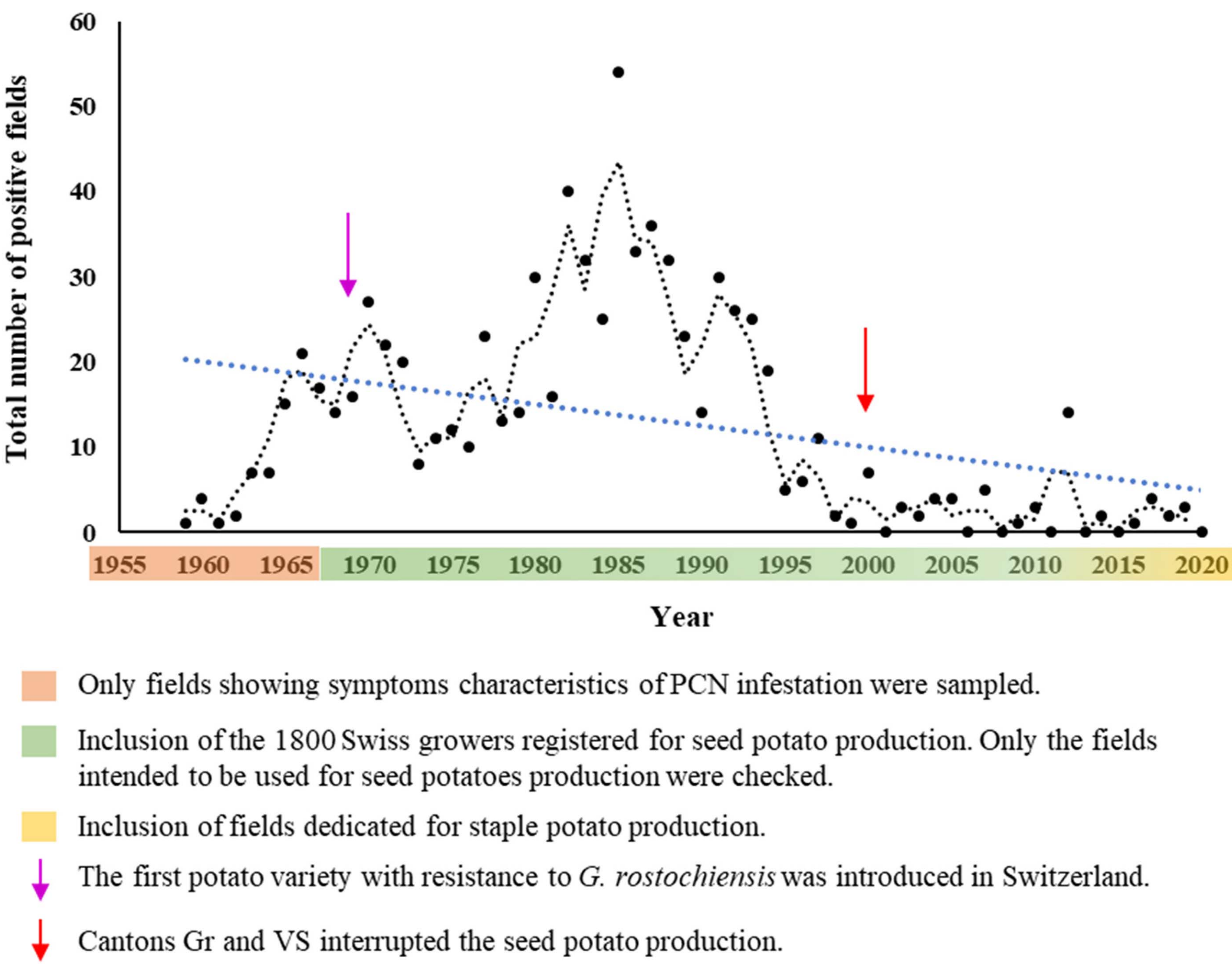

Fig. 1. Overview of potato cyst nematodes (PCNs) in Switzerland. Total number of PCN-positive fields by year (black). The overall trend reflecting the decrease in the number of positive fields since 1995 is represented by the trend line (blue dotted line). The number of sampled fields varied by year, depending on the intention of the farmers to produce seed potatoes and on the availability of the fields because of the crop rotation cycles. Gr, Graubünden; VS, Valais.

removal of all potential host plants, including weeds, and control of volunteer potatoes (as an additional measure to reduce existing PCN populations in the fields).

