

Leibniz
Universität
Hannover



Reactions of starch potato to *Alternaria* leaf spot disease

Research Thesis Proposal

By

Ayman Hosny Mohamed

Institute of Horticulture Production

Supervisors:

Prof. Dr. Traud Winkelmann

Dr. Christin Bündig

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ABSTRACT

The potato was ranked by the Food and Agriculture Organization of the United Nations (FAO) as the world's fourth most important food plant with a total production of three-hundred million tons and total planted area of nineteen million hectares. Potato is affordable staple food for over one billion people. Potato is a crop of considerable nutritional significance, rich source of carbohydrates, provides good amount of essential amino acids, vitamins, minerals, and resistant starch of prebiotic benefits. Moreover, the high content of starch in potato makes it a crop of crucial industrial importance.

Fungal diseases as biotic stressors are very common in almost all potato varieties worldwide. Early blight is a fungal infection mainly triggered by *Alternaria alternata* and *Alternaria solani*, which viciously attacks potato-growing areas in Europe and inflicts serious reduction on tubers yield and quality. When the environmental conditions are in favor of the pathogen with no or poor agronomic control, total defoliation of a potato field can be reached in less than week. The chemical control is so far the main method to partially contain the disease, which is neither cost efficient nor environmentally friendly, thus breeding for resistance and biological control for early blight are two solutions of high demand.

The full production potential of potato cultivars can be achieved by over-coming the threat of biotic and abiotic stresses. As part of the planned project AiPPARENT, the effect of combined stresses, namely drought and leaf spot infection, will be analyzed. To enable this, this study aims at comprehensive understanding of the morphological, histological and proteomic reactions of commercial potato varieties (Bintje and Norvarno) to different isolates of *Alternaria alternata* and *Alternaria solani*.

An inoculation protocol will be optimized by variation of plant parts and inoculum concentrations. This protocol will be then used to inoculate potato genotypes in vitro to assess their reaction by taking photos to be investigated by special software and by histological analysis.

The differentially abundant proteins revealed by proteomic comparison could contain potential biomarkers for resistance to early blight.

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INTRODUCTION

Potatoes (*Solanum tuberosum*) are the most important non-cereal crop in the world and are a significant part of the diet of over 1.5 billion people across the globe (Vreugdenhil et al., 2007) with total planted area of approximately 19.26 million hectares worldwide (STATISTA 2017) and around 385.07 million metric tons of production (STATISTA 2017) Fig. 1. The starch content of potatoes is widely used for industrial processes, such as in the production of paper, glue, building materials, plastics, pharmaceuticals and bio-fuel (Roper, 1996; Liang and McDonald 2014).

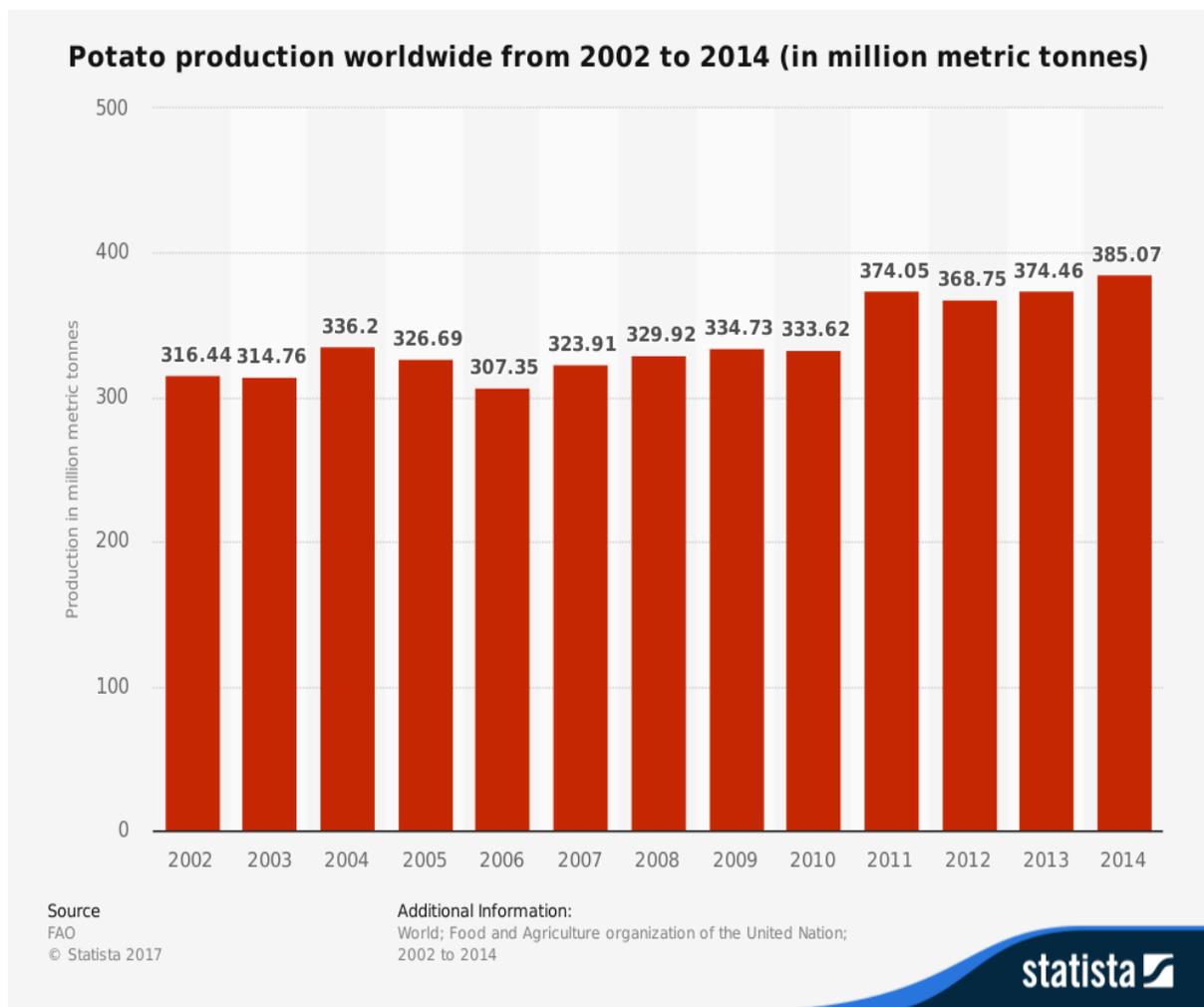


Figure 1 World potato production, 2002-2014 (Source STATISTA 2017) (accessed 26 Dec. 2017)

World food supplies are tightening and there is no balance between food production and population growth (Brown, 1981). Despite the continued expansion of the world population and the limitation of the available resources needed to produce food, global warming and climate changes linked with it, output abiotic and biotic stress combinations, which sorely affect crop

production (Mittler, 2006; Prasad et al., 2011; Atkinson et al., 2013; Narsai et al., 2013; Prasad and Sonnewald, 2013; Suzuki et al., 2014; Mahalingam, 2015; Pandey et al., 2015; Ramegowda and Senthil-Kumar, 2015). Regarding biotic stresses, *Alternaria* species most importantly *A. alternata* (Ardestani et al., 2010) and *A. solani* (van der Waals et al., 2004) are crucial fungal pathogens affecting potato production (Shtienberg & Blachinsky, 1996; Ardestani et al., 2010). The symptoms of alternaria leaf spot appear initially as brown spots on basal leaves and spread progressively to upper leaves. Spots eventually agglomerate, and the infected leaves dry up (Lagopodi & Thanassouloupoulos, 1998).

Alternaria solani causes early blight of potato species (van der Waals et al., 2004). Additionally, *Alternaria alternata* was reported to cause brown spot on potato leaves in Israel (Droby et al., 1984).

Both *A. solani* and *A. alternata* can cause foliar diseases on potato in Germany (Leiminger et al., 2014) and different European countries (Hansen et al., 2016)

The objectives of this project are to study the morphological, histological and proteomic plant reactions of different starch potato genotypes to *Alternaria spp.* as biotic stress. Hence, this study will pave the way for later documentation of combinational stress reactions of the *Alternaria* leaf spot and drought stress.

