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REVIEW ARTICLE

Potato soil-borne diseases. A review

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Abstract Potato crop is the fourth main food crop in the world and it will certainly feed a big part of the global population in the next years. The economical outlets for this crop are great; however, numerous diseases either soil- or air-borne can cause huge losses in the production. Worldwide, about 40 soil-borne diseases affect potato and cause severe damages especially on tubers, the economically most important part of the plant. The occurrence and development of soil-borne diseases depend on very diverse factors affecting either the pathogen or the plant. Favorable conditions for potato diseases development are frequently the same as the conditions needed for potato growth: temperature between 10°C and 25°C, high humidity, medium pH, etc. Adapted cultural practices such as a rotation longer than 4 years, appropriate fertilization and water management, an adapted delay between haulm killing and harvest, and dry and cool conditions for tuber storage are good ways to control potato diseases. In most cases, potato pathogens develop specific survival forms, dissemination ways and host penetration methods. The genetic variability of the pathogens implies the use of adapted diagnostic and control methods. Decision support systems developed to predict yield losses allow choosing good control methods such as the use of healthy seeds, adapted pesticides, cultural practices, and biological control agents for each potato disease. The complexity of the interactions between a pathogen and its host, influenced by biotic and abiotic factors of the environment, make the control of the diseases often very difficult. However, deep knowledge of pathosystems allows setting up integrated pest management systems allowing the production of healthy and good quality potatoes.

Keywords Cultural practices · Decision support system · Pathogen ecology · Pedologic and climatic factors · Plant microorganism interaction · Soil · Soil suppressiveness

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1 Introduction

Potato crop, the world's number one non-grain food commodity, is the fourth main food crop in the world after maize, rice and wheat, with 325 million tons produced in 2007. Potatoes are grown in more than 100 countries, mainly in Asia (135 million tons) and Europe (130 million tons; FAO 2008). They have good gustative and nutritional qualities and can be grown under various climates. This is the reason why Food and Agriculture Organization (FAO) has declared the year 2008 the international year of the potato. Indeed, potato can help fulfill the first United Nations Organization's (UNO) millennium development goal that aims at eradicating extreme poverty and hunger in the world. However, potato (*Solanum tuberosum*) crop can suffer more than 40 pests and diseases caused by insects, nematodes, viruses, bacteria, and fungi. Those pathogens are air- or soil-borne and cause damages on all parts of the plant. In this review, we will focus on soil-borne fungi, bacteria, and nematodes (Table 1, Fig. 1).

Indeed, diseases caused by viruses or viroïds provoke generally foliar symptoms: leaf distortion, mosaic, crinkling, leaf and vein necroses, dwarfing. and leaf rolling. Only some viruses—tobacco rattle virus (TRV), potato mop-top virus, potato virus Y, and tobacco necrosis virus—can cause damages on tubers such as blemishes or rots in tuber flesh (Table 1). They will be briefly mentioned in Table 1 as well as the vectors (aphids, fungi, or nematodes) involved in their transmission but they will not be detailed in this review.

Soil-borne diseases affecting potato crop can be divided into two groups depending on symptoms: symptoms damaging tubers and those damaging other parts of the plant (Gudmestad et al. 2007).

Diseases affecting stems or roots affect the crop development and may lead to a reduction of the yield (Table 1). Stem lesions can be watery and may develop into the stem pith with (stem rot) or without (blackleg, white mold) the formation of sclerotia. Other lesions can appear like more discrete light brown lesions but nevertheless affecting the yield of the crop (skin spot, stem canker). Some soil-borne pathogens sometimes cause aerial symptoms like necroses or chloroses (*Phoma* leaf spot, *Verticillium* wilt) occasionally associated with wilting and rolling (bacterial ring rot). Finally, root lesions, mainly caused by nematodes feeding on the roots, lead to necroses or rots. Nematodes feeding sites are good entry points for other soil microorganisms.

Among diseases affecting tubers, symptoms can be divided into three categories: galls, blemishes, and rots (Table 1). Galls consist in outgrowth and tuber deformation. The most frequent galls are provoked by powdery scab, wart, Common Scab, root-knot nematode, and false root-knot nematode. Blemishes affect only the tuber skin but they are now economically important since consumers' habits have changed and tubers are washed before selling. Blemishes can appear on the tuber surface as spots called black dot, black scurf, skin spot or powdery scab, or as areas of atypical appearance presenting a more or less pronounced scabby (common or netted scab) or silver (silver scurf) aspect. Rots, which affect the tuber flesh more deeply, include different types such as dry rots, soft rots (charcoal rot, leak, bacterial soft rot, black leg, and stem rot), flesh discoloration (pink rot) or vascular ring discoloration (ring rot, brown rot, *Verticillium* wilt, and *Fusarium* dry rots). Dry rot diseases also damage stored potatoes.

Potato is becoming a more and more important foodstuff in the world, it is therefore essential to control diseases which cause direct yield losses and decrease of farmer's incomes due to downgrading the quality of affected tubers. Therefore, knowledge about the pathogens as well as factors influencing disease severity is needed to setup efficient control strategies. Before reviewing the different causes of occurrence and development of the main soil-borne potato diseases, it is important to recall the concepts of soil inoculum potential and soil suppressiveness which describe the complex interactions between the soil, the pathogens, and the plant. While the former evaluates what the actual indigenous pathogenic inoculums could do in the rhizosphere towards the host plants if all conditions were favorable to its pathogenic activity, the second

Table 1 Potato soil-borne pathogens

Pathogen	Disease	Host range	Main symptoms						Pathogenicity test	Distribution	References
			Tubers			Other parts					
			Gall	Blemish	Rot	Stem lesions	Leaf lesions	Root lesions			
Fungi and oomycetes											
Colletotrichum coccodes	Black dot	Moderate: 35 hosts from 13 families including *Cucurbitaceae*, *Fabaceae* and *Solanaceae*		X		X		X	X	Worldwide	Tsror (2004); Aqeel et al. (2008)
Fusarium spp.	Fusarium dry rots	*Fusarium sambucinum* : Wide : potato, hop, leguminous plants, cereals *F. coeruleum* : Wide : potato, cereals and many other hosts			X				X	Worldwide	Peterset al. (2008)
Helminthosporium solani	Silver scurf	Potato		X					X	Worldwide	Cunha and Rizzo (2004)
Macrophomina phaseolina	Charcoal rot	Wide: 284 recorded hosts both cultivated and wild			X					America, Europe, Asia	
Phoma andigena var. *andina*	Phoma leaf spot	Narrow : potato, *S. goniocalyx*, *S. medians*, *S. phureja*, tomato, solanaceous weeds					(X)			South America (Bolivia and Peru)	
Phoma spp.	Gangrene	*Phoma exigua* var. *exigua*, wide									
		Phoma exigua var. *foveata*; narrow, potato and some weeds	X				X			North America, Europe, Asia, Oceania	Bain et al. (1987)
Phytophthora erythroseptica	Pink rot	Narrow : potato, tomato, spinach, and tulip			X				X	Worldwide	Peters et al. (2004); Stamps (1978)
Polyscytalum pustulans	Skin spot	Narrow : Solanaceous species		X		X			X	Europe, North America, Oceania, Asia	Vico et al. (1997)
Pythium ultimum var. *ultimum*	Leak	Wide including many crops			X				X	Worldwide	Perez et al. (1994)
Rhizoctonia solani	Black scurf/Stem canker	Narrow : Solanaceous species		X		X			X	Worldwide	Woodhall et al. (2008)
Rosellinia sp.	Rosellinia black rot	Wide : plants in over 63 genera in 30 families			X			(X)		South America, Africa	
Sclerotinia sclerotinium	White mold	Wide : approximately 400 species of dicots			X	X					
Sclerotium rolfsii	Stem rot	Wide : cultivated and wild plants including ferns			X	X			X	Worldwide	Garibaldi et al. (2006)
Spongospora subterranea	Powdery scab (PMTV vector)	Wide : Solanaceous species, cabbage and related species	X	X				X	X	Worldwide	Nakayama et al. (2003); Hims and Preece (1975); Merz and Falloon (2009)
Synchytrium endobioticum	Wart	Potato	X						X	Worldwide	
Thecaphora solani	Thecaphora smut	Narrow: Solanaceous species, *Datura stramonium*	X		X				X	South America and Mexico	Mordue (1988); Andrade et al. (2004)
Verticillium dahliae and *Verticillium albo-atrum*	Verticillium wilt	*Verticillium dahliae*; moderate : artichoke, bell pepper, cabbage, cauliflower, chili pepper, cotton, eggplant, lettuce, mint, potato, strawberry, tomato, watermelon, etc. *Verticillium albo-atrum*, narrow : alfalfa, hops, potato			X	X	X		X*	Worldwide	Stevenson et al. (2001), Ochiai et al. (2008)

Table 1 (continued)

Pathogen	Disease	Host range	Main symptoms						Pathogenicity test	Distribution	References
			Tubers			Other parts					
			Gall	Blemish	Rot	Stem lesions	Leaf lesions	Root lesions			
Bacteria											
Clavibacter michiganensis ssp. *sepedonicus*	Ring rot	Narrow : potato, sugar beet, tomato, eggplant			X		X		X	Worldwide	Nissinen (2000)
Clostridium spp.	Bacterial soft rot	Wide: animals and plants			X					Worldwide	
Pectobacterium atrosepticum, *Pectobacterium carotovorum* subsp. *carotovorum*, *Dickeya* spp.	Black leg, soft rot	*Pectobacterium* spp. and *Pectobacterium carotovorum* subsp. *carotovorum*; wide : potato, rapeseed, sugar beet, chicory witloof, carrots, radish, weeds *Pectobacterium atrosepticum*; narrow : potato tomato, cabbage, weeds *Dickeya* spp.: potato, ornementals, maize, chicory witloof, tomato, weeds			X	X	X		X	Worldwide	Franco et al. (2007); Bradbury (1977); Helias (2008)
Ralstonia solanacearum	Brown rot	Wide: plants in over 200 species in 28 families			X	X			X	Asia, Africa, South America (probably worldwide)	Park et al. (2007)
Streptomyces scabiei, *S. acidiscabiei*, *S. europeiscabiei*	Common and netted scab	Moderate : potato, beets, radish, rutabaga, turnip, carrot, parsnips, etc.	X	X				X	X	Worldwide	Bouchek-Mechiche et al. (2006); Lambert et al. (2006); Zhao et al. (2008)
Nematodes											
Belonolaimus longicaudatus	Sting nematode	Wide : vegetables (carrot, corn, crucifers, beans, potato, etc.), fruits (citrus, strawberry, etc.), agronomic crops (cotton, peanut, sorghum, soybean, etc.), turf grasses and forest crops						X		North America	
Ditylenchus destructor, *Ditylenchus dipsacii*	Potato rot nematode Stem and bulb nematode	Wide : almost all plants, feed also on soil fungi potato, onions, pea, beans, rye			X			X		Europe, Africa, America	Vreugdenhil (2007)
Globodera pallida, *Globodera rostochiensis*	Potato cyst nematode	Narrow : potato, tomato, eggplant, wild solanaceous weeds		X				X	X	Worldwide	Vreugdenhil (2007); Pylypenko et al. (2008)
Meloidogyne spp.	Root-knot nematode	Wide : about 2000 species (Solanaceae, Cucurbitaceae, leguminous plants, carrots, scorsoneras, lettuces, chicory witloofs, artichokes, Swiss chards, celery, etc.)	X					X	X	Worldwide	Vreugdenhil (2007); Vovlas et al. (2005)
Nacobbus aberrans	False root-knot nematode	Wide : potato, *Brassica oleracea*, *Capsicum*, carrots, cucumbers, lettuces, *Opuntia* spp. and other Cactaceae, sugarbeet, tomato, etc.	X					X		America	Inserra et al. (2005); Stevenson et al. (2001); Vreugdenhil (2007)

Table 1 (continued)

Pathogen	Disease	Host range	Main symptoms						Pathogenicity test	Distribution	References
			Tubers			Other parts					
			Gall	Blemish	Rot	Stem lesions	Leaf lesions	Root lesions			
Paratrichodorus and *Trichodorus* spp.	Stubby root nematode (TRV vector)	*Paratrichodorus* spp; wide : alfalfa, azalea, boysenberry, vegetables, corn, tomato, potato, onion, wheat, sugarcane, rice, grasses, etc. *Trichodorus* spp.; wide : trees, shrubs, crops, turf grasses		X				X		Europe, North America	
Pratylenchus spp.	Root-lesion nematode	Wide: a lot of fruit trees, some citrus fruits and cereals, ornamental plants, crops (potato and vine)						X	X	Worldwide	France and Brodie (1995)
Virus	**Means of transmission**										
Tobacco necrosis virus (TNV)	Mechanical, Olpidium brassicae	Narrow : potato, tobacco, bean, tulip		X	X					Worldwide	Stevenson et al. (2001)
Tobacco rattle virus (TRV)	Stubby root nematodes	Wide : potato, gladiolus, lettuce, sugar beet, tobacco, tulip, etc.		X	X					Europe, Japan, New Zealand, North America, Russia	Stevenson et al. (2001); FNPPPT, GNIS (2000)
Potato mop-top virus (PMTV)	*Spongospora subterranea*	Narrow : mainly Solanaceous species		X	X	X	X			Andean region, Canada, China, North Europe, Japan	Stevenson et al. (2001); FNPPPT, GNIS (2000)

evaluates in which ways the environmental conditions may limit in situ the expression of this pathogenic activity, including the saprotrophe development, if required by the inoculum (Alabouvette et al. 2006).