Certified Seeds

Swiss potato certification benefits from public and foreign organizations based in Switzerland, such as the International Seed Testing Association, the International Union for the Protection of New Varieties of Plants, and the United Nations Economic Commission for Europe. All aspects related to seed potato certification, from a common terminology to the minimum commercial quality requirements, are covered by the United Nations Economic Commission for Europe. In addition, the land used for the production of seed potatoes must be tested and found to be free of PCNs. Switzerland is following these guidelines in the framework of the European plant passport, a document issued for trading of pest-free plant material (Direktzahlungsverordnung SR 916.201). In Switzerland, the plant passport certificate is granted for seed potatoes free of PCNs that have followed Directive no. 1 of the Federal Department of Agriculture.

Resistant Potato Varieties

Pathogen-resistant cultivars have been widely used but with different limitations for *G. rostochiensis* or *G. pallida*. Some resistance genes have been introduced into commercial potato cultivars: *H1* from *S. tuberosum* spp. *andigena* (Gebhardt et al. 1993) and *Gro1-4* from *Solanum spegazzinii* (Paal et al. 2004) for *G. rostochiensis*, the *Gpa2* gene from *S. tuberosum* spp. *andigena* conferring partial resistance to *G. pallida* (van der Voort et al. 1999), and the potato resistance locus *Grp1* with broad-spectrum resistance against *G. rostochiensis* and *G. pallida* (Finkers-Thomczak et al. 2009). Potato cultivars resistant to *G. rostochiensis* are widely used as a successful control method. However, breeding for resistance to *G. pallida* is more complex, because no single gene confers complete resistance to all populations and pathotypes with different levels of virulence (Dalton et al. 2013).

As current legislation prescribes in case of fields infected with PCNs, it is important to determine the PCN population (pathotype) in the field to define the best resistant potato cultivars to be used. PCN DNA barcode regions are currently evaluated to support the time-consuming evaluation of PCN pathotypes for future routine processes. However, a bioassay of a set of resistant potato cultivars is still necessary to determine pathotypes (EPPO 2018). Continuous use of resistant cultivars (three or four crops) can greatly reduce the number of viable eggs in the soil (Varypatakis 2019). However, this practice can lead to strong selection in favor of other species (e.g., more virulent pathotypes), as observed for *G. pallida* in the United Kingdom and the Netherlands (Whitehead and Turner 1998) and more recently in Switzerland. In 2014, virulent populations of *G. pallida* were described as having outcompeted all known resistant