2 LITERATURE REVIEW

2.1 Introduction of *Solanum tuberosum*

The preliminary introduction of the potato in Europe was to the Canary Islands in 1567 (Hawkes and Francisco-Ortega, 1993). It was recorded that, potato was fed to patients in the Carmelite hospital in Seville, Spain with noteworthy therapeutic results. Accordingly, speculating that potatoes were grown in some way and acknowledged as medicinal food within a few years after its introduction is possible (Salaman, 1949). Gaspard Bauhin or “Caspar Bauhin” is a famous Swiss botanist who was the first to name the potato “*solanum tuberosum esculentum*” (Hawkes 1956). In German, the potato was called “kartoffel”, a possible sound-alike of tartouffli. In Swiss, it was called erdäpfel, while in Italian it was called truffe, or tartouffli. In France, it became known as “pomme de terre”, and in the Netherlands aardappel (Navarre and Pavék 2014).

2.1.1 Botanical characterization and distribution

Taxonomy of the genus *Solanum*

Classifications of the family typically recognized two subfamilies, *Cestroideae* and *Solanoideae* (D’Arcy, 1979, 1991; Hunziker, 1979, 2001; Olmstead & Palmer 1992). An additional subfamily, *Nolanoideae*, has been segregated by some taxonomists as a distinct family, *Nolanaceae* (Cronquist, 1981; Thorne, 1992; Hunziker, 2001). *Solanum* is categorized within the subfamily *Solanoideae* and considered as one of the largest genera of family *Solanaceae* of an estimate of 1500 species, 1000 of which are contemplated to be originated in America (Hunziker, 1979; Frodin 2004; Bohs 2001). Tuber and non-tuber bearing *Solanum* are categorized within two subsections of section *Potatoe*, *Potatoe* and *Estolonifera* (Hawkes 1990). The subsection *Potatoe* contains all tuber-bearing potatoes, including common potato *S. tuberosum*. Moreover, *Solanum* species have been a material of many taxonomical studies (Hawkes 1956; Heiser et al. 1965; Bohs and Olmstead 2001; Bohs 2005; Levin et al., 2006; Weese and Bohs 2007; Vorontsova and Knapp 2012). *S. tuberosum* the focus of this study is divided into two subspecies *tuberosum* and *andigena*. The subspecies *tuberosum* is the cultivated potato in North America and Europe for example. Furthermore, subspecies *andigena* also contains cultivated

species, but cultivation is restricted to Central and South America (Hawkes, 1990; Hanneman, 1994).

Geographical distribution and wild species

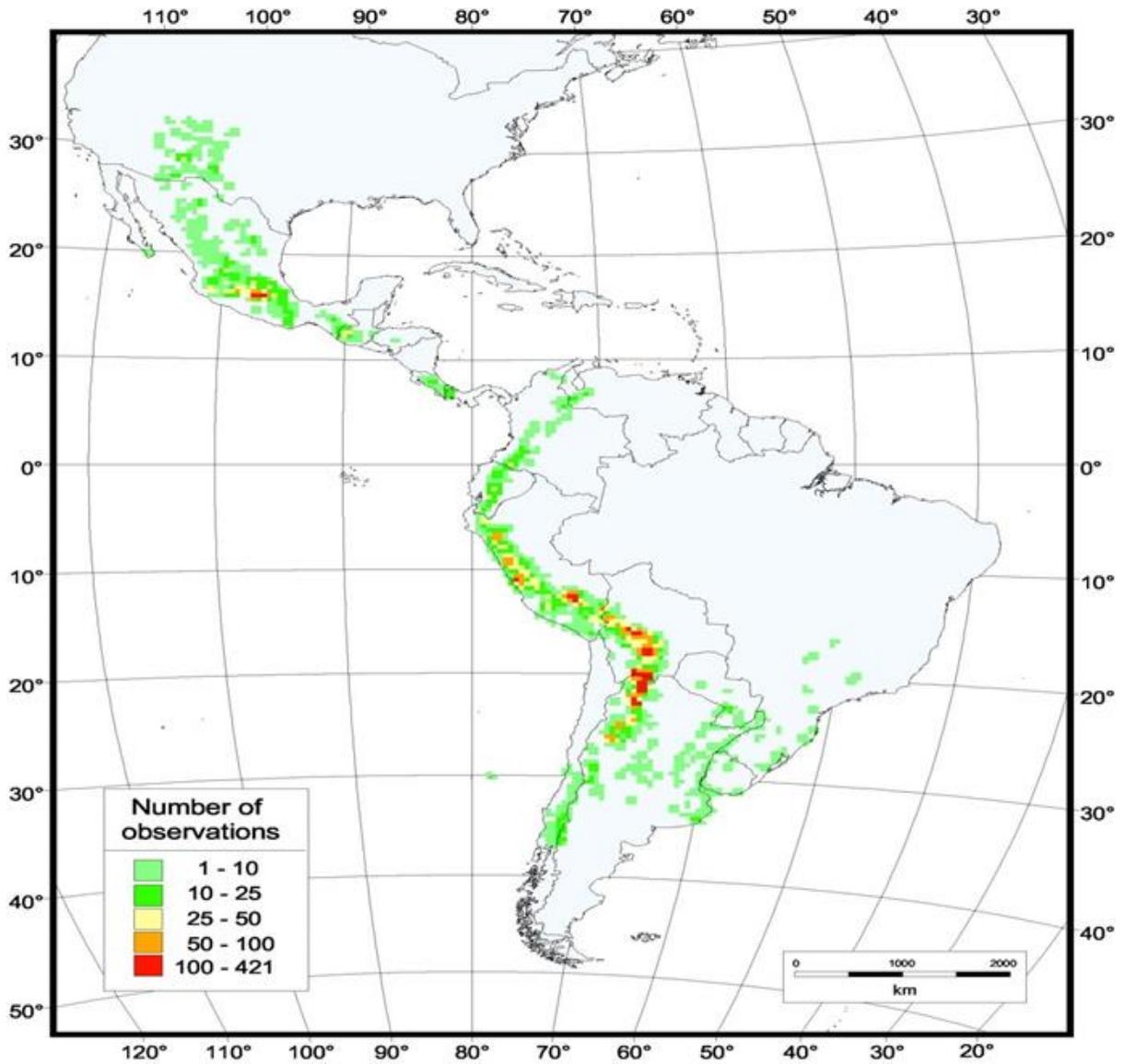


Figure 2 Number of observations of wild potato species per 50×50 km grid cell. A circular neighborhood with a radius of 50 km was used to assign observations to a grid cell. There are 1317 grid cells with observations (Hijmans & Spooner 2001).

Species within the genus *Solanum* that form more than 1000 members (D'Arcy 1991; Burton 1989) are distributed in different continents around the world Fig. 2. *Solanum* contains several crops of high economic importance (Bohs 2005; Weese & Bohs 2007) prominently, potato *Solanum tuberosum* which occur in 16 countries as a wild type, 88% of the observations are from Argentina, Bolivia, Mexico, and Peru (Hijmans 2001). Some wild *Solanum* species can tolerate

zero temperature or even below (*S. acaule* and *S. megistacrolobum*), on another extreme, *S. berthaultii*, *S. neocardenasii*, and *S. gracilifrons* are species adapted to hot and dry conditions (Hawkes 1990). These adaptations to a wide range of habitats have made the wild species tolerant to different environmental stresses and resistant to a broad range of pests and diseases (Hawkes 1994).

Morphology

S. tuberosum subsp. *tuberosum* is a herbaceous perennial with weak stems that grow to about 60 cm in length and vary according to the variety. They carry pink, purple, red, white or blue flowers with yellow short-filaments stamens and long pinnate spirally arranged leaves. The fruits are spherical yellowish or green, significantly variable in seed content and less than one inch in diameter (Anonymous, 1996; Hawkes, 1990).

A typical potato leaf consists of mid-rib, on which, two to four pairs of primary leaflets and secondary leaflets positioned between the primary ones in an irregular form are found. Tiny unobtrusive tertiary leaflets can also be noticed along the mid-rib which is attached to the plant by a petiole (McCauley et al., 1988).

A potato plant consists of a variable number of main stems, which will exhibit a variable degree of branching depending on genotype, physiological age of the mother tuber and environmental conditions. The growth nature of each individual stem is certain: it produces leaves and completes its development with forming a primary inflorescence (Danert, 1957; Almekinders & Struik, 1994).