Plant diseases result from the compatible interactions between a susceptible host plant and a pathogen. These direct interactions are important but should not outshadow the key role of environmental factors, which influence these interactions and thereby disease incidence or severity. In contrast to aerial diseases, the soil-borne diseases are induced by pathogens which are embedded in the soil matrix. Thus, the soil interferes in many ways in the relationships between and among microorganisms, pathogens, and host plant. It can even modify the interactions among microorganisms themselves. In some soils, disease incidence or severity commonly remains low in spite of the presence of the pathogen, a susceptible host plant and favorable climatic conditions. They are called disease-suppressive soils (Messiha et al. 2007; Steinberg et al. 2007). Soil suppressiveness to diseases depends on the pathogen itself—its inoculum density and its intrinsic aggressiveness—and also on different soil factors, including both biotic and abiotic components.

In the first part of this paper, the influence of abiotic factors on disease severity will be reviewed. Then the characteristics of the inoculum and its relationships with the rest of the microbiota will be considered. Finally, risk assessment models, decision support systems, and control strategies based on collected data will be discussed.

2 Effects of abiotic factors on the occurrence and development of soil-borne potato diseases

Soil abiotic components such as texture, organic matter content, pH, as well as temperature and moisture greatly affect the behavior of the pathogens and determine disease incidence or severity.

2.1 Soil temperature

Temperature and moisture of the soil are obviously greatly dependent on the climatic conditions, but also on some cultural practices such as irrigation. Temperature is of major importance in disease development since it determines pathogen growth rate (Baljeet et al. 2005), kind of symptoms (Bouchek-Mechiche et al. 2000), and geographical distribution of the diseases. Most of the potato pathogens can grow at soil temperatures between 10°C and 25°C, the optimal potato growth temperatures (Table 2). However, gangrene, black scurf, and powdery scab are favored by mean temper-

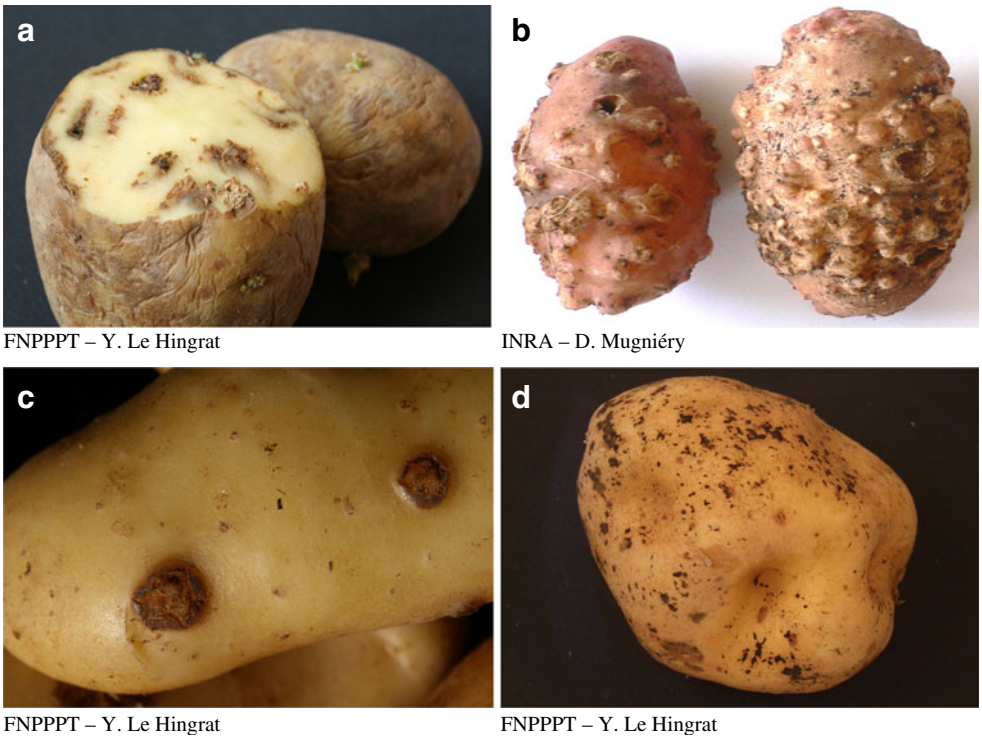

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Fig. 1 Symptoms caused by some potato soil-borne diseases, **a** tobacco rattle virus (TRV, transmitted by nematodes), **b** root-knot nematode (*Meloidogyne incognita*), **c** common or netted scab (*Streptomyces scabies*), **d** black scurf (*Rhizoctonia solani*)

atures below 15°C (Baker 1970; Gindrat 1984; Harrison 1997); on the contrary, black dot, black leg, stem rot, and charcoal rot are favored by temperatures above 27°C. Similarly, sting and root-knot nematodes reproduce better between 25°C and 30–35°C depending on the origin of the populations.

2.2 Soil moisture

Soil moisture which depends on the climate and cultural practice is also determined by the soil texture (see below). In the literature dealing with interactions between soil moisture and potato diseases, many different terms are used to characterize the soil water content.

Soil moisture content, moisture–weight percentage, and water-holding capacity are used to evaluate the volume of water contained in soil. It is generally expressed as a percentage of the soil dry weight. Other publications refer to water activity which is a dimensionless quantity (between 0 and 1) describing the amount of free water in soil for biochemical reactions. Water activity, which depends on soil texture, is related to moisture content in a non-linear relationship known as a moisture sorption isotherm curve.

High soil moisture due to abundant rainfall, poor drainage, heavy soils, or irrigation, influences disease development and the opening of the lenticels which are further entry points for soil-borne pathogens into the tuber (Helias 2008). Several diseases, especially bacterial diseases, are enhanced by high moisture content (Table 2), but few diseases are favored by low levels of moisture. This is the case for black dot, some dry rots induced by *Fusarium* spp., stem rot, wart, common scab, and sting and root-knot nematodes. High soil moisture generally has indirect effects which might favor disease severity. This is the case of flooding that provokes oxygen depletion and CO_2 enrichment resulting in an increase of *Spongospora subterranea* (powdery scab) development (Harrison 1997). In some cases, the influence of soil moisture on disease severity is not clearly demonstrated. Depending on the studies, black scurf, stem canker, silver scurf (*Helminthosporium solani*), and *Thecaphora* smut (*Thecaphora solani*) are either positively or negatively correlated with soil moisture (Adams et al. 1987; Hide and Firmager 1989; Sepulveda et al. 2000; El Bakali and Martin 2006; Wale et al. 2008). Conversely, high relative humidity during storage of tubers has always a negative impact (Table 2).

2.3 Soil texture

The soil texture describes the relative percentage of sand, loam, and clay contents. Most of fungal diseases are enhanced in light sandy soils (Table 3). Conversely, it is generally accepted that clay soils favor bacterial activity (Marshall 1975; Alabouvette et al. 1996) explaining that clay or heavy soils are conducive to bacterial soil-borne diseases (ring rot, soft rot, brown rot, and netted scab). Concerning nematodes, no general rule can be drawn up as some species are more prevalent in heavy soils (root-knot

Table 2 Favorable climatic conditions for potato soil-borne diseases development

Pathogen	Disease	Optimal temperatures (°C)	Optimal level of humidity		Optimal light duration			References
			low	high	Continuous	12:12 h (light/darkness)	Darkness or short day	
Fungi and oomycetes								
Colletotrichum coccodes	Black dot	25–30; optimum: 27	X (whc <50%)	X (storage)			Colonization, sclerotia	Davet (1970); Lees (2003); Tsror (2004)
Fusarium spp.	Fusarium dry rots	15–20	X (9.2% whc)	X (27.9% whc)		Mycelial growth		Tivoli (1983); Kong et al. (2006)
Helminthosporium solani	Silver scurf	15–32	X	X (sporulation)				Adams et al. (1987); Errampalli (2001)
Macrophomina phaseolina	Charcoal rot	>30		X (RH>52%)	Mycelial growth	Pycnidia production, mycelial growth	Germination tube elongation	Gindrat (1984); Vishwa and Sarbhoy (1989); Muthukrishnan et al. (1995); Somani and Chauhan (1996); Amadioha and Adisa (1999); Mehta et al. (2006); Chowdary and Govindalah (2007)
Phoma andigena var. *andina*	Phoma leaf spot							
Phoma spp.	Gangrene	5–18; optimum: 10		X	Pycnidial and conidial productions	Pycnidial production		Fox et al. (1978); Gindrat (1984); Bang (1989); Coelho et al. (1997); Lo et al. (2000)
Phytophthora erythroseptica	Pink rot	15–30		X (waterlogged soil)				Salas et al. (2000)
Polyscytalum pustulans	Skin spot	5–20		X (storage)				Hide and Cayley (1987); Vico et al. (1997)
Pythium ultimum var. *ultimum*	Leak	20–30		X (RH 95% in storage)				Lui (2003)
Rhizoctonia solani	Black scurf/Stem canker	10–18	X (45% whc)	X	Sclerotia formation			Baker (1970); Hide and Firmager (1989); Xu et al. (1997); El Bakali and Martin (2006); Panka et al. (2007)
Rosellinia spp.	Rosellinia black rot							
Sclerotinia sclerotinium	White mold	15–27	No effect of RH					Young et al. (2004); Harikrishnan and del Rio (2006)
Sclerotium rolfsii	Stem rot	25–35; optimum: 30	X (30% whc)		Sclerotia production		Mycelial growth, sclerotia production	Chowdhury et al. (1993); Prithiviraj et al. (2000); Blum et al. (2002); Gupta et al. (2007)
Spongospora subterranea	Powdery scab	Tuber galls: 12–15 Root gall: 17		X Constant dampness				Harrison (1997)Graaf et al. (2005); Merz and Falloon (2009)
Synchytrium endobioticum	Wart	12–18		X annual rainfall greater than 700 mm				Hampson and Coombes (1997); Stachewicz and Enzian (1998)
Thecaphora solani	Thecaphora smut	5–20		X				EPPO (1990); Sepulveda et al. (2000); Wale et al. (2008)
Verticillium dahliae and *Verticillium albo-atrum*	Verticillium wilt	22–26; optimum: 25		X (a_w=0.995)		Sporulation		Jong-Tae et al. (2001); Santamarina and Rosello (2006)

Table 2 (continued)

Pathogen	Disease	Optimal temperatures (°C)	Optimal level of humidity		Optimal light duration			References
			low	high	Continuous	12:12h (light/darkness)	Darkness or short day	
Bacteria								
Clavibacter michiganensis ssp. *sepedonicus*	Ring rot	10–20		X				Wolf and Beckhoven (2004)
Clostridium spp.	Bacterial soft rot			X				Suyama et al. (1990)
Pectobacterium atrosepticum, *Pectobacterium carotovorum* subsp. *carotovorums*, *Dickeya* sp.	Black leg, soft rot	*Pectobacterium atrosepticum*: 15–25 *Pectobacterium carotovorum* subsp. *carotovorum*: 20–35 *Dickeya* spp: 25–35		X				Jaggi et al. (1991); Serfontein et al. (1991); Vries and Vuurde (1993), Latour et al. (2008); Helias (2008)
Ralstonia solanacearum	Brown rot	23 (temperate strains) 30–35 (tropical strains)		X (whc 60%)				Shekhawat and Perombelon (1991); Sunaina et al. (2000); Tomlinson et al. (2005)
Streptomyces scabiei, *S. acidiscabiei*, *S. europeiscabiei*	Common and netted scab	Common scab: 19–24 Netted scab: 13–17	X	X				Adams et al. (1987);Bouchek-Mechiche et al. (2000); Pasco et al. (2005); Panka et al. (2007)
Nematodes								
Belonolaimus longicaudatus	Sting nematode	25–35	X (RH 7%)					Robbins and Barker (1974)
Ditylenchus destructor	Potato rot nematode	20–37; optimum: 21		X (RH 41–66%)				Mugniery and Phillips (2007); Shojaei et al. (2006)
Globodera pallida, *Globodera rostochiensis*	Potato cyst nematode	10–28	No effect of soil humidity					Inserra et al. (1996); Muhammad (1996)
Meloidogyne spp.	Root-knot nematode	*Meloidogyne incognita* 25–32 *Meloidogyne hapla*: 25–30 *Meloidogyne chitwoodi*: 20–25	X (30% whc)					Stevenson et al. (2001); Chandel et al. (2002); Pandey et al. (2002); Wu et al. (2006)
Nacobbus aberrans	False root-knot nematode	10–25; optimum: 20						Anthoine et al. (2006)
(*Para*)*trichodorus* spp.	Stubbyroot nematode							
Pratylenchus spp.	Root lesion nematode	Optimum: 21		X				Jauhari and Lal (2001); Pudasaini et al. (2007)