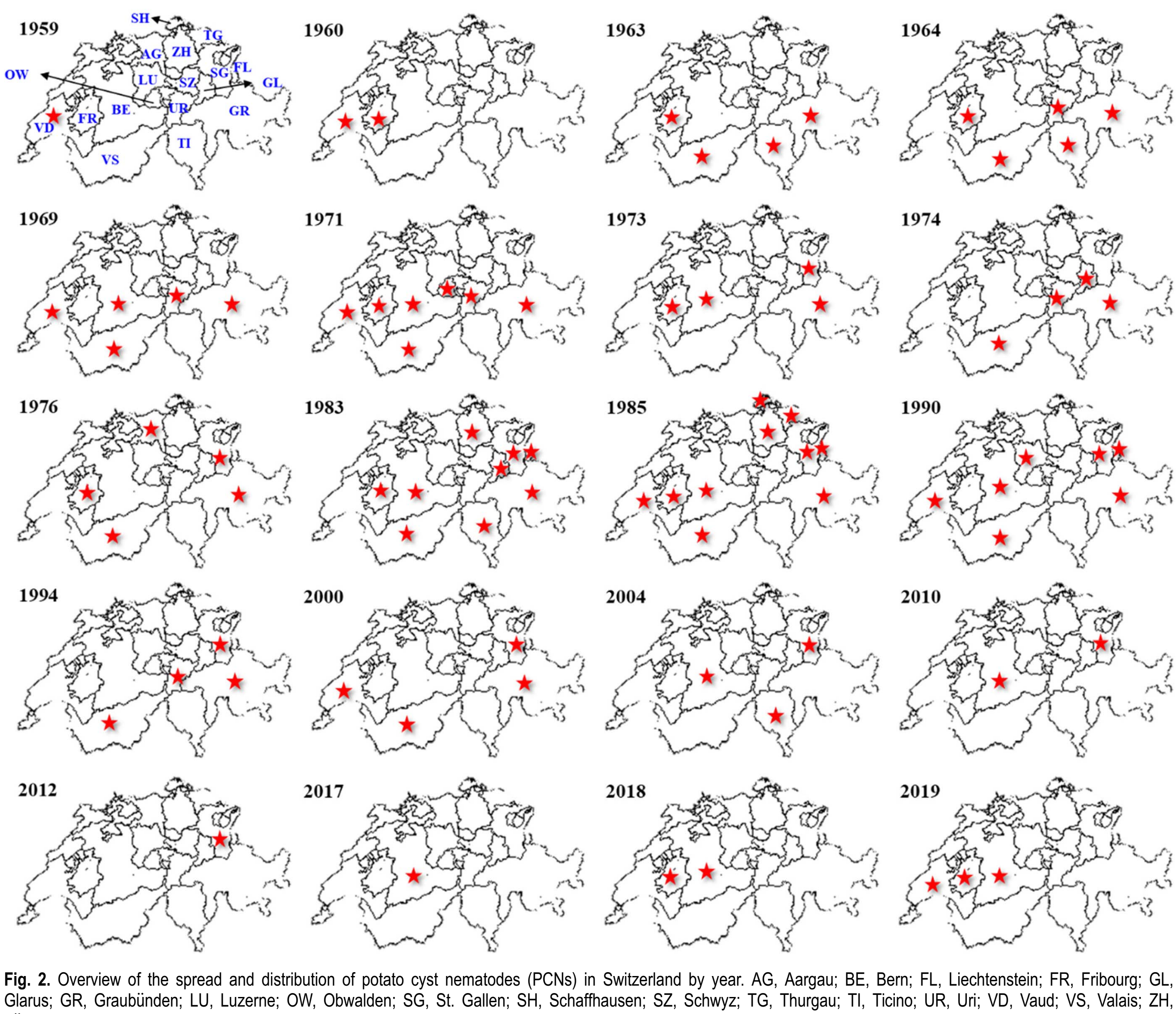

Fig. 2. Overview of the spread and distribution of potato cyst nematodes (PCNs) in Switzerland by year. AG, Aargau; BE, Bern; FL, Liechtenstein; FR, Fribourg; GL, Glarus; GR, Graubünden; LU, Luzerne; OW, Obwalden; SG, St. Gallen; SH, Schaffhausen; SZ, Schwyz; TG, Thurgau; TI, Ticino; UR, Uri; VD, Vaud; VS, Valais; ZH, Zürich.

potato cultivars in Europe available at that time: 'Iledher', 'Seresta', 'Aveka', 'Innovator', 'Cardoso', 'Ivetta', or 'Amanda' (Grenier et al. 2020; Mwangi et al. 2019; Niere et al. 2014). Consequently, breeding for resistant cultivars must be constantly adapted. The emergence of genetic variants with the ability to break down resistance has begun to be seen in the Netherlands, where growers have planted potato varieties resistant to *G. pallida* in tight rotations in areas dedicated to starch production, reinforcing the importance of an integrated management plan for the control of PCNs that uses resistant potato cultivars suitable for the detected PCN population in combination with long crop rotations.