Potato inflorescences are single or compound cymes and the number of flowers per inflorescence and per cyme depends on the genotype, the environment and the position of the inflorescence in the shoot system (Almekinders & Wiersema, 1991; Almekinders & Struik, 1994). Tubers are located at the end of stolons under the soil surface which are true stems, not roots. The general appearance of tubers are white or cream to yellow color, the skin of the tuber is light brownish to red (Hawkes 1988 and 1994).

Potato tubers are the only edible part of the plant and are greatly shortened and thickened stems that bear scale leaves, each one with a bud in its axil (Ewing and Struik 1992). The stolons are modified lateral shoots, usually developed from the basal nodes of the main and secondary

stems “branching from the basal part of the main stem”. Environmental factors, such as temperature, nutrients and water availability and darkness have a pronounced effect on stolon development (Clark 1921; Booth 1959 and 1963).

When the physiological maturity of a potato tubers is reached, potato tubers may enter a state of dormancy. Dormancy define as the physiological state of the tuber in which even when placed in optimum germination conditions it does not sprout (Reust 1986; Sonnewald and Sonnewald, 2014). Various parameters of potato tuber dormancy have been described. The duration of innate dormancy depends largely on the cultivar and to some extent on the conditions during tuber growth (Davidson 1958; Lindblom 1970; Burton 1978; Harkett 1981).

Tuberization is a complex developmental process that requires the interaction of environmental, biochemical, and genetic factors (Kolomiets et al. 2001). Regarding the biochemical factors, different important hormones for tuber induction ex. gibberellic acid (GA), cytokinin, jasmonic acid and related compounds, or abscisic acid (ABA) were reviewed in many studies (Ewing and Struik 1992; Ivana et al., 1997; Xu et al., 1998; Suttle, 2004).

2.1.2 Breeding, propagation and production

Breeding & Propagation

Potato species constitute a polyploid series ranging from diploids ($2n=2x=24$) to hexaploids ($2n=6x=72$) however, most potato cultivars are tetraploids (Douches and Jastrzebski 1993; Carputo et al. 2003). Modern potato breeding began in England with hybridization between varieties using artificial pollination (Knight 1807) and it burgeoned between the nineteenth and twentieth centuries where many new cultivars were produced (Vreugdenhil and Bradshaw 2007). In the World Catalogue of Potato more than 4500 varieties are registered (Pieterse and Hils 2009; Pieterse and Judd 2014).

The variability and adaptability of wild potato types to different environmental conditions, both gave the ability to the cultivated potato species to be grown in short and long days climates and survive relatively high and low temperatures (Hawkes 1990).

Potato traditional breeding is time intensive and complicated process due to many facts, most notably: Many wild potato species are cross-incompatible with each other and with *S. tuberosum* cultivars (Hermsen, 1978; Pandey, 1962). $2n$ gametes are common in wild *Solanum*

species, they likely contributed to the production of spontaneous tetraploids (Marks, 1966; Quinn et al., 1974). Tetraploid Potato species are highly heterozygous and tetrasomic in nature and suffer inbreeding depression upon selfing (Bradshaw, 2006; Muthoni et al., 2015). The selection cycle, from initial crosses to variety release, requires approximately 10 years or sometimes more than 30 years (Gebhardt 2013, Haverkort et al. 2009).

Potato can be propagated vegetatively by tubers, tissue culture and by cuttings (Harris 1978), Also can propagate sexually by what so called “TPS” or true potato seed (Pallais 1991).

While diploid wild species are often self-incompatible (Hosaka and Hanneman 1998, Pal and Nath 1942), the tetraploid cultivars and polyploidy species are self-compatible (Hawkes, 1990). Moreover, many polyploidy species are disomic polyploids with a selfing nature, but they have the potential to produce selfed true seed and tubers (Watanabe et al., 1994).

Nevertheless, crossing of incompatible potato species may also be achieved using polyploidy manipulation and different special techniques such as, embryo rescue and rescue pollination (Valkonen et al., 1995; Watanabe et al., 1995).

There is a continuing need for new improved potato cultivars to combine high levels of durable disease and pest resistance with acceptable yields and the quality demanded by processors and supermarkets (Bradshaw et al. 1998). Furthermore, Haverkort and Verhagen (2008) reviewed the likely consequences of climate change on potato production based on the International Panel on Climate Change report (IPCC, 2007) hence, breeding for drought and heat tolerance are of a great importance because of the adverse effect of high temperatures on irrigation water availability and tuberization (Bradshaw, 2010).

Recent research projects are aiming for marker assisted breeding, protoplast fusion, genetic mapping and transcriptome data as the next mean of practicing breeding on potato cultivars.

The Solanaceae Coordinated Agricultural Project (SolCAP) developed an Infinium SNP array with 8303 SNPs (Felcher et al., 2012; Hamilton et al., 2011), which is used to examine population structure, diversity, and heterozygosity in a panel of 250 clones (SolCAP Diversity Panel) representing a wide-range of cultivars, including historical and recently released cultivars, advanced breeding lines, and many wild species (Hirsch et al., 2013).

One recent approach to sequence the potato genome was done by Xu et al., (2011), they sequenced a unique doubled-monoploid potato clone and were succeeded to generate a high-quality draft potato genome sequence which provides better understanding for eudicot genome evolution. Using a combination of data from the vigorous, heterozygous diploid RH “*S. tuberosum* group Tuberosum RH89-039-16” and relatively weak, doubled-monoploid DM “*S. tuberosum* group Phureja DM1-3 516 R44”

2.1.3 Potato production & economic relevance

Ninety three percent of the world’s potatoes are grown in the northern hemisphere (Hijmans, 2001). The two-major global potato production zones are temperate climates with a latitude between 45°N and 57°N, where potato varieties are grown as a summer crop, such as Western and Eastern Europe, northern China, northern USA, and southern Canada, and subtropical lowlands with a latitude between 23°N and 34°N, where potato varieties are grown as a winter crop, such as the Ganges plain, southern China, southern USA, northern Mexico, and Egypt (Hijmans, 2001).

Potatoes can be grown at different temperatures, ideally, average daily temperature range below 21°C and above 5°C, and another requirement is adequate water from rain or irrigation (Gopal and Khurana, 2006).

S. tuberosum species can be successfully grown under very diverse environmental conditions however general parameters can be determined for the cultivation, some of which are:

- The *S. tuberosum* subsp. *tuberosum* tuber cannot survive -3°C and lower temperature as the leaves die at -4°C (van Swaaij et al., 1987). Potato tubers are destroyed by a frost period of 25 hours at -2°C or a frost period of 5 hours at -10°C (Dale 1992).
- Potatoes are very sensitive to soil water deficiency and can tolerate a wide range of soil pH, normally 5 and higher but good production was observed at a pH of 3.7 (Vayda, 1994; Ackerson et al., 1977; Epstein and Grant 1973).
- Short days <14 hours and moderate ground temperatures (15-18°) enhance tuber formation. Longer days (14-16 hours) and higher (day) temperatures (20-25°) enhance flowering and seed formation (Beukema and van der Zaag, 1979; Burton, 1989).
- As potatoes have a shallow root system in comparison to other crops (Iwama and Yamaguchi 2006; Iwama 2008), a comprehensive fertilization management especially regarding nitrogen

and phosphorus is essential for high tuber yield and quality (Ojala et al., 1990; Rosen et al., 2014).

The commercial value of potatoes is increased considerably when they are processed into edible products that appeal to consumers on flavor, texture, appearance, and most of all convenience (Kirkman, 2007). In industrialized countries, direct consumption of potatoes has greatly declined, whereas consumption of potato products (e.g. chips) has increased. For example, in Germany consumption of fresh potatoes declined from 87 kg/cap/year in 1971 to 42 kg/cap/year in 1999, however during the same period consumption of potato products increased from 14 kg/cap/year to 29 kg/cap/year (OECD 2015).

Since the first potato starch plant was established in the USA in the 1830s (Treadway, 1962), the industry has developed in North America and Europe, particularly in the Netherlands, Poland, France, and Germany (Burton, 1989). Today potato starch is the starting material for the preparation of more than 500 different commercial products (Davies, 2002).