RH relative humidity, *whc* water holding capacity

Table 3 Favorable edaphic conditions for the development of potato diseases

Pathogen	Disease	Optimal soil texture		Optimal soil pH	Optimal soil nutrient content	Optimal organic matter content	References
		Mainly sandy or light soils	Mainly clay or heavy soils				
Fungi and Oomycetes							
Colletotrichum coccodes	Black dot	X		6–7	Low nitrogen level		Kang et al. (2003); Nitzan and Tsror (2003); Tsror (2004)
Fusarium spp.	Fusarium dry rots	X		*F. solani* >5.3 *F. roseum*, no effect	High Fe level Low Ca, borax and P levels	Variable	Combrink et al. (1975); Tivoli et al. (1987); Tivoli et al. (1990); Alabouvette et al. (1996)
Helminthosporium solani	Silver scurf	X	X				Lennard (1980); Lutomirska and Szutkowska (2004)
Macrophomina phaseolina	Charcoal rot	X		6.5			Singh and Kaiser (1994)
Phoma andigena var. *andina*	Phoma leaf spot						
Phoma spp.	Gangrene	X		3.8–5.6		2.9–7.6‰	Tivoli et al. (1987)
Phytophthora erythroseptica	Pink rot						
Polyscytalum pustulans	Skin spot						
Pythium ultimum var. *ultimum*	Leak			No effect		No effect	Vivoda et al. (1991)
Rosellinia spp.	Rosellinia black rot						
Rhizoctonia solani	Black scurf/Stem canker	X		High?		High	El Fahl and Calvert (1976); Rudkiewicz et al. (1983); Lutomirska and Szutkowska (2005)
Sclerotinia sclerotinium	White mold					High	
Sclerotium rolfsii	Stem rot	X		~ 6.5	High nitrogen, organic carbon and low phosphorus and potassium levels		Sheoraj et al. (2007); Banyal et al. (2008)
Spongospora subterranea	Powdery scab	X organic or over irrigated soils	X poorly drained soils	4.7–7.6	High aluminum level		Zambolim et al. (1995); Graaf et al. (2005); Gilchrist et al. (2009); Merz and Falloon (2009)
Synchytrium endobioticum	Wart		X	Variable			Hampson (1985); Hampson and Coombes (1997)
Thecaphora solani	Thecaphora smut				High salt level		EPPO (1990)
Verticillium dahliae and *Verticillium albo-atrum*	Verticillium wilt	X		6–9	High Ca, low K, Mg and total soil C level	Low	Baard and Pauer (1981); Höper and Alabouvette (1996); Davis et a. (2001)
Bacteria							
Clavibacter michiganensis ssp. *sepedonicus*	Ring rot		X				Moffett and Wood (1984)
Clostridium spp.	Bacterial soft rot						

Table 3 (continued)

Pathogen	Disease	Optimal soil texture		Optimal soil pH	Optimal soil nutrient content	Optimal organic matter content	References
		Mainly sandy or light soils	Mainly clay or heavy soils				
Pectobacterium atrosepticum, *Pectobacterium carotovorum* subsp. *carotovorum*, *Dickeya* spp.	Black leg, soft rot	X Black leg	X Soft rot		Low Ca concentration		Zielke et al. (1974); Lucke (1975); Lambert and Manzer (1991)
Ralstonia solanacearum	Brown rot	X	X	variable	No ammonium intake		Hsu (1991); Shekhawat and Perombelon (1991); Messiha et al. (2007); Michel and Mew (1998); Yi and Sul (1998); Keshwal et al. (2000); Muller et al. (2004)
Streptomyces scabiei, *S. acidiscabiei*, *S. europeiscabiei*	Common and netted scab		X	5.2–7	Low Mn level		Rudkiewicz et al. (1983); Alabouvette et al. (1996); Loria et al. (1997); Milosevic et al. (2005); Lazarovits et al. 2007
Nematodes							
Belonolaimus longicaudatus	Sting nematode	X					Mashela et al. (1991)
Ditylenchus destructor	Potato rot nematode						
Globodera pallida, *Globodera rostochiensis*	Potato cyst nematode	X		6.1	Low nitrogen level	High	Pelsmaeker and Coomans (1987); Ruijter and Haverkort (1999); Trifonova (2001)
Meloidogyne spp.	Root-knot nematode	X	X	7.5		High	Kumar and Vadivelu (1996); Kandji et al. (2001); Pandey et al. (2002); Melakeberhan et al. (2004)
Nacobbus aberrans	False root-knot nematode						
Paratrichodorus and *Trichodorus* spp.	Stubby-root nematode (TRV vector)	*For both P. pachydermus and T. similis*	*Only in the case of T. primitivus*	low	High level of Fe		Barbez (1983); Spaull and Cadet (2001)
Pratylenchus spp.	Root-lesion nematode		X	variable	Low level of Fe		Pelsmaeker and Coomans (1987); Spaull and Cadet (2001)

nematodes) and other species in light soils (sting nematodes). Soil texture also influences soil structure, through the distribution of different pore sizes, determining the actual living space for bacteria, fungi, and predators. It also influences the water activity; water retained in pores of narrow diameter being less available for organisms that water present in large pores.

2.4 Soil pH

Disease development is also influenced by soil pH linked to soil nutrient availability (Table 3). Soils with extreme pH values are often highly suppressive to several plant diseases (Höper and Alabouvette 1996). However, pH fluctuations resulting from amendments influence pathogens and disease development. Decreasing pH increases the availability of phosphorus, nitrogen, and aluminum ions and decreases potato cyst nematode, brown rot, and common scab damages, respectively (Mulder et al. 1997; Michel and Mew 1998; Ruijter and Haverkort 1999; Mizuno et al. 2003). On the contrary, addition of urea in soil induces a very large increase in pH and a good control of *Synchitrium endobioticum*, the fungal pathogen causing wart (Hampson 1985).

2.5 Soil organic matter

Soil organic matter is both the substrate for and the result of microbial activity. In addition, together with clay, organic matter affects soil structure and thus moisture content and aeration. The quantity of organic matter in a soil has an effect on the appearance and the development of diseases but its quality is also an important point which has been too poorly addressed (Alabouvette et al. 1996).

Most physico-chemical factors are not independent from one to the others, which makes experiments and data interpretation very difficult. Soil texture can affect humidity, soil amendments impact on pH, and all those factors influence availability of chemical elements. Thus, the pathogenic inoculum present either in the soil or on the tuber surface has to find the optimal climatic and edaphic conditions to develop.

3 Effects of biotic factors on the occurrence and development of soil-borne potato diseases

3.1 Autecology of pathogens

3.1.1 Inoculum sources, survival and dissemination pathways

The survival of soil-borne pathogens during periods without potato crop depends on their ability to resist to unfavorable conditions. Most of them survive in soil under the form of resistant structures able to directly infect the new host crop. Some pathogens can also survive as saprophytes on host crop residues or on alternative hosts during winter. Finally, inoculum can also be introduced into the field by the seeds; it is called seed- or tuber-borne inoculum. Inoculum sources are diverse and for many diseases several inoculum sources can play a role (Table 4). Soil-borne fungi produce different conservation structures. *Fusarium* spp. forms chlamydospores resistant to adverse conditions, *Rhizoctonia solani*, *Verticillium* spp., *Sclerotinia sclerotinium* overwinter as sclerotia. Bacteria can survive over winter with favorable moisture, temperature, and soil type (Ficke et al. 1973; Bradbury 1977; Loria et al. 2008). Nematodes can survive and persist in soil as protective cysts surrounding the eggs (*Globodera* spp.) or as juveniles in host roots (*Meloidogyne* spp.; Qian et al. 1996; Wharton and Worland 2001).

In the absence of resistant structures and of efficient saprophytic abilities, some pathogens need alternative hosts to survive in absence of potatoes. These alternative hosts frequently belong to the *Solanaceous* family and act as a long-term reservoir of the pathogen (Chang et al. 1992; Tomlinson et al. 2005).

Fungal dissemination occurs frequently as spores (conidiospores, chlamydospores, pycnidiospores, sporangiospores, oospores, and zoospores) or mycelium transported by water (rain, irrigation, and flow in soil), by soil adhering to farm equipment or introduced by contaminated seed tubers (Zambolim et al. 1995; Stevenson et al. 2001; Bae et al. 2007). Moreover, some pathogens liberate mobile dissemination forms such as zoosporanges. Zoospores of *Phytophthora erythroseptica*, *S. subterranean*, and *S. endobioticum* are responsible for short-distance dissemination of these pathogens (Wharton et al. 2007; Merz and Falloon 2009). Adult nematodes such as *Pratylenchus penetrans* are able to migrate on quite long distances better than do larvae (Pudasaini et al. 2007).

3.1.2 Relationship between inoculum density and disease severity

Although there is not always a clear and linear relationship, the severity of the disease generally increases with an increasing level of inoculum (Table 4). Sometimes, a minimum inoculum threshold is needed to initiate the disease development. This is the case, for instance, for potato cyst nematodes (Samaliev et al. 1998). Conversely, the disease severity of black dot does not increase any more beyond a maximum threshold of inoculum density (Nitzan et al. 2008). In fact as stated above, the relationship between inoculum density and disease severity greatly depends on the environmental factors which determine the level of soil suppressiveness.

Table 4 Inoculum sources and correlation between inoculum density and soil-borne potato diseases severity

Pathogen	Disease	Inoculum source	Correlation between inoculum density and disease severity (minimum value used for the calculation)	References
Fungi and oomycetes				
Colletotrichum coccodes	Black dot	Soil >Seed tuber	Disease severity remains constant above a threshold of soil-borne inoculum (0.5–1.7 g inoculum per liter of soil)	Lees (2003); Nitzan et al. (2008)
Fusarium spp.	Fusarium dry rots	Soil, seed tuber	Positive correlation (10^4 conidia·ml^{-1} soil for *F. sulphureum* 10^5 conidia·l^{-1} soil for *F. coeruleum*)	Tivoli et al. (1987); Stevenson et al. (2001); (2005)
Helminthosporium solani	Silver scurf	Seed tuber, soil	Negative correlation	Lennard (1980); Bains et al. (1996); Geary and Johnson (2006)
Macrophomina phaseolina	Charcoal rot			
Phoma andigena var. *andina*	Phoma leaf spot			
Phoma spp.	Gangrene	Seed tubers>plant residues		Adams (1980); Tivoli et al. (1987); Carnegie (1991)
Phytophthora erythroseptica	Pink rot	Seed tuber		Salas et al. (2000)
Polyscytalum pustulans	Skin spot	Seed tubers; crop debris, dust in store and soil		Wale et al. (2008)
Pythium ultimum var. *ultimum*	Leak	Soil	Positive correlation (10 propagules·ml^{-1} soil)	Triki et al. (2001)
Rhizoctonia solani	Black scurf/Stem canker	Sclerotia on seed tubers, in soil and in plant residues	Positive correlation	Rahman et al. (1996); Tsror and Peretz-Alon (2005)
Rosellinia sp.	Rosellinia black rot			
Sclerotinia sclerotinium	White mold	Soil, seed tuber		US Canola Association
Sclerotium rolfsii	Stem rot		Positive correlation	Rahman et al. (1996)
Spongospora subterranea	Powdery scab	Soil, seed tuber, manure	No significant/positive correlation (100 sporosori·g^{-1} soil)	Zambolim et al. (1995); Graaf et al. (2005), Nakayama (2007); Merz and Falloon (2009)
Synchytrium endobioticum	Wart	Soil, seed tubers	Positive correlation (1/25 sporangium·g^{-1} soil)	Hampson et al. (1994); Baayen et al. (2005)
Thecaphora solani	Thecaphora smut	Seed tuber, soil, infested plant parts		Mordue (1988); Wale et al. (2008)
Verticillium dahliae and *Verticillium albo-atrum*	Verticillium wilt	Soil microsclerotia, infected plant residues	Positive correlation	Nicot and Rouse (1987); Mol and Scholte (1995); Vallad et al. (2004)
Bacteria				
Clavibacter michiganensis ssp. *sepedonicus*	Ring rot	Seed tuber, soil, equipment	No significant correlation	Nelson (1982); Westra et al. (1994)
Clostridium spp.	Bacterial soft rot			
Pectobacterium atrosepticum, *Pectobacterium carotovorum* subsp. *carotovorum*, *Dickeya* spp.	Black leg, soft rot	Mainly seed tubers but also soil, water, insects	Positive correlation (10^3 cell per tuber)	Naumann et al. (1974); Perombelon (2000); Helias (2008)
Ralstonia solanacearum	Brown rot	Seed tuber, soil, water		Hsu (1991)
Streptomyces scabiei, *S. acidiscabiei*, *S. europeiscabiei*	Common and netted scab	Seed tuber and soil-borne	Positive correlation	Wilson et al. (1999); Wang and Lazarovits (2005)
Nematodes				
Belonolaimus longicaudatus	Sting nematode			
Ditylenchus destructor	Potato rot nematode	Seed tuber or soil		
Globodera pallida, *Globodera rostochiensis*	Potato cyst nematode	(cysts in) soil or soil-carrying seeds/seedlings/equipment	Positive correlation (2 eggs·g^{-1} soil)	Samaliev et al. (1998); Anaya et al. (2005)
Meloidogyne spp.	Root-knot nematode	(Eggs or larvae in) soil or soil-carrying seeds/seedling/equipment	Positive correlation (0.5 eggs·cm^{-3} soil)	Mohsin et al. (1989); Nagesh (1996); Vovlas et al. (2005)
Nacobbus aberrans	False root-knot nematode	Seed tuber		Franco et al. (1992)
Paratrichodorus and *Trichodorus* spp.	Stubby root nematode (TRV vector)	Soil or soil-carrying vector	Positive correlation	Perez et al. (2000)
Pratylenchus spp.	Root-lesion nematode	Soil	Positive correlation (0.4 eggs·g^{-1} soil)	Holgado et al. (2009)

3.1.3 Mechanisms of infection

Potato plants are essentially composed of cellulose, a very solid polymer and tubers are enveloped in a protective covering called periderm made of a suberin biopolymer providing the primary barrier against diseases, insects, dehydratation, and physical intrusions (Lulai 2001). Soil-borne pathogens of potato have various ways to penetrate the host plant and break physical barriers. They enter the roots, young sprouts, underground stems, stolons, or tubers. Some pathogens cannot infect intact tuber periderm or lenticels and penetrate through wounds (Stevenson et al. 2001; Taylor et al. 2004) whereas other pathogens can penetrate either directly by mechanical and/or enzymatic degradation of the host's cells or through natural openings (stomata, lenticels, eyes) (Table 5).