Every year a list of recommended potato varieties is created in Switzerland by a collaboration between Agroscope and Swisspatat. Swisspatat is an interprofessional organization representing the interests of the potato industry in Switzerland, and Agroscope is responsible for updating the descriptions of varieties and their disease susceptibility based on variety trials and empirical research (Schwärzel et al. 2019). However, no mention to resistance, relative to PCNs, is made in the recent annual lists. We reviewed the list of recommended potato varieties for Switzerland and added information about resistance against *G. rostochiensis* and *G. pallida* and their pathotypes (Table 1). Of the 42 potato varieties recommended in the main list, 30 are resistant to *G. rostochiensis*, one is resistant to *G. pallida*, two are resistant to both PCN species, and nine are susceptible to both PCN species.

The main potato variety planted in Switzerland is Agria (21% of the planted area), followed by Erika (8%), Innovator, Fontane, and Victoria (5% each), Jelly, Lady Rosetta, Markies, and Charlotte (4% each), and Lady Claire, Ditta, Agata, Annabelle, Amandine, and Celtiane (3% each) (Swisspatat Statistische Angaben 2019). Of the varieties listed above, Charlotte is susceptible to both PCN species, Innovator is resistant to *G. pallida*, and all others are resistant to *G. rostochiensis* (Table 1).