Pests & diseases

Some important insects that commonly transmit potato diseases or damage the plants include:

Potato tuber moth (PTM, *Phthorimaea operculella* Zeller): is one of the most damaging pests of potatoes in field and storage and is generally of greatest importance in warmer climates (Raman 1988)

Colorado potato beetle (*Leptinotarsa decemlineata*): is one of the most serious insect pest and considered as threat to potato crops in most potato-growing areas of the world (Weber and Ferro 1994)

Andean potato weevil (*Premnotrypes* spp.), are the most important insect pests of potatoes throughout the Andean region (Parsa et al., 2006).

Cyst nematodes (*Globodera pallida* and *G. rostochiensis*): which penetrate and feed on roots are most damaging nematodes worldwide (Di Vito et al., 1982).

Diseases to which potato varieties are susceptible to can be fungal, bacterial and viral diseases. Potato crop can be affected by approximately 160 diseases and disorders of which 50 are caused by fungi, 10 by bacteria, 40 by viruses and others by non-parasitic, or due to unknown causes. (Arora & Khurana 2004).

Fungi produce various secondary metabolites (SMs) which affect their host plants at different stages of pathogenesis (Berestetskiy, 2008; Friesen et al., 2008a,b; Meena et al., 2015).

Late blight is one of the most important fungal diseases which is caused by *Phytophthora infestans* which devastated potato production for the last century and a half, it has been claimed that, it is the most important potato disease in the world (Niederhauser 1993). late blight has been reviewed in detail by Ehrlich and Ehrlich (1966) and Akino et al. (2014).

Early blight which occurs in in Asia, Africa, Australia, Europe, North, Central and South America (Miller 1978) and caused by *Alternaria solani* (Harrison 1974; Rotem 1981). The first reference to the fungus as a parasite and its association with potato leaf blight was by Galloway (1891) in Australia.



Figure 3 Pathogenicity of the representative isolates of three *Alternaria* species on detached potato leaflets. (a,b) *A. tenuissima*; (c,d) *A. alternata*; (e,f) *A. solani*; (a,c,e) upper surface; (b,d,f) lower surface. The experiment was conducted using detached apical leaflets of the compound leaves from 45-day-old plants of potato cv. Favorite. A drop of 20 μ L spore suspension was inoculated on the upper surface of each leaflet (one point per leaflet). Disease severity (DS) was scored on a 4-point rating system after 7 days incubation at 25°C and 90% relative humidity (Zheng et al., 2015).

With special focus on *Alternaria spp.* causing fungal diseases, the eight *Alternaria* species documented to cause potato foliar diseases worldwide comprise *A. solani* (van der Waals et al.,

2004), *A. alternata*, *A. tenuissima* (Fig. 3 a,b), *A. dumosa*, *A. arborescens*, *A. infectoria* (Ardestani et al., 2010), *A. grandis* (Rodrigues et al., 2010) and *A. interrupta* (Taheri et al., 2009). *Alternaria solani* causes early blight of potato and other *Solanum* crop species (van der Waals et al., 2004) (fig. 3 e,f). *Alternaria alternata* was reported to cause brown spot on potato leaves in Israel (Droby et al., 1984). *Alternaria grandis* has been recorded as the cause of early blight on potato in Brazil (Rodrigues et al., 2010). In addition, *A. tenuissima*, *A. dumosa*, *A. arborescens*, *A. infectoria* and *A. interrupta* have been reported to cause potato leaf spot in Iran (Ardestani et al., 2010). Brown leaf spot disease caused by (*Alternaria alternata*) (Fig. 3 c,d) is one of the destructive and common diseases of the cultivated potato particularly in areas with frequent rainfall and high relative humidity (Nash and Gardner 1988). This disease progressively weakens the plant and increases its susceptibility to infection as it reduces the photosynthetic leaf area and increases the imbalance between nutrient demand in the tubers and nutrient supply from the leaves, subsequently leading to reduced yields (Simmons 2000).

2.2 Biology of *Alternaria* spp.

2.2.1 Morphology of *Alternaria* spp.

Conidiophores of the majority of the *Alternaria* species produce asexual spores (conidia) measuring between 160 and 200 μm long (Mamgain et al., 2013).

The key taxonomic feature of the genus *Alternaria* is the production of large, multicellular, dark-colored conidia with longitudinal as well as transverse septa. These conidia are broadest near the base and gradually taper to an elongated beak, providing a club-like appearance (Fig. 4) (Singh Saharan 2016).

According to a recent study by Zheng et al. (2015), potato leaves with disease symptoms were collected from 193 locations in 16 provinces, autonomous regions or municipalities in China. A small piece of leaf tissue (5×5 mm) was taken from the margin of a lesion, surface disinfected with 0.3% sodium hypochlorite for 2 min and 70% ethanol for 40s, rinsed with sterile distilled water three times and placed onto Petri dishes containing potato dextrose agar (PDA) amended with streptomycin sulphate (50 mg L^{-1}). The PDA plates were incubated for 7 days at 25°C in the dark. Multiple fungal colonies were obtained from each leaf lesion and only those

with different morphologies were selected as individual isolates. One hundred and eighty-two *Alternaria* isolates were classified into three morphological groups: *A. tenuissima* (A-ten), *A. alternata* (A-alt) and *A. solani* (A-sol).

Spore suspensions of the three smallspored *Alternaria* species were harvested by flooding the cultures on PDA “potato carrot agar” plates with sterile distilled water, gently scraping the colony surface and collecting the suspension. After filtering through four layers of cheesecloth, the spore suspension was adjusted to 10^6 conidia mL^{-1} using a haemocytometer.

For preparation of spore suspensions of *A. solani*, the mycelium of the test isolates were incubated on V8 juice agar for 7 days in the dark at 22°C and were then transferred to a growth chamber with a 16 h light cycle at 20°C (Langsdorf et al., 1990). After removing the aerial mycelium with a brush, spores were collected 2 days later from the cultures and spore suspensions were prepared following the same steps as for the small spored *Alternaria* species. The sporulation patterns on PCA plates also differed accordingly among the groups (Fig. 4 d,e,f).

A hundred and ten isolates were attributed to group A-ten, developing loose cottony and greyish-green to olive brown colonies on PDA plates, these isolates were characterized by formation of unbranched conidial chains up to 12 conidia in length with one or two lateral branches on PCA plates. Conidiophores were short, arising singly, $16.0\text{-}71.2\ \mu\text{m}$ long and $2.6\text{-}6.2\ \mu\text{m}$ wide. The conidia were $22.5\text{-}43.4 \times 8.2\text{-}14.2\ \mu\text{m}$ and typically ovoid to obclavate in shape. The number of transverse septa and longitudinal septa of conidia varied from 1 to 6 and from 0 to 2, respectively. Based on these features, isolates in this group were identified as *A. tenuissima* (Fig. 4a,d,g).

Forty-two isolates attributed to group A-alt were dark grey to black brown and densely turfy on PDA plates. On PCA plates, these isolates produced conidial chains 8-12 spores in length with numerous secondary and occasionally tertiary chains branching from apical and median cells. Conidiophores were single or fasciculate, straight or bent, $22.5\text{-}79.6\ \mu\text{m}$ long and $2.0\text{-}4.9\ \mu\text{m}$ wide. Conidia were obpyriform to ellipsoid, $20.8\text{-}40.5 \times 7.6\text{-}12.0\ \mu\text{m}$, with 3-8 transversal and 0-3 longitudinal septa. These isolates were identified as *A. alternata* (Fig. 4b,e,h).

Thirty isolates attributed to group A-sol had a dense dark grey to black colony with sparse aerial mycelium, and produced simple conidiophores bearing dark, multiseptate conidia with 9-11 transverse septa and 1-2 longitudinal septa. Conidia with one beak were long-ovoid, 102.7-

115.0 × 15.0-25.3 μm with a beak 80.5-110.6 μm in length (beak width tapered from 5.0-8.0 μm to about 2.5 μm at the tip). Conidia with two beaks were shorter in length, 82.5-105.0 × 16.7-20.5 μm with an initial beak 60.0-84.7 μm long and a second beak 62.8-85.5 μm long. Based on these characters, the isolates were identified as *A. solani* (Fig. 4e,h).