Once they have penetrated the host, pathogens colonize plant tissues. Fungi grow through the parenchyma of the cortex and often reach the vascular vessels. *T. solani*, *S. endobioticum*, and *Streptomyces* spp. penetration provokes hypertrophy of the colonized tissues resulting in galls. They grow in the plant, induce cell death, and feed on them saprophytically. They secrete phytotoxins—for example thaxtomin produced by *Streptomyces* spp.—inducing the formation of several layers of suberized corky cells, creating a large lesion firmly integrated within the tuber skin (Stevenson et al. 2001; Mulder et al. 2008; Perez and Torres 2008). Compared to common scab development, powdery scab pustules formation is a relatively short process, at the end of which a single wound cork layer remains that covers the entire lesion. After hardening off, this layer can be easily removed from the lesion without any damage of the underlying tissues (Delleman et al. 2005). *Colletotrichum coccodes*, *H. solani*, *Polyscytalum pustulans*, *R. solani*, *S. subterranea*, and *Streptomyces* spp. are responsible for several superficial alterations called blemishes. Colonization by those pathogens is usually limited to superficial layers of tuber periderm (Harrison 1997; Stevenson et al. 2001; Cunha and Rizzo 2004; Lehtonen et al. 2008; Loria et al. 2008) but they can colonize other parts of the plant until they reach vascular system. *Streptomyces* spp. responsible for netted scab blemishes has pathogenic mechanisms that are assumed to not implicate thaxtomin but rather a necrotic protein (Bouchek-Mechiche et al. 2006).

Fungi and bacteria-causing rots produce a wide range of hydrolytic enzymes such as cellulases, pectinases, xylanases, and proteases (Olivieri et al. 2004). They are responsible for tissue maceration and cell death, after which the microorganisms have access to the nutritional resources of the dead plant tissues (Amadioha 1997; Aveskamp et al. 2008). *Pectobacterium* spp. develop an original pathogenic strategy based on quorum sensing, which utilizes freely diffusible chemical signal molecules allowing pathogenic bacteria to synchronize the production of virulence factors and make the pathogenic attack more efficient (Liu et al. 2008). Finally, nematodes attacking potatoes can be classified into two categories: ectoparasites and endoparasites. Ectoparasites nematodes (*Belonolaimus longicaudatus*, *Paratrichodorus* spp., and *Trichodorus* spp.) are mobile and feed on potato roots in the area of cell division and elongation without penetrating the root (Stevenson et al. 2001; Mugniéry 2007). The endoparasitic nematodes of potato, *D. destructor* and *P. penetrans* are migrating endoparasites; they feed from cell to cell within the host, whereas *Globodera* spp., *Meloidogyne* spp., and *N. aberrans* are sedentary endoparasites, they induce specialized feeding sites in plant roots. *D. destructor* and *P. penetrans* penetrate underground parts of the plant, feed on the cortical cells, and migrate into the roots, destroying cell after cell. *Globodera pallida*, *Globodera rostochiensis*, *Meloidogyne* spp., and *N. aberrans* develop feeding cavities in host root, causing galls (Mugniéry 2007).

3.1.4 Genetic variability

A soil-borne disease can be caused by several species of pathogens belonging to a single genus, by one species, or even by a subgroup of a species. Each species or subspecies is adapted to particular conditions or variety. Knowledge of the genetic diversity of pathogens is useful for precise diagnosis and control of potato diseases.

Since *Erwinia* has been renamed and divided into two different genera, *Pectobacterium* and *Dickeya* (Helias 2008), bacterial soft rot previously attributed to *Erwinia carotovora*, *Erwinia atroseptica*, and *Erwinia chrysanthemi* is in fact one disease caused by several species belonging to different genera (Table 5). *Pectobacterium* spp. and *Dickeya* spp. are frequently associated with bacteria of the genus *Clostridium* which includes very numerous Gram-positive anaerobic bacteria. *Clostridium puniceum* is one of the few well-characterized pectolytic clostridia isolated from rotting potato tubers (Stevenson et al. 2001; Prescott et al. 2003).

Within a same species, the pathogen may belong to different groups with various genetic, pathogenic, and physiological traits leading to the characterization of races, biovars and, recently, genomovars—strains which are phylogenetically differentiable, but are phenotypically indistinguishable—phylotypes and sequevars— one or several strains with a given sequence (Nouri et al. 2009). Fungi without sexual reproductive stage related to the potato disease cycle, such as *Colletotrichum* spp., *Fusarium* spp., or *Verticillium* spp., are classified in vegetative compatibility groups (VCGs). Within a VCG, hyphae belonging to different isolates can anastomose and form stable heterokaryons, whereas hyphae from isolates belonging to

Table 5 Genetic variability, strategies of conservation and attack of the pathogens and detection methods

Pathogen	Disease	Genetic variability	Conservation and overwintering	Main penetration ways	Detection methods	References
Fungi and oomycetes						
Colletotrichum coccodes	Black dot	6 or 7 VCG pathogenic for potato	At least 8 years at 10 cm depth in the soil as sclerotia	Mechanical	Q and RT-PCR, Fourier transform infrared (FT-IR)	Dillard and Cobb (1998); Cullen (2002); Heilmann et al. (2006); Erukhimovitch (2007); Shcolnick et al. (2007); Nitzan et al. (2008)
Fusarium spp.	Fusarium dry rots	13 species, especially *F. sambucinum* and *F. solani* var. *coeruleum* (15 VCGs)	Microconidia, chlamydospores and mycelium on plant debris	Wounds, enzymatic	Isolation and morphology, RT-PCR, PCR enzyme-linked immunosorbent assay, volatile profile	Tivoli et al. (1987); Ouellette et al. (1990); Stevenson et al. (2001); Oliveri et al. (2004); Cullen et al. (2005); Burlakoti et al. (2007); El-Hassan et al. (2007); Peters et al. (2008b); Sharifi et al. (2008); Recep et al. (2009)
Helminthosporium solani	Silver scurf		At least 4 years in the soil	Enzymatic	Classical detection methods, PCR	Bains et al. (1996); Errampalli (2001); Martinez et al. (2004); Geary et al. (2007)
Macrophomina phaseolina	Charcoal rot		Until 3 years under unfavorable climatic conditions as microsclerotia	Enzymatic		Dhingra and Sinclair (1977); Amadioha (1997)
Phoma andigena var. *andina*	Phoma leaf spot					
Phoma spp.	Gangrene	2 sub-species: *P. exigua* var. *foveata* and *P. exigua* var. *exigua*		Enzymatic	Conventional and RT-PCR	McDonald et al. (2000); Stevenson et al. (2001); Giebel and Dopierala (2004); Cullen et al. (2007)
Phytophthora erythroseptica	Pink rot	One species with few genetic variations	Oospores	Enzymatic		Lucas and Pitt (1974); Peters et al. (2004); Peters et al. (2005); Cullen et al. (2007); Taylor et al. (2008)
Polyscytalum pustulans	Skin spot		7 years or more in soil as sclerotia	Mechanical	RT-PCR	Lees et al. (2009)
Pythium ultimum var. *ultimum*	Leak		Many years in the soil and in the infected plant debris as oospores	Wounds	Conventional and RT-PCR, Conventional and RT-PCR	Cullen et al. (2007); Taylor et al. (2008)
Rhizoctonia solani	Black scurf/Stem canker	One species with 13 anastomosis groups pathogenic for potaotes (AG3 being predominant)	Sclerotia	Enzymatic	Classical bioassays, PCR, immunochromatographic lateral flow	Tsror et al. (1993); Gilligan et al. (1996); Carling et al. (2002); Lees et al. (2002); Gvozdeva et al. (2006); Hughes (2008)
Rosellinia spp.	Rosellinia black rot	3 species: *R. bunodes*, *R. necatrix* and *R. pepo*		Enzymatic	Conventional and Scorpion-PCR	Stevenson et al. (2001); Schena et al. (2002); Ten Hoopen and Krauss (2006)
Sclerotinia sclerotinium	White mold			Mechanical		Wharton, Michigan potato diseases
Sclerotium rolfsii	Stem rot		Sclerotia	Enzymatic		Madalageri et al. (1991); Ohazurike and Arinze (1992)
Spongospora subterranea	Powdery scab		For >10 years in cold areas as cistosori	Mechanical	Classical methods, conventional and RT-PCR, ELISA	Zambolim et al. (1995); Stevenson et al. (2001); Graaf et al. (2003); Ward (2004); Merz (2005); Qu et al. (2006); Nakayama (2007)

Table 5 (continued)

Pathogen	Disease	Genetic variability	Conservation and overwintering	Main penetration ways	Detection methods	References
Synchytrium endobioticum	Wart	One species with 43 pathotypes	>30 years as winter sporangia	Mechanical	Conventional and RT-PCR	Boogert et al. (2005); Baayen et al. (2006)
Thecaphora solani	Thecaphora smut		7 years or more in the soil	Mechanical	PCR	Andrade et al. (2004); Perez and Torres (2008)
Verticillium dahliae and Verticillium albo-atrum	Verticillium wilt	2 species: *V. dahliae* (4 VCGs) and *V. albo-atrum* (VCG02 attacking potato)	≈63 months		Classical methods, PCR, Q-PCR	Nelson (1984); Correll et al. (1988); Joaquim and Rowe (1991); Platt and Mahuku (2000); Tsror et al. (2000); Strausbaugh et al. (1992); Zhang et al. (2005); Atallah et al. (2007)
Bacteria						
Clavibacter michiganensis ssp. *sepedonicus*	Ring rot	One species with few genetic variation	≈18 months in plain soil	Enzymatic	Immuno-fluorescence antibody, staining (IFAS), (ELISA), RT-PCR; LMW RNA profiles	Nelson (1984); Logan et al. (1987); Eichenlaub et al. (1991); Palomo et al. (2000); Smith et al. (2001); Stevenson et al. (2001); Vasinauskiene and Baranauskaite (2003); Hukkanen et al. (2005); Gudmestad et al. (2009)
Clostridium spp.	Bacterial soft rot	Several species among which *C. puniceum*		Enzymatic		Perombelon et al. (1979); Stevenson et al. (2001); Prescott et al. (2003)
Pectobacterium spp., *Dickeya* spp.	Black leg, soft rot	2 genera: *Pectobacterium* spp. among which *P. atrosepticum* and *P. carotovorum* subsp. *carotovorum* and *Dickeya* spp.	Overwintering possible (on crop debris or weeds) but varying between bacteria, seasons and areas	Enzymatic	Conventional and RT-PCR, isolation (CVP), volatile profile, biochemical tests, ITS-RFLP profiles, 16 S rRNA analysis, ELISA	Bradbury (1977); Ouellette et al. (1990); Tsror et al. (1993); Helias et al. (2000); Lazy and Lukezic (2003); Atallah and Stevenson (2006); Latour et al. (2008); Pitman et al. (2008); Helias (2008)
Ralstonia solanacearum	Brown rot	One species with several biovars (1, 2, and 2T) and races (1 and 3) attacking potato	Water, weeds, (soil?)	Enzymatic	Isolation, PCR, immunofluorescence and fluorescent in-situ hybridisation (FISH)	Hsu (1991); Ronda et al. (1999); Rangaswami and Mahadevan (2004); Messiha et al. (2007); Loria et al. (2008); Nouri et al. (2009); Smith and de Boer (2009)
Streptomyces spp.	Common and netted scab	Common scab: *S. scabies*, *S. europaeiscabiei*, *S. stelliscabiei*, *S. acidiscabiei*, *S. turguidiscabiei* and maybe some others Netted scab: *S. reticuliscabiei* and some isolates of *S. europaeiscabiei*	Conidia	Enzymatic	Conventional and RT-PCR, RFLP, rRNA sequence analysis, carbon source utilization, repetitive BOX profiles	Rudkiewicz and Sikorski (1984); Bouchek-Mechiche et al. (2000); Flores-Gonzalez et al. (2008); Loria et al. (2008); Mulder et al. (2008); Zhao et al. (2008)
Nematodes						
Belonolaimus longicaudatus	Sting nematode			Mechanical	Centrifugal-flotation method, morphological detection	Crow et al. (2000)
Ditylenchus destructor	Potato rot nematode		About 4 months in favorable conditions	Mechanical	Extraction in water, morphological identification, PCR-RFLP	Shojaei et al. (2006); EPPO (2008); Ilyashenka and Ivaniuk (2008)
Globodera pallida, *Globodera rostochiensis*	Potato cyst nematode	2 species: *G. pallida* and *G. rostochiensis*	Until 8 years in the soil as cysts	Mechanical and enzymatic	Soil extraction and, morphological identification, allele-specific PCR	Wharton and Worland (2001); Moxnes and Hausken (2007); Achenbach et al. (2009); Reid (2009); Rehman et al. (2009)