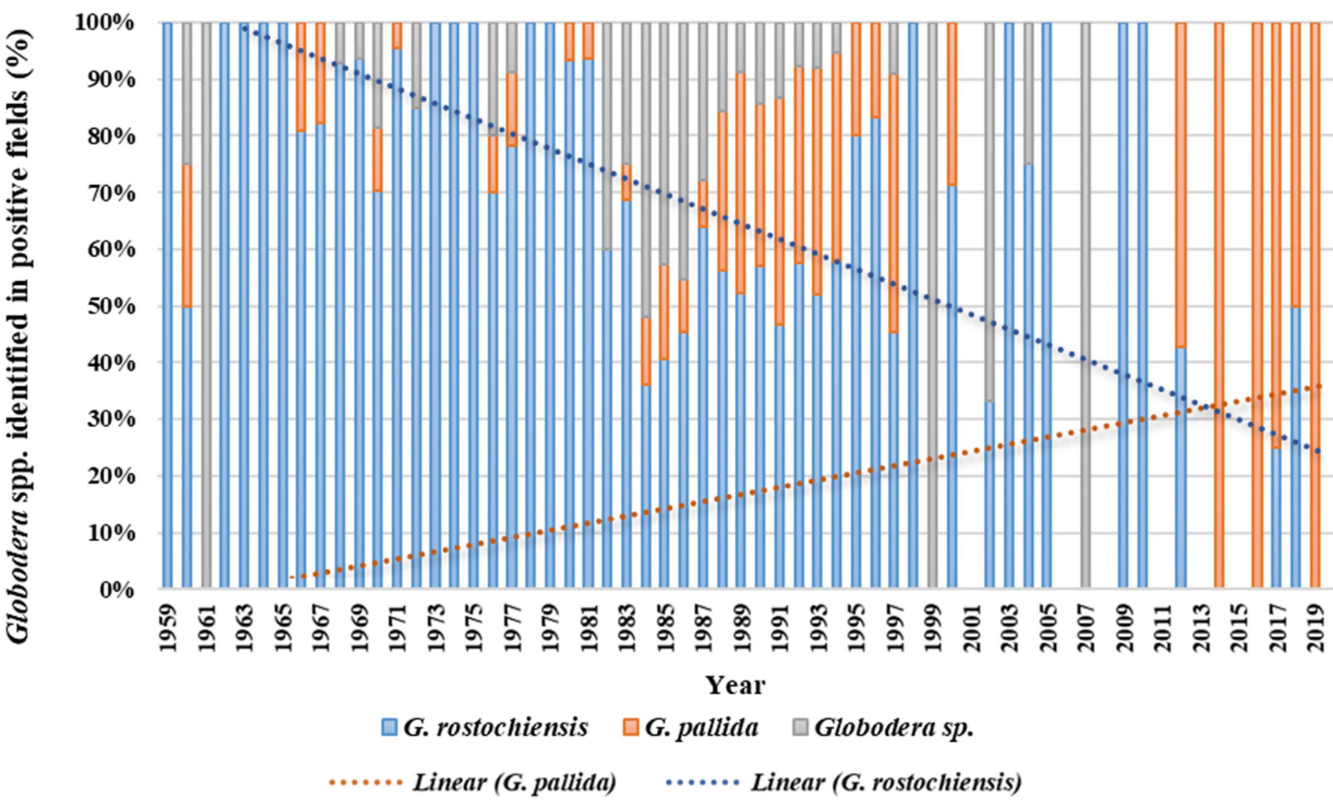

Fig. 3. Dynamics of *Globodera* species in Switzerland from 1959 to 2019. Linear trends in *G. rostochiensis* ($y = -1.2238x + 2,494.3$) and *G. pallida* ($y = 0.582x - 1,141.6$) were calculated via the function FORECAST.LINEAR in Excel version 2016, which predicts a future value along a linear trend.

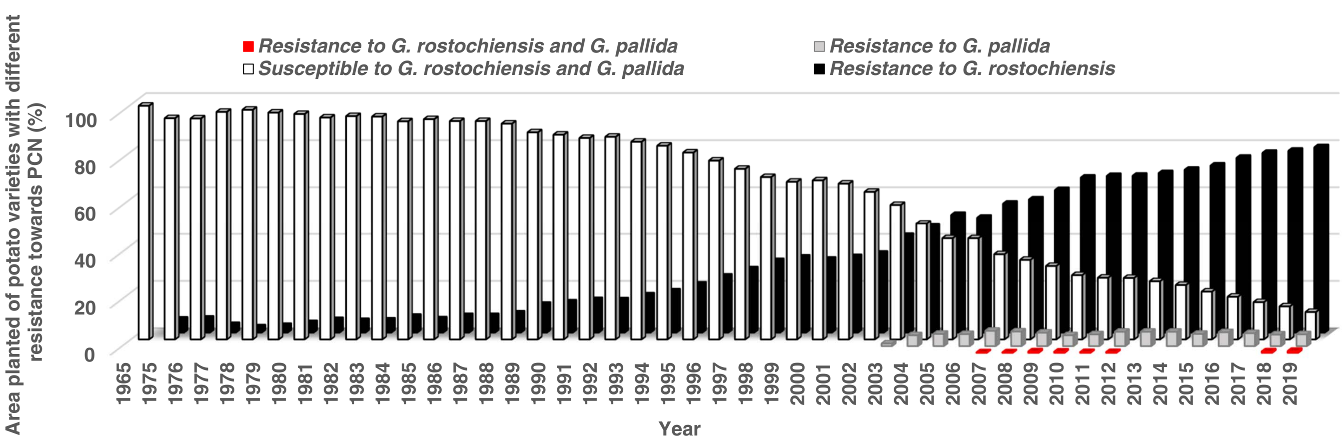

Fig. 4. Evolution of the area planted with potato cyst nematode (PCN)-resistant potato varieties in Switzerland over time (1965, 1975 to 2019).

Since the establishment of the list of recommended potato varieties in Switzerland in 1954, 109 have been recommended to Swiss farmers, of which 55 susceptible to both PCN species, 50 resistant to *G. rostochiensis*, one resistant to *G. pallida*, and three resistant to both *Globodera* species. The first variety to show resistance to *G. rostochiensis*, Marijke, was introduced to the list in 1968, followed by Prominent and Saturna in 1971, Aula in 1977, and Christa in 1978. The first variety having resistance to *G. pallida* was introduced in 2002 (Innovator), and potato varieties with resistance to both PCN species were introduced to the list of recommended potato varieties in 2007 (Lady Jo) and later in 2018 (Figaro and Ivory Russet) (Supplementary Tables S1 to S3). Potato varieties recommended in Switzerland, before the detection of PCN in seed potatoes and the discovery of PCN in Swiss soil, originated from Germany, the United Kingdom, and the Netherlands, indicating that if the seed potatoes were purchased directly from their country of origin, these are probably the places from which PCNs were introduced into Switzerland. This would exclude Denmark from the likely origin for the introduction of PCN on Swiss soil, as suggested earlier by Högger (1984).