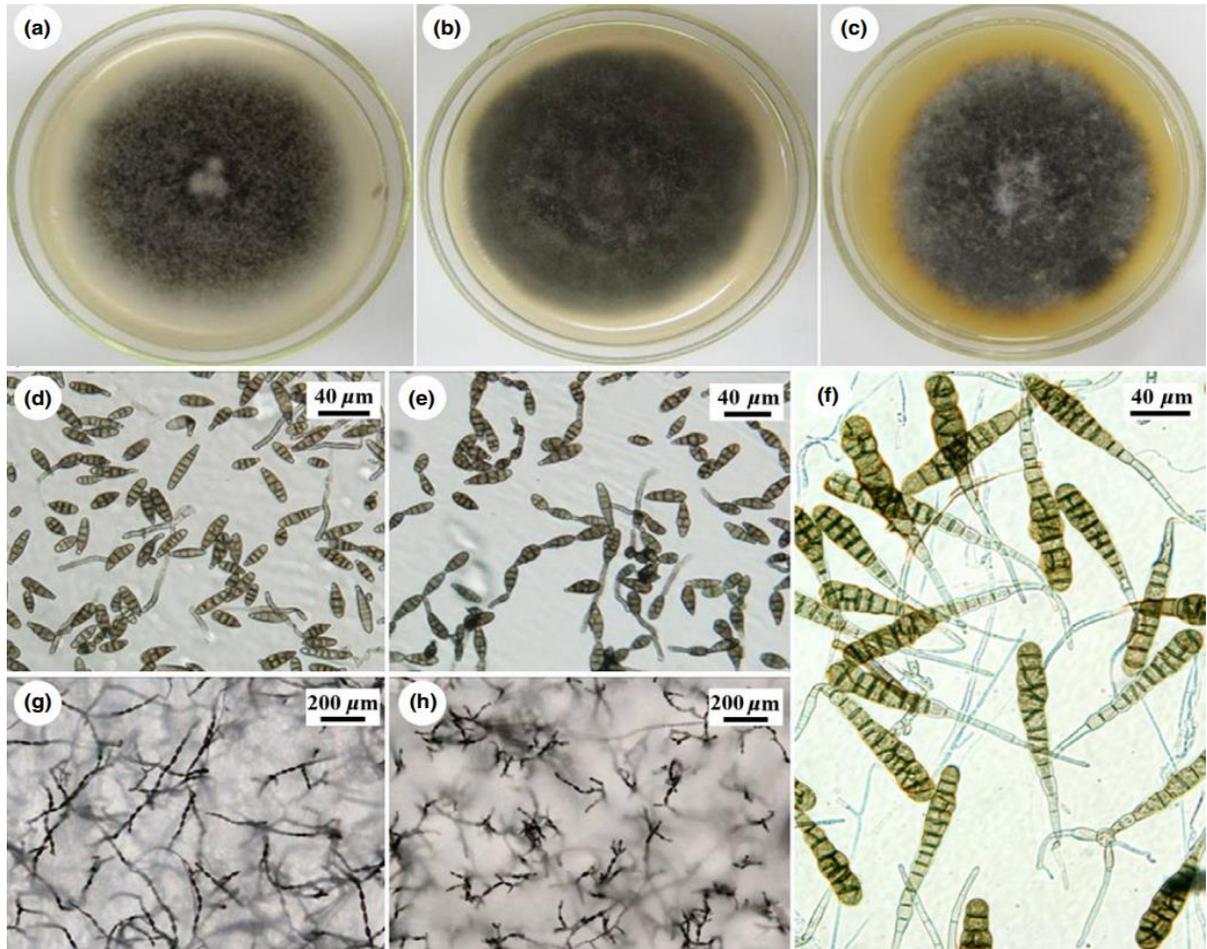


Figure 4 Colonies, conidia and sporulation patterns of the representative isolates of three *Alternaria* species. (a–c) Colonies of the representative isolates of *A. tenuissima*, *A. alternata* and *A. solani* observed on potato dextrose agar plates, respectively; (d–f) conidia of the representative isolates of *A. tenuissima*, *A. alternata* and *A. solani* observed on potato carrot agar (PCA) plates, respectively; (g–h) sporulation patterns of the representative isolates of *A. tenuissima* and *A. alternata* observed on PCA plates, respectively (Zheng et al., 2015).

2.2.2 Life cycle and propagation

The plant pathogenic fungi are divided into biotrophic, hemibiotrophic, and necrotrophic pathogens. These different pathogenic life styles require different molecular infection mechanisms. Necrotrophic fungi infect and kill host tissue and extract nutrients from dead host cells. Bio-

trophic fungi colonize living host tissue and obtain nutrients from living tissue; whereas hemibiotrophic fungi display two phases during the infection process; first is an initial biotrophic phase followed by a necrotrophic stage (Lo Presti et al., 2015). Early blight is caused by the fungus, *Alternaria solani*, producing dark to black conidia (asexual spores and has not been found to produce sexual spores) which survives in infected leaf or stem tissues on or in the soil (Fig. 5) (Schultz and French, 2009). The pathogen overwinters as mycelium or conidia in plant debris ex. (potatoes or tomatoes), soil and infected tubers or on other host plants of the same family. Conidia are spread by wind and splashing water. Wind, rain and insects are the principle methods of dissemination of *A. solani* (van der Waals, 2002). Spores landing on leaves of susceptible plants germinate and may penetrate tissues directly through the epidermis, through stomata and or through wounds such as those caused by sand abrasion, mechanical injury or insect feeding. Incubation periods (time from infection to symptom development) vary greatly, depending on age and susceptibility of plants. Epidemics increase in severity after sandstorms, due to increased wounding of the epidermis. The primary infections become necrotic with chlorotic halos. Mycelium from necrotic lesions produces conidia that infect healthy leaves and begin secondary infections (Fig. 5) (van der Waals, 2002). Potato tubers become infected as they are lifted through infested soil at harvest. Tuber infection usually occurs through wounds and/or through natural openings (lenticels), which tend to open when the soil is wet (Fig. 5) (Sikora, 2004). *Alternaria* produces host-specific toxins as well as non-host specific toxins (nHSTs) (Thomma, 2003). Generally, nHSTs toxins have relatively mild phytotoxic effects, they are not absolutely required for establishing disease since they are also toxic to plant species outside the host range of the pathogen affect a broad spectrum of plant species and are thought to be an additional factor of disease alongside, for instance, penetration mechanisms and enzymatic processes (Meena et al., 2017). More than 70 phytotoxins produced by *Alternaria spp.* have been characterized, and include virulence factors that have both non-specific and specific host interactions (Meena et al., 2017). Determination of the exact mode of action of phytotoxic compounds in pathogenesis or virulence is critical and it can be determined by studying virulence and sensitivity of toxins produces by different isolates on host genotypes (Strange 2007, Meena

et al., 2012). Host-selective toxins (HSTs) are mycotoxins which are often essential for both host specificity and pathogenicity.