Table 5 (continued)

Pathogen	Disease	Genetic variability	Conservation and overwintering	Main penetration ways	Detection methods	References
Meloidogyne spp.	Root-knot nematode	At least 7 species: *M. hapla*, *M. chitwoodi*, *M. fallax* (Mediterranean and temperate areas), *M. arenaria*, *M. incognita*, *M. javanica* and *M. mayaguensis* (Mediterranean and tropical areas)		Mechanical and enzymatic	Morphometrics, host range, biochemical and molecular (RFLP) analysis	Hlaoua and Raouani (2007); Melakeberhan et al. (2007); Mugniéry (2007); Dieterich and Sommer (2009); Ozarslandan et al. (2009)
Nacobbus aberrans	False root-knot nematode			Mechanical	PCR	Franco et al. (1992); Atkins et al. (2005)
Paratrichodorus and *Trichodorus* spp.	Stubby-root nematode (TRV vector)	7 species of *Paratrichodorus* spp. and 5 species of *Trichodorus* spp.			Morphometric and molecular analysis	Riga and Neilson (2005); Riga et al. (2007)
Pratylenchus spp.	Root-lesion nematode	11 species of *Pratylenchus* spp.		Enzymatic	Morphometric and molecular (PCR-RFLP) analysis	Brown et al. (1980); Saeed et al. (1998),Stevenson et al. (2001); Mugniery and Phillips (2007)

VCG vegetative compatibility group, *AG* anastomosis group, *RT-PCR* reverse transcriptase polymerase chain reaction, *Q-PCR* quantitative PCR, *FT-IR* Fourier-transformed infrared spectroscopy, *ELISA* enzyme-linked immunosorbent assay

different VCGs cannot. This mechanism is the only known mechanism of genetic exchange between individuals of asexual fungi (Hiemstra and Rataj-Guranowska 2003). Hyphal anastomosis is also used to categorize the isolates of *R. solani* into anastomosis groups (AG). Presently, 13 AGs have been described, several of which being divided into subgroups. Individual AGs are not strictly associated with a specific host but rather with a family of hosts which can be in turn narrow or very broad, for example AG 1 with rice mainly and AG 8 with various cereals. AG 3 isolates, and more specifically isolates from the AG 3 PT subgroup, are often associated with potato diseases (Fiers et al. in press; Kuninaga et al. 2000; Carling et al. 2002). However it was shown, in Great Britain and France, that AG 2–1 and AG 5 can cause disease in potato crops but with a much lower incidence than AG 3 PT (Campion et al. 2003; Woodhall et al. 2007).

As a result of the genetic evolution of pathogens, new pathotypes are regularly discovered. Conversely, some populations such as *P. erythroseptica* and *Clavibacter michiganensis* subsp. *sepedonicus* vary slightly in pathogenicity and in genetic diversity suggesting a relatively recent introduction of a small founding population of the pathogen (Smith et al. 2001; Peters et al. 2005). Genetic evolution can be achieved by vertical or horizontal gene transfer. *Meloidogyne* populations originally did not possess the cell wall-degrading enzymes required to invade host roots. Although the mechanism of horizontal gene transfer remains largely elusive, it has been speculated that a gene coding for a cell wall-degrading enzyme was horizontally transferred from a rhizobial bacterium to the nematode and was kept in the genome of the nematode by strong selection pressures representing important initial steps facilitating the invasion of plants by nematodes (Dieterich and Sommer 2009). By genetic evolution, pathogens can adapt to the different environmental conditions they are submitted to. This enables them to skirt control measures and continuously forced farmers to use new control methods.

3.1.5 Diagnosis and detection methods

Rapid detection of plant parasitic pathogens enables to set up adapted control measures and avoid disease expansion and yield losses, even if the infestation level is low. Classical detection methods begin with visual observation and characterization of symptoms followed by identification using morphologic traits for nematodes (Crow et al. 2000; Riga and Neilson 2005; Melakeberhan et al. 2007; Mugniéry 2007) or isolation on selective media for fungi and bacteria. Carbon source utilization, sugar degradation, and production of specific enzymes allow the biochemical identification of bacteria (Flores-Gonzalez et al. 2008; Pitman et al. 2008). However, these classical methods are often not accurate enough to distinguish between different

strains or pathovars of the same species. Molecular biology based-diagnosis and detection methods are expected to complement classical diagnosis. The most developed detection methods are based on polymerase chain reaction (PCR), which amplifies DNA regions specific of the pathogen of interest (Table 5). The quantitative reverse transcriptase PCR is currently among the most powerful methods for the diagnosis of pathogens in complex environments. Indeed, it enables to quantify the ARN of the pathogen present in a sample. Fingerprinting methods—restriction fragment length polymorphism or amplified fragment length polymorphism—are used for intraspecific identification of pathovars or races of bacteria, fungi, or nematodes (Abeln et al. 2002; Cullen et al. 2007; Flores-Gonzalez et al. 2008; Pitman et al. 2008). Fluorescent in situ hybridisation or stable low molecular weight DNA profiles were developed to detect *R. solanacearum* and *C. michiganensis* var. *sepedonicum*, respectively (Ronda et al. 1999; Palomo et al. 2000). Immunological techniques such as immunochromatographical lateral flow, enzyme-linked immunosorbent assay and immunofluorescence are based on the recognition of specific markers at the surface of pathogenic cells to detect and identify the pathogens (Ronda et al. 1999; Merz 2005; Hughes 2008). Fungal pathogens display typical infrared spectra that differ from the spectra of substrate material such as potato; they can be early and rapidly detected by Fourier transform infrared microscopically based technique (Erukhimovitch 2007). Finally, monitoring of normal and disease-induced volatile profiles in stored potatoes or of the light reflected from plant in fields are valuable techniques to detect stress and thus potential pathogenic infections (Ouellette et al. 1990; Heath et al. 2000).

3.2 Interactions between microorganisms, organisms, and pathogens

Potato pathogens are not the only microorganisms living in the potato surroundings. A huge microbial biomass is associated and interacts with potatoes. About 10^7 bacteria colony forming units per gram of soil live in the potato rhizosphere and potato geocaulosphere which is the volume of soil surrounding the tubers (Lazarovits et al. 2007). The structure of microbial and nematode communities in the geocaulosphere varies according to the plant age and other factors related to cultivar, nutritional status, biotic and abiotic stresses, etc. (Al-Hazmi et al. 1993; Krechel et al. 2002; Ferreira et al. 2008; Desgarennes et al. 2009; Manici and Caputo 2009).

Earthworms and nematodes favor pathogen mobility by transporting them through the soil (Jensen 1978; Table 6). Nematodes enhance potato diseases because they act as vectors of the pathogens. They also enhance the diseases either by facilitating the development of other pathogens—acting as mechanical wound agents and providers of necrotic tissues for pathogen penetration or nutrition—or by benefiting of their attacks as opportunistic micro-organisms (Jensen 1978).

The microbial or faunal interactions in the geocaulosphere are involved in disease suppressiveness of the soil. Two classical types of suppressiveness of soil are known. General suppression is related to the global activity of the whole microbial biomass in the soil. In contrast, specific suppression is due to the specific activity of certain individuals or groups of microorganisms (Alabouvette et al. 1996; Weller et al. 2002). For instance, *Serratia plymuthica*, *Pseudomonas* spp., *Bacillus* spp., *Streptomyces* spp., and *Trichoderma* spp. (Kumar and Khare 1990; Kamensky et al. 2002; Krechel et al. 2002) are able to decrease the severity of several potato diseases (Table 6). They can be considered as biological control agents. Some biological control agents can act directly against fungal pathogens by enzymatic degradation of their cell walls (Kamensky et al. 2002; Li et al. 2002), by parasitism—as it seems to be the case against numerous nematodes—(Nunez-Camargo et al. 2003; Papert et al. 2004), by antibiotics production (Grosch et al. 2005), by siderophore secretion that reduces the availability of iron needed by plant pathogens (Bharadwaj et al. 2008) or by interfering with communication between pathogens, i.e., by degrading molecules involved in the ”quorum sensing” mechanisms of *Pectobacterium* spp. (Dong et al. 2004). Indirectly, biological control agents can lead to the plant strengthening and a better resistance to pathogen attacks by producing plant growth hormone or by inducing the production of plant defense molecules such as phytoalexins and PR proteins (Stevenson et al. 2001; Larkin 2008). Mycorrhizal fungi also have a beneficial effect; inoculation with arbuscular mycorhizal fungus suppressed tuber dry rot and reduced stem canker and black scurf (Bharadwaj et al. 2008).

3.3 Interactions between plants and pathogens

The major method to control potato diseases is to find resistant cultivars to a majority of pathogens especially since the use of chemicals is limited (INRA and Cemagref 2005; Paillotin 2008). Different levels of resistance towards most of the soil-borne potato diseases have been observed among potato cultivars. Wild species of *Solanum* provide excellent sources of disease resistance genes that may be introgress into *S. tuberosum* genome by interspecific crossing (Jansky and Rouse 2003; Table 7) and international structures such as the International Potato Center in Peru are aiming at preserving the genetic diversity of native potatoes. Varieties of potato which contain color pigments are more and more utilized in current breeding programs

Table 6 Detrimental beneficial and associations of microorganisms with potato soil-borne pathogens