Data on the planted area of potato varieties from 1965, 1975, and all subsequent years until 2019 were retrieved (Supplementary Tables S1 to S3). The evolution of the area planted of different potato varieties in Switzerland with respect to their resistance to *Globodera* species is shown in Figure 4. From 1965 until 2003 susceptible potato varieties dominated. However, there has been a gradual increase in the area planted with potato varieties resistant to *G. rostochiensis* since its introduction in 1968. In 2005, the area planted with potato varieties resistant to *G. rostochiensis* exceeded that of susceptible varieties and continued to increase. The area planted with potato varieties resistant to *G. pallida* has remained constant since 2004, and the area planted with varieties resistant to both PCN species is still very limited. A fact that probably contributes to the scarce cultivation of potato varieties resistant to *G. pallida* or both PCN species is that these varieties, because of their characteristics, are produced mainly for industrial use, whereas in Switzerland potatoes are produced mainly for fresh consumption. Although there has been an increase in the availability of cultivars with resistance to *G. pallida* in Europe, especially in Germany and the Netherlands, the number of resistant cultivars is still low when the end use of the

Table 1. Revised list of potato varieties recommended for Switzerland 2020, including information about resistance to potato cyst nematodes (PCNs) *Globodera rostochiensis* and *G. pallida*

					Assessment of resistance to PCN pathotypes and virulence groups[a]							
Year	**Potato variety**	**Maturity**	**Use**	**Parentage**	**Ro1**	**Ro2**	**Ro3**	**Ro4**	**Ro5**	**Pa2**	**Pa3**	**Reference**
2001	Agata	Early	Table potato, floury, boiling	BM 52-72 × Sirco	9	–	–	R	–	2		Schwärzel et al. 2019 Agriculture and Horticulture Development Board (AHDB) 2020
1988	Agria	Medium-early	Transformation, fries	Quarta × Semlo	9	–	–	–	–	2		Schwärzel et al. 2019 AHDB 2020
1999	Amandine[b]	Early	Table potato, hard, boiling	Marian × Charlotte	S	–	–	–	–	S		Schwärzel et al. 2019
2008	Annabelle	Early	Table potato, hard, boiling	Nicola × Monalisa	8	R	R	–	–	2		Schwärzel et al. 2019 AHDB 2020
2020	Ballerina	Medium-early	Table potato, hard, boiling	Agria × Obelix	–	–	–	–	–	–	–	Landwirtschaftliches Technologiezentrum Augustenberg 2019 Schwärzel et al. 2019
2020	Belmonda	Medium-early	Table potato, floury, boiling	Marabel × Leyla	R	–	–	R	–	–	–	Gündermann 2014; Ordon 2019 Schwärzel et al. 2019
1935	Bintje	Medium-early	Table potato, floury, boiling	Munstersen × Fransen	S	–	–	–	–	S		Schwärzel et al. 2019
2010	Celtiane[b]	Early	Table potato, hard, boiling	Amandine × Eden	9	–	–	–	R	2		Schwärzel et al. 2019 AHDB 2020
2011	Challenger	Medium-early to late	Table potato, floury, boiling	Aziza × Vicoria Hansa × Danaé	2	–	–	–	–	2		Schwärzel et al. 2019 AHDB 2020
1984	Charlotte	Medium-early to late	Table potato, hard, boiling	(156-91-1 × Roseval)	2	–	–	–	–	2		Schwärzel et al. 2019 AHDB 2020
2016	Cheyenne[b]	Early Medium-early	Table potato, hard, boiling	× Altesse	9	–	–	–	–	2		Schwärzel et al. 2019 AHDB 2020
2017	Concordia	Medium-early	Table potato, floury, boiling	B 1019/2/95 × Jelly	R	–	–	R	–	S		Gündermann 2014; Ordon 2019 Schwärzel et al. 2019
1961	Desirée	Medium-early	Table potato, floury, boiling	Urgenta × Depesche	2	–	–	–	–	2		Schwärzel et al. 2019 AHDB 2020
1998	Ditta	Medium-early	Table potato, hard, boiling	Bintje × Quarta	R	–	–	R	–	S		Gündermann 2014; Ordon 2019 Schwärzel et al. 2019
2014	Erika	Early	Table potato, hard, boiling	Marabel × AR88-156	9	–	–	9	–	S		Direction Générale de l'Alimentation 2019 Schwärzel et al. 2019
2018	Figaro	Late	Transformation, chips	00-710-3 × Omega	9	–	8	–	–	8	5	Gündermann 2014; Ordon 2019 Schwärzel et al. 2019
2001	Fontane	Medium-early	Transformation, fries	Agria × AR 76-34-3	9	–	–	R	–	2		Schwärzel et al. 2019 AHDB 2020