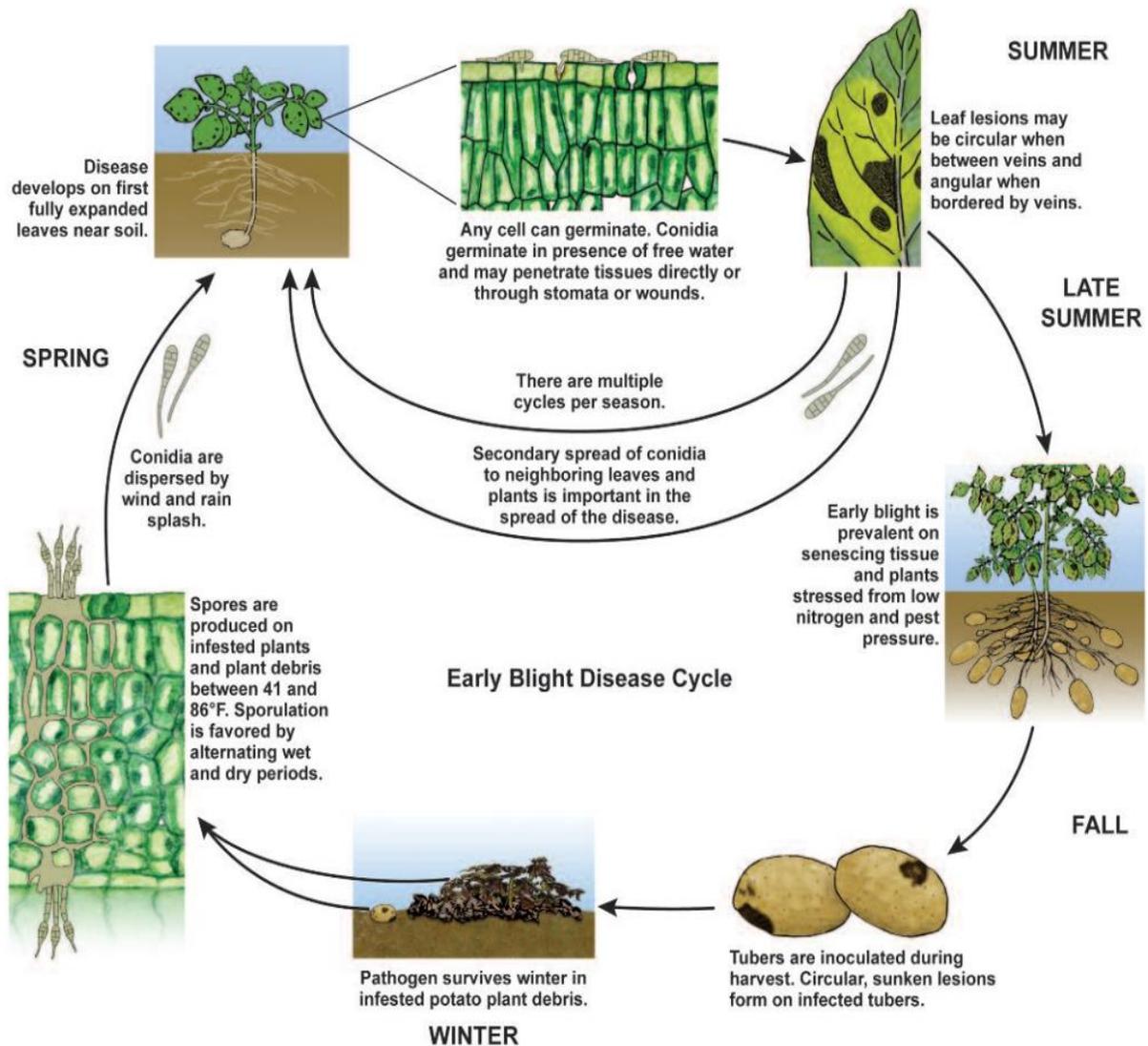


Figure 5 The diseases cycle of the early blight pathogen, *Alternaria solani*. (Warton and Wood, 2012).

HSTs are produced during germination of spores on plant surfaces (Mausunaka et al., 2005). Ten phytopathogenic fungi belonging to the genus *Alternaria*, are known to produce HSTs (Otani et al., 2011). Seven of these pathogens cannot be distinguished from ubiquitous saprophytic *A. alternata* on the basis of conidial morphology, but each pathotype can be distinguished by its unique pathogenicity (Nishimura et al. 1978, 1982). Five species and two sub-species were grouped into seven pathotypes, corresponding to their hosts Japanese pear, apple, tobacco, rough lemon, tangerine, tomato, and strawberry; these produce AK-, AM-, AT-, ACR- (ACRL-), ACT- or ACTG-, AAL- (AL-), and AF-toxins, respectively (Nishimura and Kohmoto 1983; Kohmoto and Otani 1991). AK-toxin, AF-toxin and ACT-toxin exert primary effects on the

plasma membrane of susceptible cells (Fig. 6) (Maekawa et al., 1984; Otani et al., 1985; Kohmoto et al., 1993; Park & Ikeda, 2008). A study on the structure–selectivity relationships of AK-, AF- and ACT-toxins suggested that the initial interaction between the toxin and its putative receptor site on the plasma membrane of susceptible cells probably involves a biological reaction, such as ligand binding to a receptor, rather than a simple physicochemical reaction (Nishimura & Nakatsuka, 1989). AM-toxins have two target sites for affecting susceptible apple cells: one on the plasma membrane and another on chloroplasts membrane (Fig. 6) (Park et al., 1981; Zheng et al., 2015).

However, Otani et al. (2011) suggested that the chloroplast is a primary target site of AM-toxin. In the chloroplasts of susceptible apple leaves the chloroplast disorganization is compatible with the reduction in chlorophyll content and inhibition of photosynthetic CO₂ assimilation in the toxin-treated susceptible leaves (Kohmoto et al., 1982). Because of structural and functional similarity, AAL-toxins and fumonisins are collectively referred to as sphinganine-analogue mycotoxins (SAMs) (Gilchrist et al., 1995). SAMs induce programmed cell death in susceptible

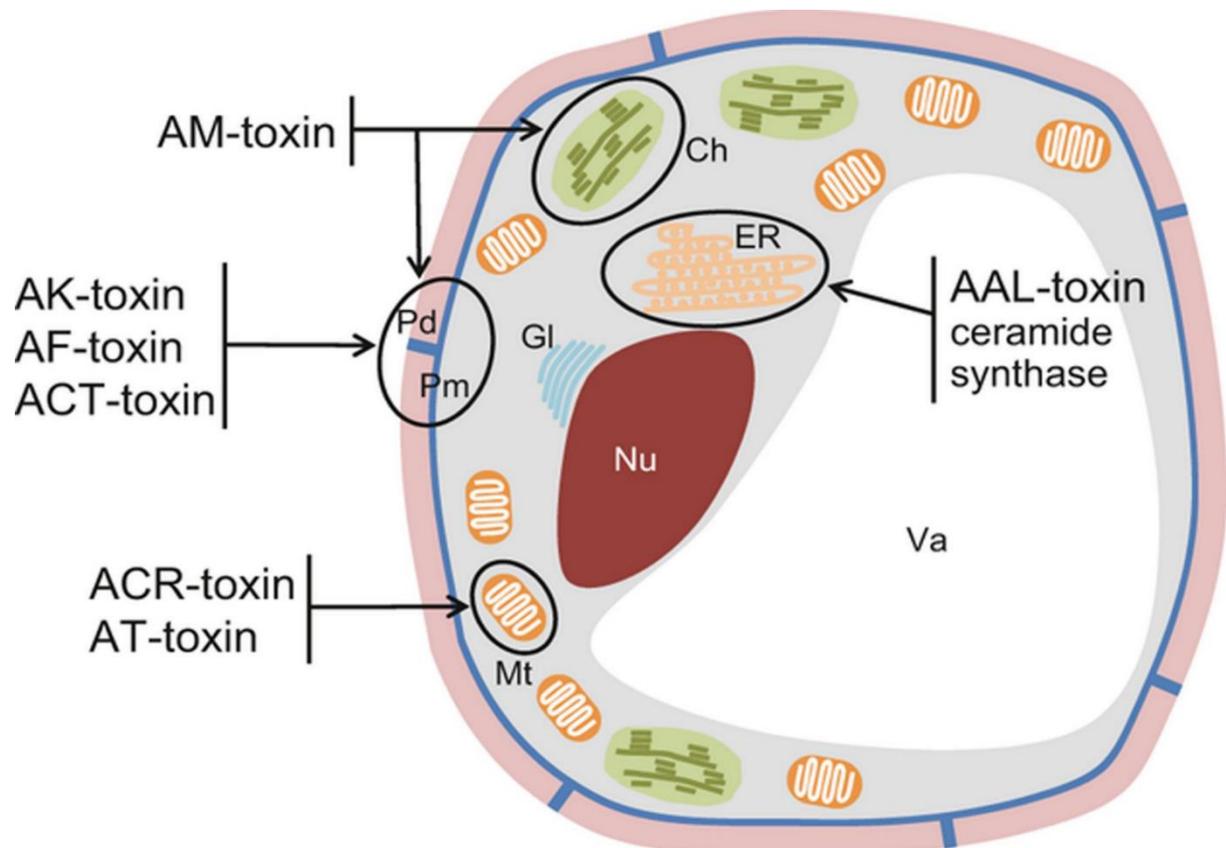


Figure 6 Schematic presentation of target sites of HSTs produced by *Alternaria alternata*. Ch, chloroplast; ER, endoplasmic reticulum; Gl, Golgi apparatus; Mt, mitochondrion; Nu, nucleus; Pd, plasmodesma; Pm, plasma membrane; Va, vacuole (Tsuge et al., 2013).

tomato cells throughout inhibiting ceramide biosynthesis by ceramide synthases proteins in the endoplasmic reticulum (Wang et al., 1996; Spassieva et al., 2002, 2006). ACR-toxin caused uncoupling of mitochondrial oxidative-phosphorylation with a loss of membrane potential, and also caused leakage of the cofactor NAD⁺ from the tricarboxylic acid cycle which takes place in the matrix of the mitochondria (Akimitsu et al., 1989).