Pathogen	Disease	Organisms enhancing diseases	Organisms reducing diseases	References
Fungi and oomycetes				
Colletotrichum coccodes	Black dot	*V. dahliae*, *S. subterranea*		Tsror (2004); Merz and Falloon (2009)
Fusarium spp.	Fusarium dry rots	*P. atrosepticum*, *Meloidogyne* spp. *D. destructor*, *S. subterranea*	*S. plymuthica*, *D. destructor*	Munzert et al. (1977); Jensen (1978); Gould et al. (2008); Merz and Falloon (2009)
Helminthosporium solani	Silver scurf		*Acremonium strictum*, *Pseudomonas putida*, *Nocardia globerula*, *Xanthomonas campestris*	Elson et al. (1997); Rivera-Varas et al. (2007)
Macrophomina phaseolina	Charcoal rot		*Trichoderma harzianum*, *Bacillus subtilis*, *P. aeruginosa*	Kumar and Khare (1990); Gupta et al. (1999)
Phoma andigena var. *andina*	Phoma leaf spot			
Phoma spp.	Gangrene			
Phytophthora erythroseptica	Pink rot	*S. subterranea*	*Enterobacter* sp., *E. cloacae*, Pseudomonas sp., *P. fluorescens*	Merz and Falloon (2009); Schisler et al. (2009)
Polyscytalum pustulans	Skin spot			
Pythium ultimum var. *ultimum*	Leak		*Pseudomonas fluorescens*, *Burkholderia ambifaria*	Li et al. (2002); Bardin et al. (2004)
Rhizoctonia solani	Black scurf/stem canker	*G. rostochiensis*, *Meloidogyne* spp. + *V. dahliae*, *Pratylenchus neglectus* + *V. dahliae*	*Paenibacillus polymyxa*, *Bacillus licheniformis*, *P. fluorescens*, *Chryseobacterium gleum*, *Lysobacter enzymogenes*, *Streptomyces* spp., *Verticillium biguttatum* + *Gliocladium roseum* + *Azotobacter chroococcum*, *Trichoderma* spp., non pathogenic *Rhizoctonia* spp.	Scholte and S'Jacob (1989); Krechel et al. (2002); Grosch et al. (2005); Back et al. (2006); Grosch et al. (2006); Santamarina and Rosello (2006); Mahmoud et al. (2008); Wilson et al. (2008)
Rosellinia sp.	Rosellinia black rot		*Trichoderma* spp.	Al-Chaabi and Matrod (2002)
Sclerotinia sclerotinium	White mold		*S. plymuthica*, *Penicillium* strain PY-1, *Gliocladium* sp., *Fusarium* spp., *Coniothyrium minitans*, *Trichoderma harzianum*	Phillips (1989); Kamensky et al. (2002); Yang et al. (2008)
Sclerotium rolfsii	Stem rot		*Bacillus subtilis* *Trichoderma* spp.	Kumar and Khare (1990); Dey et al. (2004)
Spongospora subterranea	Powdery scab	*C. coccodes*	*Trichoderma harzanium*	Merz and Falloon (2009)
Synchytrium endobioticum	Wart	Earthworms		Hampson and Coombes (1989)
Thecaphora solani	Thecaphora smut	*Meloidogyne incognita*		Bazan de Segura and Carpio (1974)
Verticillium dahliae and V. albo-atrum	Verticillium wilt	*C. coccodes*, *Meloidogyne* spp. + *R. solani*, *P. neglectus* + *R. solani*, *P. penetrans*, *G. rostochiensis*, *G. pallida*	*T. harzianum*, *Pseudomonas* spp., *Streptomyces* spp.	Jensen (1978); Franco and Bendezu (1985); Scholte and S'Jacob (1989); Krechel et al. (2002); Rotenberg et al. (2004); Tsror (2004); Santamarina and Rosello (2006); Bharadwaj et al. (2008)
Bacteria				
Clavibacter michiganensis ssp. *sepedonicus*	Ring rot			
Clostridium spp.	Bacterial soft rot	*Pectobacterium* spp.		Perombelon et al. (1979)
Pectobacterium atrosepticum, *Pectobacterium carotovorum* subsp. *carotovorum*	Black leg, soft rot	*Clostridium* spp, *F. solani* var. *coeruleum*	*Bacillius* spp., *Pseudomonas* spp	Munzert et al. (1977); Perombelon et al. (1979); Dong et al. (2004); Bharadwaj et al. (2008)
Ralstonia solanacearum	Brown rot	*G. pallida*	*P. fluorescens*, *P. putida*, *B. subtilis*	Jensen (1978); Mahmoud (2007)
Streptomyces scabiei, *S. acidiscabiei*, *S. europeiscabiei*	Common and netted scab		Non pathogenic *Streptomyces*	Wanner (2007)

Table 6 (continued)

Pathogen	Disease	Organisms enhancing diseases	Organisms reducing diseases	References
Nematodes				
Belonolaimus longicaudatus	Sting nematode			
Ditylenchus destructor	Potato rot nematode			
Globodera pallida, *G. rostochiensis*	Potato cyst nematode	*V. dahliae*, *R. solani*, mycorhization	*V. dahliae*, *F. oxysporum*, *P. exigua*	Jensen (1978); Wronkowska and Janowicz (1989); Ryan and Jones (2003); Back et al. (2006); Mugniéry and Phillips (2007)
Meloidogyne spp.	Root-knot nematode	*P. neglectus*, *R. solani*, *V. dahliae*	*Pseudomonas* sp., *Streptomyces* sp., *Rhizobium* sp.; *Bacillus megaterium* var. *phosphaticum B. penetrans*, *Glomus mossae*	IPC (1978); Scholte and S'Jacob (1989); Hafez and Sundararaj (2000); Sankaranarayanan and Sundarababu (2001); Krechel et al. (2002)
Nacobbus aberrans	False root-knot nematode			
Paratrichodorus and *Trichodorus* spp.	Stubby-root nematode (TRV vector)			
Pratylenchus spp.	Root-lesion nematode	*V. dahliae*, *R. solani*		Scholte and S'Jacob (1989); Saeed et al. (1998)

because cultivars producing anthocyanins can provide better resistance to soft rot or other diseases compared to white/yellow flesh cultivars (Wegener and Jansen 2007). Cultivars resistant to several diseases were obtained, but simultaneous resistance to all pathogens is very difficult to achieve. Moreover, for some diseases, new genotypes of pathogen appear regularly and overcome plant defense turning the former resistant cultivars into susceptible ones. Hence the levels and durability of field resistance are often highly depending on numerous abiotic and biotic factors still neither well-known or controlled.

Resistant potato cultivars counteract pathogenic attacks by plant defense reactions that generally lead to the production of suberin and antimicrobial agents, activation of defense genes and trigger hypersensitive cell death (Levine et al. 1994) delaying the pathogen development in plant tissues until a wound periderm could form. Susceptible cultivars produce non-uniform deposits of suberin making them less performing against pathogens (Finetti Sialer 1990; Ray and Hammerschmidt 1998). The anti-microbial agents produced by potatoes can be glycoalkaloids (α-chaconin and α-solanine), phenolic compounds and phytoalexins, antimicrobial compounds produced by the plant after pathogen attacks (Okopnyi et al. 1983; Lyon 1989; Ray and Hammerschmidt 1998; Zagoskina et al. 2006; Baker et al. 2008; Lerat et al. 2009). Plants also produce inhibitors of virulence factors (Kim et al. 2006). Another plant defense reaction called systemic acquired resistance (SAR) spreads a signal through the surrounding cells. It allows plants to become highly resistant to subsequent infection by the original pathogen but also by a wide variety of other pathogens. For example, foliar SAR-inducing applications of (benzo (1,2,3) thiadiazole-7-carbothioic acid S-methyl ester-BTH and harpin) reduce the numbers of root lesion nematodes (*Pratylenchus* spp.) and root knot nematodes (*Meloidogyne chitwoodi*; Collins et al. 2006).

4 Effects of cultural practices on the occurrence and development of soil-borne potato diseases

Each technical choice made by farmers concerning the way of growing potatoes plays a predominant role on the quantitative and qualitative yield. All cultural practices may impact disease development.

4.1 Rotations

The most traditional way to control diseases is to use crop rotations including a nonhost plant that can "sanitize" the soil (Alabouvette et al. 1996). Several studies show good results when potatoes are grown only once every 3 or 4 years and, as the other practices, it should be thought in a systemic approach (Table 8). The

Table 7 Some wild potato cultivars harboring resistance towards pathogens

Cultivar	Resistance	References
Solanum vernei	*Spongospora subterranea*	Merz and Falloon (2009)
Solanum acaule	*Clavibacter michiganensis* var. *sepedonicus*	Laurila et al. (2003)
Solanum commersonii	*Ralstonia solanacearum*	Kim-Lee et al. (2005)
Solanum bulbocastanum	*Meloidogyne chitwoodi*	Nitzan et al. (2009)
Snowder (*Solanum tuberosum* x *Solanum berthaultii*)	*Pythium ultimum* and *Phytophthora erythroseptica*	Salas et al. (2003); Thompson et al. (2007)
Solanum brevideus	*Pectobacterium* spp.	Ahn et al. (2001)

beneficial effect of crop rotation depends on the host range of the pathogen and its ability to survive in soil in the absence of its host plant thanks to dormant structures such as sclerotia or chlamydospores. Crop rotation must avoid including alternative hosts for the pathogen (Peters et al. 2004). Susceptible weeds—such as hairy nightshade (*Solanum sarrachoides*)—have to be eliminated as they enable the pathogen to survive during the absence of the main host (Boydston et al. 2008). Crop rotation can also fail to control highly specialized pathogens, such as *Globodera* spp., *S. endobioticum*, or *S. subterranea*. These organisms are able to survive for long periods, either saprophytically or as dormant structures, in soil, and a very low inoculum density is sufficient to induce disease (Samaliev et al. 1998; Merz and Falloon 2009). Rotations with potatoes can include very diverse crops (Table 8). If some of those crops have beneficial effects towards potato crop, other might favor pathogen development and should not enter the rotation, or at least not as the crop preceding the potatoes.

4.2 Fertilization and amendments

Supplying plants with micronutrients and macronutrients can be achieved with organic or inorganic fertilizers, either through soil application, foliar spray, or seed treatment (Davis et al. 1994; Panique et al. 1997; Malakouti 2008). Adapted fertilization and amendment allow strong and healthy crops, which are less susceptible to pathogens (Khomyakov and Kostin 1981). Fertilization may also indirectly favor diseases by enhancing foliar development that maintains high level of humidity needed for example for the growth of *Pectobacterium* spp. (Rousselle et al. 1996). Amendments contribute to control diseases by modifying soil properties, especially pH (see Section 2.2) and microbial activities. That could result in specific suppression caused by the stimulated specific antagonistic populations or in general suppression caused by increased microbial activities or both (Lazarovits et al. 2001; Steinberg et al. 2007; Termorshuizen et al. 2006).

For some diseases, such as stem rot, organic fertilizers are more efficient than mineral ones in terms of disease suppression (Amitava and Maiti 2006; Table 8). Among organic fertlizers, composts are known to have the capacity to suppress diseases, depending on their degree of maturity (organic matter content and microbial activities). The causal agents of disease suppression brought into the soil by compost amendment are complexes of bacterial and fungal populations, which invade the pile during the curing stage, although some residual activity is probably related to fungistatic compounds occurring in the composts (Raviv 2008).

4.3 Tillage management

Potato cultivation traditionally involves intensive soil tillage throughout the cropping period. Mechanical tillage, ridging, and harvesting entail intensive soil disturbance and modify the environmental conditions especially the microbial characteristics of soil, both on quantitative and qualitative aspects (FAO 2008; Vian 2009). As an example, plowing contributes to redistribute vertically the inoculum, which increases the probability of infection (Taylor 2005). Over the last decades, there is a trend to replace plowing by techniques without soil inversion, i.e., no tillage or superficial tillage. It seems that this strategy could lead to some efficient disease suppression by stimulating microbial activity but conversely may limit the nutrient uptake by the plant (Klikocka 2001; Peters et al. 2004; Vian 2009). Therefore, a combination of both biotic and abiotic factors should be clearly balanced (Table 8). Indeed, rotation and conservation tillage practices can improve disease suppression by enhancing the antibiosis abilities of endophytic and root zone bacteria (Peters et al. 2003). On the other side, the plant growth and the macronutrient (N, P, K, Ca, and Mg) contents in potato plant respond positively to a deeper soil caused by plowing (Boligowa and Glen 2003; Nunes et al. 2006).

4.4 Planting, haulm destruction, lifting, and harvesting

Planting, dehaulming, lifting, and harvesting are decisive for disease expression (Table 8). For example, low planting density increases the yield per plant because the foliage has more space to grow. Also, sparse plants are less exposed to

Table 8 Cultural practices favorable to reduce disease development

Pathogen	Disease	Rotation	Fertiliaation and amendments	Tillage	Planting, lifting, and harvesting methods	Pesticides	Cultural systems	Storage	References
Fungi and oomycetes									
Colletotrichum coccodes	Black dot	Long rotations (>5 years) With wheat, red clover, alfalfa, rye, maize, orchard grass, fallow, barley Without yellow mustard, soybean, spring canola		Mouldboard plowing at 30 cm	Avoid water stress, Early harvesting Short interval between haulm destruction and harvesting	Increased by oxamyl Decreased by imazalil, tolchlofos-methyl, mancozeb, thiabendazole, fenpiclonil and propiconazole		Dry curing and/or temperatures below 5°C	Hide and Read (1991); Andrivon et al. (1997); Denner et al. (2000); Esfahani and Bak (2004); Glais-Varlet et al. (2004); Cwalina-Ambroziak and Czajka (2006); Nitzan et al. (2006)
Fusarium spp.	Fusarium dry rots	No monoculture, minimum 3 years of rotation with red clover	Composted manure	Minimum tillage	Early harvesting Short interval between haulm destruction and harvesting, wound healing	Chlorine dioxide, fenpiclonil and a mixture of thiabendazole and imazalil, mancozeb	Organic	Dry curing and/or low temperatures below 4°C	Khomyakov and Kostin (1981); Povolny (1995); Carnegie et al. (2001); Lui and Kushalappa (2002); Carter et al. (2003); Olsen et al. (2003); Peters et al. (2004); Cwalina-Ambroziak and Czajka (2006); Raviv (2008)
Helminthosporium solani	Silver scurf	Minimum 3 years of rotation with red clover		Minimum tillage	low planting density. Late planting and early harvesting,	Mancozeb, imazalil, prochloraz, chlorine dioxide, thiabendazole, fenpiclonil, benomyl		Dry conditions, and/or temperatures below 4°C	Lennard (1980); Hide and Read (1991); Firman and Allen (1995); Carnegie et al. (1998); Carter et al. 2003; Olsen et al. (2003); Peters et al. (2004); Geary and Johnson (2006)
Macrophomina phaseolina	Charcoal rot					Captan, benomyl, copper oxychloride			Amadioha (1998)
Phoma andigena var. *andina*	Phoma leaf spot								
Phoma spp.	Gangrene				No evident effect of planting time. Early haulm destruction. Lifting at >8°C	2-aminobutane, thiabendazole	Organic	Wet conditions and/or temperatures above 15°C	Meredith et al. (1975); Fox and Dashwood (1979); Croke and Logan (1982); Copeland et al. (1980); Ostergaard and Henriksen (1983); Bang (1989); Povolny (1995); Carnegie et al. (1998)
Phytophthora erythroseptica	Pink rot	3 years with barley and red clover			Planting in well-drained fields, harvesting in cool weather, minimizing damages	Mefenoxam, metalaxyl-m		Drying after harvesting	Peters et al. (2005); Al-Mughrabi et al. (2007); Taylor et al. (2008)
Polyscytalum pustulans	Skin spot				Early harvesting	Imazalil, prochloraz (seed), 2-aminobutane, benomyl, thiabendazole		Curing in dry conditions at high temperatures	Lennard (1980); Hide and Cayley (1987); Hide and Read (1991); Carnegie et al. (1998)
Pythium ultimum var. *ultimum*	Leak		Composted manure		Planting in well-drained fields, harvesting in cool weather, minimizing damages,	Mefenoxam		Drying after harvesting	Raviv (2008); Taylor et al. (2008)