[a] Resistance was scored on a nine-point scale, where 9 indicates the highest level of resistance according to the EU Council Directive 2007/33/EC, or graded as R, resistant or S, susceptible.
[b] Contract production with marketing protection.

potatoes is taken into consideration. For industrial use (for the production of fries and chips or for starch production), ≥100 potato varieties resistant to *G. pallida* are available in Europe, whereas only 19 potato cultivars are available for fresh consumption (Supplementary Table S4). In Switzerland, the first potato varieties for fresh consumption with resistance to *G. pallida* have become available only in recent years (2011 to 2018; Hockland et al. 2012) and are registered mainly in Germany and the Netherlands (Supplementary Table S4). Because Switzerland does not have a breeding program dedicated to the development of potato varieties with resistance to PCNs, Swiss farmers rely on other European breeding programs. Thus, because of the time required for inspection and approval until the variety is included in the annual list of potato varieties released by Agroscope, there is a delay in the introduction of resistant potato varieties in Switzerland (Schwärzel et al. 2019). Consequently, only a limited number of cultivars resistant to *G. pallida* are available in Switzerland (Table 1).

Crop Rotation

Crop rotation by definition is a "system of growing different kinds of crops in recurrent succession on the same land" (Martin et al. 1976). It is an ancient agricultural technique used to break pest cycles; control diseases, pests, and pathogens; promote soil fertility; and increase crop and market diversity (Baldwin 2006).

In Switzerland 36% of the land is devoted to agriculture (Swiss Ornithological Institute - Farmland: https://www.vogelwarte.ch/en/atlas/evolution/farmland). Farms tend to be small compared with those in neighboring countries, and crop rotations must be established on all arable farmland to prevent not only the spread of pests and diseases but also soil erosion, compaction, loss, surface washoff and leaching of fertilizers and pesticides into the groundwater.

By federal determination, farms with >3 hectares of open arable land must have at least four main crops, of which one crop must cover ≥10% of the arable land (crops planted in areas <10% are added up to constitute one crop) (Direktzahlungsverordnung; SR 910.13). For potato growers, ≤25% of arable land can be used each year, and potatoes may be replanted on the same plot only after 4 years. Records on crop rotation must be stored for ≥6 years and must include information about the crop and the sequence of crops planted for each arable field (Direktzahlungsverordnung; SR 910.13).

Given the suitability of the host to spread PCNs and the importance of the crop to the Swiss agriculture and economy, cereals (wheat, oats, rye, triticale, and sorghum) are a good crop to be used in rotation with potatoes. Cereals are Switzerland's most important arable crop, accounting for an area of about 140,000 hectares (Swiss farmers - Arable farming: https://en.agriculture.ch/knowledge-and-facts/production/arable-farming/). Other crops that are good candidates for use in rotation with potatoes include rapeseed (the most important oil seed in the Swiss agricultural sector), sugar beet, sunflower, soybean, tobacco, peas, and beans.

Climate Change and Its Potential Effects on PCNs

Understanding the factors that influence the dynamics of *Globodera* spp. populations, whether biotic or abiotic, is crucial for better control of PCNs, to limit yield losses and prevent the increase or spread of current populations.

Temperature is one of the most influential environmental factors affecting nematode development (Kaczmarek 2014; Perry et al. 2013). It is known that *G. rostochiensis* and *G. pallida* have different optimal temperatures for hatching and reproduction. *G. rostochiensis* is more successful at temperatures >20°C, whereas the optimal temperature is lower for *G. pallida* (Byrne et al. 2001; Franco 1979; Jones et al. 2017; Kaczmarek 2014; Skelsey et al. 2018). Temperature affects the multiplication rates and competition between the two species when they are present as mixed populations (Kaczmarek 2014). In this sense, climate changes, such as an increase in global average temperature, could play an important role in the dynamics of PCN species in the future.