In summary, the *Alternaria* HSTs are a diverse group of low-molecular-weight substances, most were found in culture filtrates as families of closely related compounds. The *Alternaria* HSTs cause necrosis on leaves of susceptible cultivars at concentrations as low as 10⁻⁸ to 10⁻⁹ M and no necrosis on leaves of resistant cultivars even at higher concentrations (Otani et al., 1995).

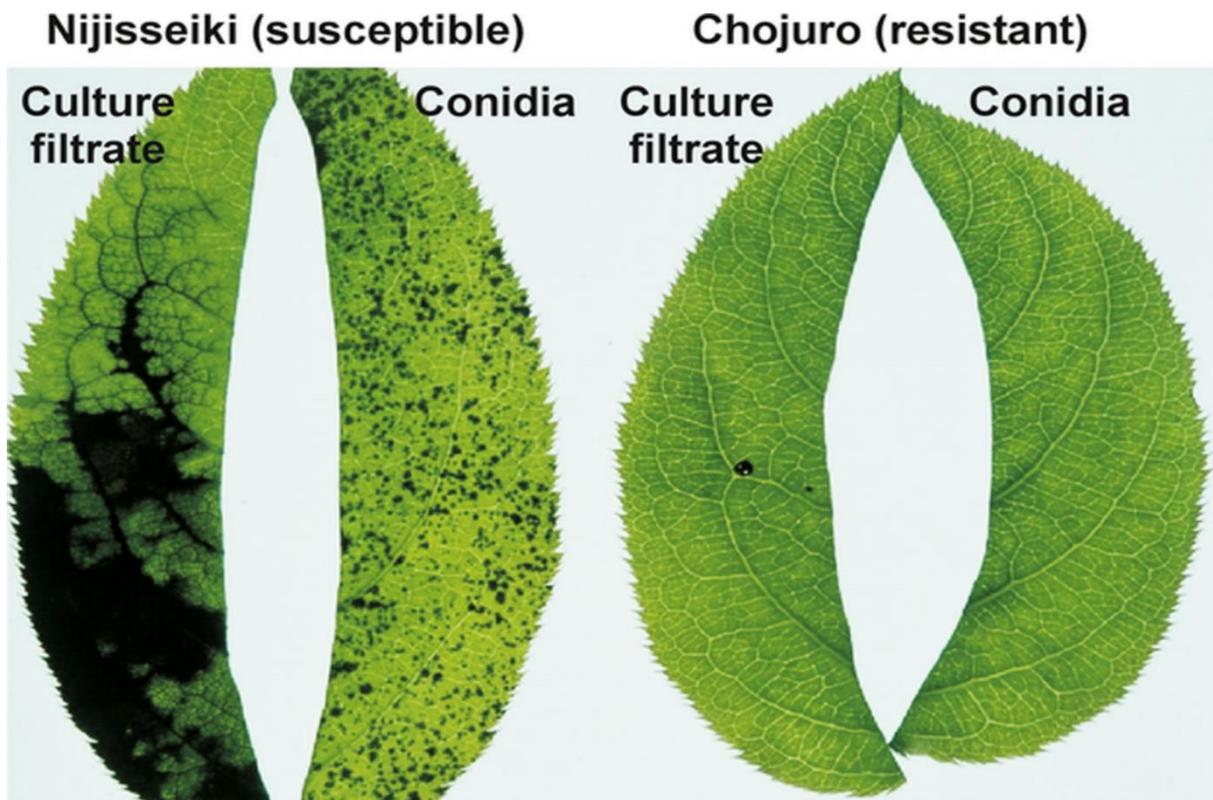


Figure 7 Toxicity of AK-toxin produced by the Japanese pear pathotype of *Alternaria alternata*. The culture filtrate of the Japanese pear pathotype was dropped on slightly wounded points of left-half leaves. Right-half leaves were spray-inoculated with a conidial suspension. Leaves were incubated for 24 h (Tsuge et al., 2013).

2.2.3 Symptoms of *Alternaria* spp. in potato

The effect of phytotoxins on plants at the physiological level is characterized by the malfunctioning of many physiological processes including respiration, transpiration, photosynthesis,

nutrients translocation, growth and development. It results in the appearance of specific symptoms including wilting, growth suppression, chlorosis (Fig. 3 c,d), necrosis (Fig. 7), and spotting of aerial portions (Taj et al., 2015).

Early blight caused by *Alternaria spp.* is a problem in many potato growing areas of the world, occurs particularly in the regions with high temperature and alternating periods of dry weather and high humidity and/or irrigated potato soils, light-textured, sandy, low in organic matter (Gudmestad and Pasche 2007).

2.2.4 Source of resistance in potato spp.

Plants defend themselves from pathogen infection through a wide variety of mechanisms that can be either local or systemic, constitutive or inducible (Dixon 1986; Keen 1990; Ryals et al., 1992; Ryals et al., 1994).

When a plant has a specific resistance (R) gene which interacts with the interrelated avirulence (avr) gene from the pathogen, an expeditious defense mechanism known as the hypersensitive response (HR) happens to suppress the infection (Flor 1971).

Plants avert pathogen infections by eliciting a cascade of defense mechanisms, including reinforcement of the cell wall (Kauss, 1987; Barber et al., 1989; Bradley et al., 1992), synthesis of phytoalexins and oxidation of phenolic compounds (Hahlbrock and Scheel, 1989; Dixon and Lamb, 1990), activation of defense-related genes (Bowles, 1990; Dixon and Harrison 1990), and localization of cell death or the hypersensitive response (Keen, 1992). Associated with these reactions, the production of active oxygen species (AOS), such as the superoxide anion radical (O_2^-), hydroxyl radical (OH), and hydrogen peroxide (H_2O_2) known as oxidative burst.

The oxidative burst has been postulated to play an important role in plant defense (Baker and Orlandi, 1995), induction of an intracellular signaling pathway (Desikan et al., 1999; Grant et al., 2000), and in the activation of systemic-acquired resistance (Alvarez et al., 1998; Hae-Jun et al., 1998). Chai and Doke (1987), showed that superoxide dismutase and peroxidase are systemically induced in potato after local infection with *Phytophthora infestans*. To study the effect of H_2O_2 in plants, Wu et al. (1995) expressed the gene encoding glucose oxidase (GO) from *Aspergillus niger* in transgenic potato plants. GO (β -D-glucose:oxygen 1-oxidoreductase, EC 1.1.3.4) catalyzes the oxidation of β -D-glucose by molecular oxygen, yielding gluconic acid

and H₂O₂. They have concluded that, the increased level of H₂O₂ in transgenic potato plants mediates strong resistance against soft rot caused by *Erwinia carotovora* subsp *carotovora* and enhanced resistance to late blight caused by *Phytophthora infestans*. Moreover, many studies have strongly suggested the crucial role in which nitric oxide (NO), β-aminobutyric acid (BABA), γ-aminobutyric acid (GABA), Laminarin (the linear β-1,3 glucan) and 2,6-dichloroisonicotinic acid (INA) play in response to biotic and abiotic stresses in plants (Arasimowicz-Jelonek et al., 2013; Moreau et al., 2010; Ton and Mauch-Mani 2004; Jakab et al., 2001; Conrath et al., 1995).