Table 8 (continued)

Pathogen	Disease	Rotation	Fertiliaation and amendments	Tillage	Planting, lifting, and harvesting methods	Pesticides	Cultural systems	Storage	References
Rhizoctonia solani	Black scurf/Stem canker	Minimum 3 years of rotation without wheat, alfalfa, ryegrass	Composted manure, straw	Minimum tillage, autumn ridging	Shallow planting (5 cm), high soil temperature, low planting density. Short time between haulm destruction and harvest.	Increased by 1,3-dichloropropene, aldicarb and ethoprophos. Decreased by pencycuron, chlorine dioxide, thiophanate-methyl, flutolanil, manco-zeb, benomyl, thia-bendazole Oxamyl soil treatments increase stem canker and decrease black scurf	Conventional		Johnston et al. (1994); Firman and Allen (1995); Hide et al. (1995); Lakra (2000); Klikocka (2001); Peters et al. (2004); Baljeet et al. (2005); Cwalina-Ambroziak and Czajka (2006); Errampalli et al. (2006); Nitzan et al. (2006); Repsiene and Mineikiene (2006); Zimny et al. (2006); Henriksen et al. (2007); Raviv (2008); Wilson et al. (2008)
Rosellinia sp.	Rosellinia black rot								
Sclerotinia sclerotinium	White mold	4–5 years With cereals, grasses Without rapeseed, peas, beans			Irrigation management	Fluazinam, iprodione, thiophanate-methyl, fluazinam, boscalid			US Canola Association; Johnson and Atallah (2006); Wale et al. (2008)
Sclerotium rolfsii	Stem rot		Composted manure			Carbendazim (resistance), quintozene, mancozeb			Bisht (1982); Solunke et al. (2001); Amitava and Maiti (2006); Raviv (2008)
Spongospora subterranea	Powdery scab	Minimum 10 years, no pasture	No cow manure	No plowing in spring	Late planting date in well-drained fields	Flusulfamide, fluazinam, mancozeb			Christ (1989); Blum and Merz (1993); Zambolim et al. (1995); Falloon (1997)
Synchytrium endobioticum	Wart	Very long rotation (30 years)	urea		Planting in well-drained fields	Carbamide = urea			Derevenko et al. (1981); Hampson (1985)
Thecaphora solani	Thecaphora smut	Long rotations				Carbendazim, thiabendazol, methyl bromide and dazomet			EPPO (1990); Wale et al. (2008)
Verticillium dahliae and *Verticillium albo-atrum*	Verticillium wilt	3 years of rotation With red clover, Sudan grass, corn and Without fallow, rape, Austrian winter pea, oat, rye, mint, weeds	Ammonium lignosulfate	Minimum tillage		Mancozeb, captan, metam sodium, 1,3-dichloropropene, chloropicrine			Johnston et al. (1994); Davis et al. (1996); Soltani et al. (2002); Tsror et al. (2005); Omer et al. (2008); Wale et al. (2008)
Bacteria									
Clavibacter michiganensis ssp. *sepedonicus*	Ring rot	With onion				Flusulfamide protects against Cms	Organic		Slack and Westra (1998); Wolf et al. (2005); Repsiene and Mineikiene (2006)
Clostridium spp.	Bacterial soft rot		Neem leaf and seed aqueous extracts						Bdliya and Dahiru (2006)

Table 8 (continued)

Pathogen	Disease	Rotation	Fertiliaation and amendments	Tillage	Planting, lifting, and harvesting methods	Pesticides	Cultural systems	Storage	References
Pectobacterium atrosepticum, *Pectobacterium carotovorum* subsp. *carotovorum*, *Dickeya* spp.	Black leg, soft rot	No monoculture, rotation with wheat, red clover, barley or orchard grass	No over nitrogen		Planting in well-drained fields, rogu-ing, and elimination of infected plants/ tubers Limiting wounds	Chlorine dioxide, aluminum and bisulfite salts, naphtoquinone naphthazarin, kasugamycin, stable bleaching powder, streptocycline, benzoic acid, sodium benzoate, copper oxychloride + metalaxyl, metiram, copper oxychloride + cymoxanil, klorocin	Conventional	Early efficient and quick drying after harvesting	Bushkova et al. (1981); Khomyakov and Kostin (1981); Lewocz (1992); Saleh and Huang (1997); Karwasra and Parashar (1998); Bartz (1999); Olsen et al. (2003); Medina et al. (2004); Yaganza et al. (2004); Repsiene and Mineikiene 2006
Ralstonia solanacearum	Brown rot	Without solanaceous plants. With barley and flax	Calcium superphosphate	4 deep plowings after harvest		Tri-potassium phosphate, bleaching powder	Depends on the soil type		Kishore et al. (1996); Mahmoud (2007); Messiha et al. (2007)
Streptomyces scabiei, *S. acidiscabiei*, *S. europeiscabiei*	Common and netted scab	With lupin, soybean, winter rye or serradilla Without: sugar beet, carrots, pasture	Ammonium lignosulfate, potassium, phosphate, compost, swine manure	Subsoiling		Increased by oxamyl, 3% boric acid, streptomycin, streptomycin sulfate, daminozide, DL-ethionine	No effect		Meredith et al. (1975); Volovik et al. (1980); Hide and Read (1991); Conn and Lazarovits (1999); Park et al. (2002); Soltani et al. (2002); Chaudhari et al. (2003); Mizuno et al. (2003); Peters et al. (2004); Scholte (2005); Repsiene and Mineikiene (2006); Henriksen et al. (2007); Al-Mughrabi et al. (2008)
Nematodes									
Belonolaimus longicaudatus	Sting nematode	Without sorghm-sundangrass With cotton				1,3-dichloropropene			Crow et al. (2000); Crow et al. (2001); Perez et al. (2000)
Ditylenchus destructor	Potato rot nematode					Oxamyl			Rojancovschi (1994)
Globodera pallida, *Globodera rostochiensis*	Potato cyst nematode	Long rotations With peas, flax, rye, oat or rye grass	phosphore		Avoiding dissemination from infected fields with equipment	Dimethyl disulphide, 1,3-dichloropropene, aldicarb, phoxim, A. C. 92100, carbofuran, A.C. 64475	Conventional		Cornejo (1977); Hague et al. (1983); Mulder et al. (1997); Trifonova (1997); Ruijter and Haverkort (1999); Molendijk (1999); Minnis et al. (2004); Coosemans (2005)
Meloidogyne spp.	Root-knot nematode	With cotton, or black fallow Without most crops (carrot, beat, salsify, red clover, cereals, vegetables,..)				Methyl bromide, metham sodium, dicloropropen-cloropicrin, metham sodium + 1,3-dichloropropene, fosthiazate + metam sodium, dimethyl disulphide	No effect		Molendijk (1999); Crow et al. (2000); Carter et al. (2003); Coosemans (2005); Hafez and Sundararaj (2006); Charchar et al. (2007); Ingham et al. (2007)
Nacobbus aberrans	False root-knot nematode				Planting in June or July	Abamectin and furateocarb, A.C. 92100, aldicarb, carbofuran, A.C. 64475			Cornejo (1977); Iriarte et al. (1999); Main et al. (2001)

Table 8 (continued)

Pathogen	Disease	Rotation	Fertiliaation and amendments	Tillage	Planting, lifting, and harvesting methods	Pesticides	Cultural systems	Storage	References
Paratrichodorus and *Trichodorus* spp.	Stubby-root nematode (TRV vector)	With beet, oats, grasses Without sorghm-sundangrass or velvetbean, maize, wheat, cabbage, rape, barley				Aldicarb (+ oxamyl), 1,3-dichloropropene			Barbez (1983); Perez et al. (2000); Crow et al. (2001); Hafez and Sundararaj (2006)
Pratylenchus spp.	Root-lesion nematode	With wheat, ryegrass, without red clover				1,3-dichloropropene, oxamyl, fosthiazate, cadusafos, carbofuran	Organic		Philis (1997); Johnston et al. (1994); Molendijk (1999); Kimpinski et al. (2001); Carter et al. (2003)

the attacks of pathogens than plants at high densities (Milic et al. 2006). Diseases can be reduced by adjusting planting, dehaulming, and harvesting dates and cultivation of early tuberizing cultivars combined with pre-harvesting desiccation of haulms and treatment of seed tubers with chemicals (Sikka and Singh 1976). Black scurf development on tubers has a positive correlation with the curing period (time between haulm destruction and harvest) because infection on tubers continues in the soil even after haulm destruction (Lakra 2000).

4.5 Pesticides

Pesticides are commonly used to control various pathogens altering potato tubers. They can be applied as soil fumigant (fumigants such as carbamates are not allowed in some European countries), sprayed or powdered directly on seed tubers after harvest or applied as granular (Hide et al. 1995; Tsror et al. 2000; Errampalli et al. 2006). The chemicals have to be carefully chosen, since pathogens can adapt and become resistant (Table 8). Thiabendazole-resistance was detected in *Fusarium avenaceum*, *F. culmorum*, *F. equiseti*, and *F. sporotrichioides* (*Fusarium* dry rot; Ocamb et al. 2007), in *P. pustulans* (skin spot; Carnegie et al. 2008) and in *H. solani* (silver scurf). Mefenoxam-resistance is known for *P. erythroseptica* (pink rot) populations (Taylor et al. 2006) and numerous treatments of carbendazim select resistant mutants of *Sclerotium rolfsii* (stem rot; Solunke et al. 2001). Moreover, the use of numerous chemicals is nowadays regulated and many of them are no longer permitted in Europe.

4.6 Organic farming versus conventional agriculture

Organic farming relies on agricultural techniques that exclude the use of chemical pesticides and recommend organic fertilization. As a result, the soil and tuber environment is quite different from the one caused by conventional practices and may induce disease suppression (Table 8). To reduce disease incidence or severity, the best adapted cultural system depends on the pathogen to control and varies strongly according to the soil type (Messiha et al. 2007). It has been reported that farmers who switch from conventional to organic system faced critical pest or disease problems during a transition period of about 5 years but managed to control soil-borne diseases on the long-term (Bruggen and Termorshuizen 2003). However, organic farmers generally faced more sanitary problems than conventional farmers.

4.7 Handling and storage

Inappropriate manipulation of tubers at harvest or during storage can provoke wounds that increase diseases such as

black dot, *Fusarium* dry rots, silver scurf, gangrene, leak, pink rot, black leg, and soft rot (Meredith et al. 1975; Hide 1994; Vanvuurde and Devries 1994; Salas et al. 2000; Marcinkowska et al. 2005; Peters et al. 2008a, b; Table 8). Significant measures of managing potato diseases include: avoiding mechanical damage to potatoes during harvesting, shipping and sorting, curing the harmed parts thereby preventing infection and disease onset, avoiding manipulation of cold potato since potato tubers are more sensitive to injuries when cold, avoiding the exposure of table potato to light, and continuously providing stored potatoes with fresh air (Milosevic and Alovic 2006; Scheid 2006). Most of the storage diseases decrease when the tubers are cured in dry conditions and stored at temperature close to 4°C or 5°C, except gangrene (Table 8). Once again, for storage as for production, a balance between biotic and abiotic conditions should be carefully setup to preserve yield and quality. Indeed, despite they have less infection when stored in a dry atmosphere, tubers show greater weight losses than when they are stored in a humid atmosphere (Lennard 1980).

5 Disease management

5.1 Risk assessment and decision support systems

Disease occurrence and development influenced by abiotic and biotic factors are difficult to predict. However, their prediction would be very useful to assess disease risk and consequently the potential yield loss and to choose the best disease control strategy. Current methods to evaluate yield losses are based on predictive models which commonly assign a value or score to each risk factor, such as cultivar resistance, inoculum density, cultural practices, and environmental factors. The maximum score that can be assigned to each factor depends on the relative importance of the factor in determining the disease. For example, cultivar resistance is considered to be a major determinant of powdery scab severity, so this factor has a higher score than the zinc content of soil, which is thought to be less important (Burgess and Wale 1994). Assessment of the risk for each factor and for each disease is performed by bioassays in fields or in growth chambers under controlled conditions. They are generally laborious, time consuming, and costly.