To assess the potential influence of temperature on the dynamics of *Globodera* spp. in Switzerland, mean annual temperature was recorded from 1959 to 2019 (MeteoSwiss Federal Office of Meteorology and Climatology 2019). From 1959 until 1968, the mean annual temperature was 4.5°C, and there was a gradual increase in *G. rostochiensis* after its first detection on Swiss soil in 1958 (Figs. 1 and 3). After the introduction of potato varieties resistant to *G. rostochiensis*, susceptible varieties were still the main cultivated potatoes in Switzerland until 2005 (Fig. 4). From 1969 until 1978 (annual average temperature of 4.4°C), *G. rostochiensis* detection remained stable (Figs. 1 and 3), and from 1979 to 1988 (annual average temperature of 4.6°C) a gradual decrease in the detection of *G. rostochiensis* and a slight increase in the detection of *G. pallida* were observed (Figs. 1 and 3). In the next 10-years, from 1989 to 1998, the mean annual temperature in Switzerland increased to 5.5°C (Figs. 1 and 3). In the same period, a further increase in *G. rostochiensis* was observed (Figs. 1 and 3), attributed mainly to new introductions and spread of *G. rostochiensis*, since it coincides with the second peak of PCN-positive field detection, as shown in Figure 1. Because the use of resistant varieties was intensified earlier, we suggest that the temperature could have favored the hatching and multiplication of *G. rostochiensis* over *G. pallida*. Over the 10-year periods from 1999 to 2008 and from 2009 to 2019, subsequent increases in the mean annual temperature were recorded, 5.7°C and 6.1°C, respectively. In contrast, the presence of *G. rostochiensis* decreased, and the presence of *G. pallida* increased (Figs. 1 and 3). These changes can be attributed mainly to the intensive use of potato varieties resistant to *G. rostochiensis* (Fig. 4), overcoming the potential effect that the increase in temperature could have had. There is no clear evidence that the increase in temperature has had a significant impact on the dynamics of *Globodera* spp. in Switzerland, but this aspect should be considered for the management and control of PCNs in the future, especially if the increases in temperature occur as predicted.

Climate change studies have shown that the hatching response is higher and faster for both *Globodera* spp. at higher temperatures. Therefore, increasing soil temperatures will probably favor the multiplication of both *Globodera* spp. (Kaczmarek 2014) if no other management strategies are applied, such as the use of resistant potato varieties. In addition, as warmer conditions arrive earlier in the year because of climate change, growers may be able to shift forward the potato-growing season (Skelsey et al. 2018), raising the risks of developing a complete second generation of PCNs, especially if late maturity potato cultivars are grown.

Increased exploitation of resistance to *G. rostochiensis* appears to be an important management and control measure to counterbalance the effects of rising temperatures. To avoid further problems caused by PCNs, breeding new potato varieties resistant to *G. pallida*, gaining knowledge about the pathotypes of PCN populations, and maintaining crop rotation are crucial for potato growers.

Conclusion

An overview of the development and status of PCNs in Switzerland since its detection on Swiss soil in 1958 was presented. Management measures; the increasing use of resistant potato varieties, especially against *G. rostochiensis*; and crop rotation cycles seem to have been crucial in the control of PCNs, and currently the spread is limited to central-west and western Switzerland. However, in the last 5 years a shift from *G. rostochiensis* to a predominance of *G. pallida* on Swiss soil has been observed. Control of *G. pallida* is more difficult because of the lack of resistant potato varieties, especially those intended for fresh consumption. Additionally, biotic and abiotic factors, such as temperature increases related to climate change, could favor multiplication rates of both PCN species similarly, favoring the competition between them in mixed soil populations in the future. Consequently, an extended monitoring program would be of interest to Swiss farmers to avoid favoring virulent genetic variants that could be present in Swiss PCN populations.

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