Tolerant cultivars are a particular risk factor in potato production as they can maintain and increase the inoculum level in fields (Merz and Falloon 2009). A tolerance threshold of the crop has to be determined. It takes into account the relationship between inoculum density and disease incidence or severity according to cultivar resistance (Table 4).

A score can also be attributed to each cultural practice in the equation of the model since they have various impacts on yield losses. For example, incidence and severity of *Verticillium* wilt decrease with long rotations (Johnston et al. 1994), but mint as a previous crop increases *Verticillium* wilt (Omer et al. 2008). Consequently, in the equation of the model, rotation length will be negatively correlated to yield losses whereas mint as previous crop will be positively correlated to yield losses due to *Verticillium* wilt.

On the same pattern, some predictable environmental factors such as nutrient contents and soil pH can be scored. However, abiotic environmental factors are difficult to predict. For example, at planting time, rainfall and temperature conditions occurring at the critical growth phase of the disease are almost impossible to foresee. As climatic conditions cannot be predicted at middle term, models of risk assessment are less reliable. However, no factor alone has a dramatic effect on the disease; and the beneficial reduction of a disease is usually achieved by the sum of optimized factors (Harrison 1997).

Mathematical modeling including all the data related to the environmental factors and to the results concerning

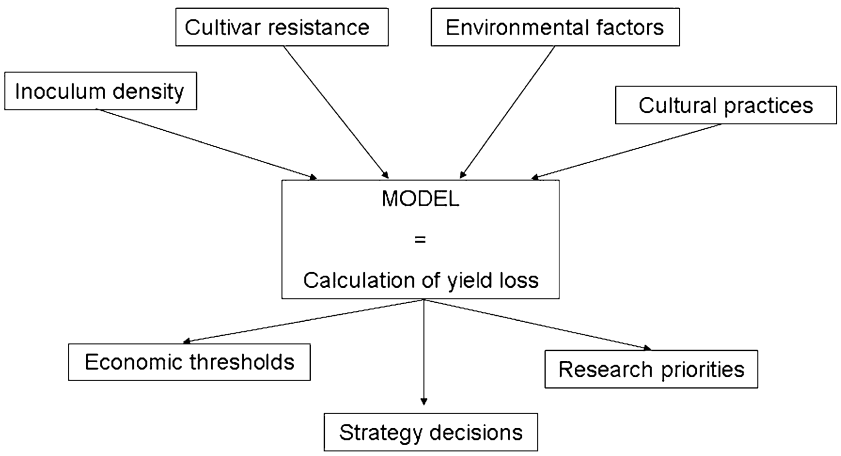

Fig. 2 Input and output parameters of yield loss calculation models

plant resistance appeared to be helpful to evaluate risk, to overcome the scaling gap between bioassays in growth chamber and field application and to simulate scenario based on crop management (Janvier et al. 2007).

Calculation of yield losses enables to identify a damage threshold and to determine the time at which disease control must be initiated. Indeed, yield loss threshold and economic threshold are different. Economic threshold is frequently higher than yield loss threshold; because up to a certain point, losing yield is less penalizing for farmers than spending money to avoid it. Calculation of economic thresholds beyond which control of diseases is profitable takes into account a damage function drift to potato yield, pathogen population density, and crop selling prices. For example, application of control measures is found to be beneficial at an initial density of *G. rostochiensis* higher than eight eggs and larvae per gram of soil, while the damage threshold is at two eggs per gram of soil (Samaliev and Andreev 1998). Economic thresholds allow taking short-term strategic decisions such as choice of the cultivar, cultural practices, timing of crop establishment, seed treatment, planting density, etc. and long-term strategic decisions such as define research priorities, design the breeding programs, or develop integrated pest management strategies (Savary et al. 2006) (Fig. 2). Predicting models are used by farmers as decision support systems (DSS) and generally provide a theoretical yield to be obtained at the end of the cropping period, a monitoring of pest populations and comments and advices in order to increase the theoretical yield as much as possible (Been et al. 2005; Jorg et al. 2006). Some DSS are able to send real time alerts to farmers when several risk factors are combined and when control measures have to be taken immediately (Dubois and Duvauchelle 2004). DSS are environmental and farmer friendly as they enable to increase economical yields by applying the right chemical doses at the right time and when disease pressure requires it, in order to reduce unnecessary environmental pollutions and treatment cost.

5.2 Control methods

Ways to control diseases are evolving since the use of chemicals is supposed to be reduced. In many cases, the most efficient long-term strategy is to use resistant cultivars when available. Otherwise, management strategies consist either in exclusion, avoiding contact between plant and pathogens, or by pest eradication, and leading to complete elimination or partial reduction of pathogen populations.

For the potato crop which is multiplied vegetatively, exclusion methods begin with the use of healthy tubers. Many soil-borne pathogens can be carried on by seed tubers and the use of certified seed potatoes is a major way to control or restrict the movement of pathogens of potato crops (Andrade et al. 2008). Seed certification programs aim at warranting seed tuber quality to potato producers and favor the diffusion of genetic progress. The certified seed production process may be 8–10 years long. Strict rules established by the national regulation institutions (i.e., National Potato Council in USA or Groupement National Interprofessionnel des Semences-Service Officiel de Contrôle in France) have to be respected and the seeds are regularly inspected for bacterial, viral, and fungal diseases, as well as varietal purity and identity. Each country is free to apply more or less severe rules. Certification systems have been developed in most of the seed producing countries to cover the production of certified seed potatoes free from pathogens and pests (McDonald 1995; Grousset and Smith 1998; Sahajdak and Uznanska 2003). An international project of commercial and phytosanitary minimal guidelines (CEE-ONU S-1) is in progress. It is intended to serve as a minimal base consensus between the various standards established at ”regional” levels (EU, NATTO, etc.; UNECE 2010).

Eradication strategies aim at eliminating an established pathogen from plant propagation material or production sites. Eradication methods involve the use of pesticides, adapted cultural practices or biological control. Application of fungicides and nematicides are protecting strategies (see Section 4.5 and Table 8) whose application time and doses can be advised by DSS. However, pesticides are sometimes inefficient against pathogens, such as *Pectobacterium carotovorum* (Latour et al. 2008), or their use is limited by environmental regulations. Consequently, alternative methods based on adapted cultural practices have to be recommended (see Section 4 and Tables 3 and 8). Some crops either susceptible or resistant may serve as baiting crop, for example, resistant potato cultivars cropped just before the main potato crop decreased black scurf (Scholte 2000). Likewise, alfalfa can be used to avoid TRV transmitted by stubby root nematode, as this crop is a host for stubby root nematode but immune to TRV (Stevenson et al. 2001). Cultivar precocity can be used to avoid some diseases. Since black dot and charcoal rot damages occur late in the growing season, early cultivars are generally recommended to control these diseases (Stevenson et al. 2001). When a disease is established in a production site, its spread must be avoided as much as possible. All diseased plants have to be eliminated or burned and tools should be properly disinfected before use in another field (Salas et al. 2000; Latour et al. 2008).

Natural interactions of plants and microorganisms with the pathogens are used as biological control to protect potato crops. There is a continuum from a conducive soil to a suppressive one (Alabouvette et al. 1996) what means that in each soil, almost each pathogen can be potentially controlled by other microorganisms either by a specific

antagonism or by competition with total microbial biomass (see Section 3.2 and Table 6). Appropriate agricultural practices, thanks to the DSS, should stimulate this potential to enhance or to maintain the soil suppressiveness to potato diseases.

Another approach consists in applying biocontrol agents. However, the choice of a biological control agent must take into account the potential risks to human health. Even if *Serratia grimesii* and *Burkholderia cepacia* decrease dry rot and black scurf and stem canker, respectively, they can cause human infections and are not recommended for biological control (Table 6; Grosch et al. 2005; Gould et al. 2008). Moreover, indirect control such as strengthening of potato plants by mycorhization increases tuber yield and allow an integrated management of potato cyst nematode and root-knot nematode (Sankaranarayanan and Sundarababu 2001; Ryan et al. 2003). Biological control may also include the use of natural toxic compounds for pathogenic agents. Fumigation of essential oils is studied to control dry rot, gangrene, black scurf, and stem canker (Bang 2007). Fish emulsion and crushed crab shell are used against *Verticillium dahliae*, *Verticillium albo-atrum*, and *S. endobioticum*, respectively (Hampson and Coombes 1995; Abbasi et al. 2006). Soil can be disinfected from pathogens by biofumigation or solar heating or both. For example, *Brassica* crops used in crop rotations and as green manure have been associated with reductions in soil-borne pests and pathogens. These reductions have been attributed to the production of volatile sulfur compounds through the process of biofumigation and to changes in soil microbial community structure (Janvier et al. 2007). Composting is also a sanitizing method which combines temperature, time, and toxic compounds to control potato diseases. The composts the most frequently used on potato crop are organic wastes (sludge, manure, tea, etc.) that have undergone long, thermophilic and, aerobic decomposition. The most effective compost composition and combinations of temperature and time have to be determined for each pathogen. As it decreases the pathogenic population and/or favors microbial enrichment of the soil, compost has generally a positive or neutral effect on disease suppression and only rarely a disease stimulating effect (Termorshuizen et al. 2006). Sanitization is also performed on tubers before planting by hot water (Janvier et al. 2007) or during storage with chemical treatments at high temperatures (Secor et al. 1988). However, heating may damage tubers resulting in fewer sprouts. Biocontrol can also be performed by disrupting pathogens molecular pathways. *P. carotovorum* quorum-sensing mechanism is controlled by a quorum-quenching strategy aiming at interrupting the quorum-sensing by using compounds or organisms able to cause interferences in the bacterial signal (Latour et al. 2008). Finally, it is also possible to enhance plant defense reactions against soil-borne pathogens by foliar spraying with different inducers such as salicylic acid, di-potassium hydrogen phosphate, and tri-potassium phosphate (Mahmoud 2007).

The different methods that were presented above are not items that have to be taken at random. Their combination generally gives better results than each of the method applied alone.

Decision support systems developed to predict yield losses allow choosing good control methods such as the use of healthy seeds, adapted pesticides, cultural practices, and biological control agents for each potato diseases.

6 Conclusions

If a disease results from the interaction between the plant and a pathogen, its severity is influenced by soil abiotic and biotic factors affecting the plant, the pathogen, or both (Alabouvette et al. 1996). Biotic and abiotic factors are not independent, the abiotic factors modulating the biotic ones. They act both on the disease epidemiology, that means the environmental conditions which make the plant growing and the pathogen, present or latent on the crop, causing or not the disease. Moreover, some unfavorable factors for a given disease can be favorable to another. The multifaceted interactions between plants, pathogens and their environment make disease management complex since controlling every factor occurring in the disease development is quite impossible. Potato producers have to aim at limiting contact between plant and pathogens by using for example healthy seeds. Moreover, pathosystems are continuously changing since the pathogens genetically adapt to their hosts or to the environmental conditions implemented by human activities or not. In a system whose parameters vary continuously, the control strategies have to be adapted to each situation at every time.

This review aimed at being as exhaustive as possible about the factors impacting the occurrence and development of the soil-borne potato diseases. Such a work putting in relation numerous potato diseases and comparing their development conditions, the ecology of the causal pathogens and their abiotic and biotic interactions responds to a clear demand from both scientists, extension services, breeders, and farmers. Studies dealing with potato diseases frequently consider only one or few diseases at the same time. Thus, this review constitutes by itself a decision support system since the optimal factors limiting disease development are listed. Nevertheless, the data collected here deal more with diseases known in developed counties and those which cause severe economical losses. Knowledge about minor diseases such as *Phoma* leaf spot, *Rosellinia* black rot, and *Thecaphora* smut are extremely rare, probably because these diseases occur in very isolated areas. *Phoma* leaf spot was

recorded only in Bolivia and Peru, *Rosellinia* black rot was described in South America and Africa, and *Thecaphora* smut in South America and Mexico.

Moreover, soil-borne diseases are difficult to study because soil is a complex environment in which numerous interactions occur and where detection of pathogens is not easily performed. However, researches on those diseases could be beneficial at long-term in case they would spread throughout the world. It would have been rather complex to consider air-borne diseases in addition to soil-borne diseases of potato. However, air-borne diseases such as late blight caused by *Phytophthora infestans* and early blight caused by *Alternaria solani* are responsible for huge economical losses and have to be considered with as much attention as soil-borne diseases. Finally, since few years, importance of potato tuber quality raised in developed countries where tubers are washed before selling. Indeed, washing tuber makes visible some superficial blemishes that were previously hidden by adhering soil. Consumer's habits changing, blemished tubers cannot be sold anymore and the losses take seriously damaging proportions for potato market.

The previous considerations acknowledge the fact that the plant disease problem can be reduced in short term thanks to solid knowledge in epidemiology and pathogens ecology; but in longer term, control strategies must be adapted with the constant evolution of pathosystems.

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