In another study by Yoshioka et al. (2001), The results of treating potato tubers with hyphal wall components (HWC) elicitor from *Phytophthora infestans*, caused a rapid but weak transient accumulation of H₂O₂ (phase I), followed by a massive oxidative burst 6 to 9 h after treatment (phase II). The team have isolated homologs of gp91 phox, a plasma membrane protein of the neutrophil NADPH oxidase, from a potato cDNA library. Molecular cloning of the cDNA showed that there are two isogenes, designated StrbohA and StrbohB, respectively. RNA gel blot analyses indicated that StrbohA is constitutively expressed at a low level, whereas StrbohB is up-regulated during the phase II burst. DPI (Diphenylene iodonium) blocks both bursts, while pretreatment of the protein synthesis inhibitor cycloheximide with the tuber nullify only the second burst. These data suggest that StrbohA and StrbohB contribute to phase I and phase II bursts, respectively.

Genetic studies indicate that Rboh (Respiratory burst oxidase homolog) gene is a key regulator of ROS production and displays pleiotropic functions in plants (Sagi et al., 2004; Torres and Dangl, 2005).

The control of early blight is largely dependent on fungicidal treatment. Because of the polycyclic nature of the disease (Shuman, 1995), several applications of fungicides are required to offer sufficient protection for potatoes from early blight attack (Teng & Bissonnette 1985).

The use of resistant cultivars in the control of early blight offers an economical and environmentally friendly alternative (Spiertz et al., 1996).

In a recent study by Abuley et al. (2017) in Denmark, the team conducted field experiments in 2015 and 2016 using randomized complete block design with four replicates to classify the resistance level to early blight of the main potato cultivars in Denmark. Conidia and mycelium

of both *A. solani* and *A. alternata* were used for the inoculation. The disease progress curves (DPC) of early blight on the cultivars with different maturity classes were compared to that of Bintje as susceptible, early-medium maturity class control cultivar.

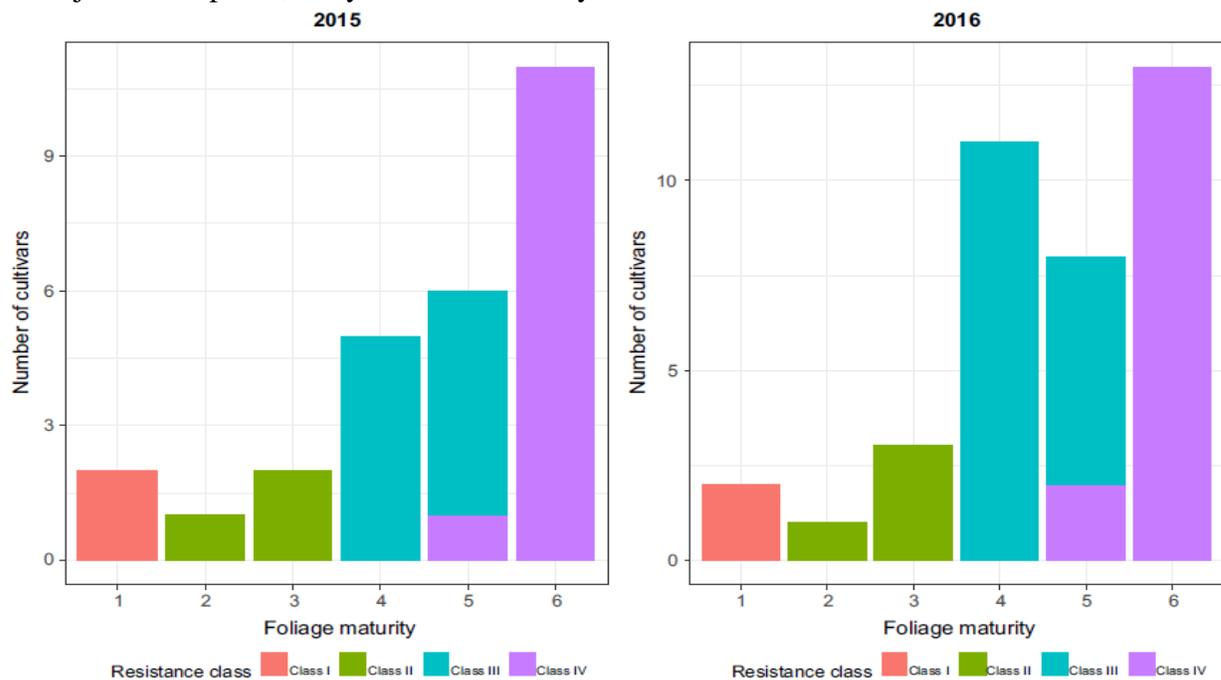


Figure 8 The number of cultivars in the different resistance classes according to the foliage maturity of the cultivars in 2015 and 2016. The values 1, 2, 3, 4, 5 and 6 on the x-axis represent very-early, early, early-medium, medium, medium-late and late maturing classes, respectively. The resistance classes I, II, III and IV represent ‘very susceptible’, ‘susceptible’, ‘moderately slow blighting’ and ‘slow blighting’, respectively. (Abuley et al., 2017).

In order to classify the resistance level of the cultivars, the team investigated different factors which are: multivariate analysis was with the apparent rate of infection, the time to reach 50% severity, the relative area under the DPC, the daily defoliation, the disease severity in the middle of the epidemic and the duration of the epidemic. None of the cultivars showed complete resistant to early blight according to analysis of the DPC. However, the cultivars showed different levels of epidemic development. Accordingly, the resistance levels of the cultivars were classified into four classes, I, II, III and IV interpreted as ‘very susceptible’, ‘susceptible’, ‘moderately slow blighting’ and ‘slow blighting’, respectively. The team concluded that, the late maturing cultivars were more resistant than the early maturing cultivars Fig. 8.

2.3 Protein analysis

2.3.1 Introduction to proteomics

The term proteomics was suggested by Marc Wilkins, back during the 1994 Siena Meeting, to simply refer to the “PROTEin complement of a genOME” (Wilkins et al., 1996). Similar to genomics and transcriptomics, proteomics has evolved to incorporate high-throughput techniques, protocols and methods that contribute to a faster analysis of large numbers of proteins in a relatively short time frame (Washburn et al., 2001; Wolters et al., 2001). Proteomics offers the possibility of studying simultaneously the total set of proteins that is present in a biological unit (from subcellular organelles to ecosystems), together with its arrangement (descriptive proteomics), its abundance (quantitative proteomics), genotype dependent variations (population proteomics), implication in development and environmental responses changes (differential or comparative proteomics), post-translational modifications (PTMs), and interactions with other proteins and molecular entities (interactomics) (Afroz et al., 2011; Bhadauria et al., 2010; Tan et al., 2009; Jorin-Novo et al., 2007).

2.3.2 Proteomic studies of potato

Throughout time, plants have developed acclimatization ability to different biotic and abiotic stresses (Jones and Dangl 2006; Chinnusamy et al., 2004). This ability depends mainly on different proteins, the most important of which are phytoalexins, AOS, enzyme inducing the synthesis of phytohormones (salicylic acid, ethylene, abscisic acid and jasmonic acid) and pathogenesis related proteins (PR) (Baker and Orlandi, 1995; Ewing and Struik 1992; Ivana et al., 1997; Xu et al., 1998; Suttle, 2004; López-García et al., 2012).

Proteomics has been used to study potato tuber life cycle and development (Lehesranta et al., 2006; Agrawal et al., 2008), proteins in potato tubers (Lehesranta et al., 2007) and potato skins (Barel and Ginzberg 2008; Chaves et al., 2009). Since many pathogens, such as *Alternaria alternata* and *A. solani* infect leaf tissues (Ardestani et al., 2010; van der Waals 2004, 2011) a study of biological activities in potato leaves using proteomics becomes important. Lim et al., (2012).

Generally, the standard work flow of a plant fungal pathogens proteomic experiments includes few steps: experimental design, sample preparation, protein extraction and purification, protein

separation, mass spectrophotometry analysis, protein identification, statistical analysis, validation of the identified proteins and data analysis management followed by database storage Fig 9. However, the exact protocol for different proteomics experiments should be optimized according to the study purpose (González-Fernández et al., 2010).

In fungal proteomics, the most used technique is two-dimensional gel electrophoresis (2-DE), with an important advantage of separating the proteins with a high resolution of up to 10,000 spots also the ability to making large-scale protein-profiling experiments (Görg et al., 2004; Jungblut and Thiede 1997; Klose and Kobalz 1995; O'Farrell et al., 1977).

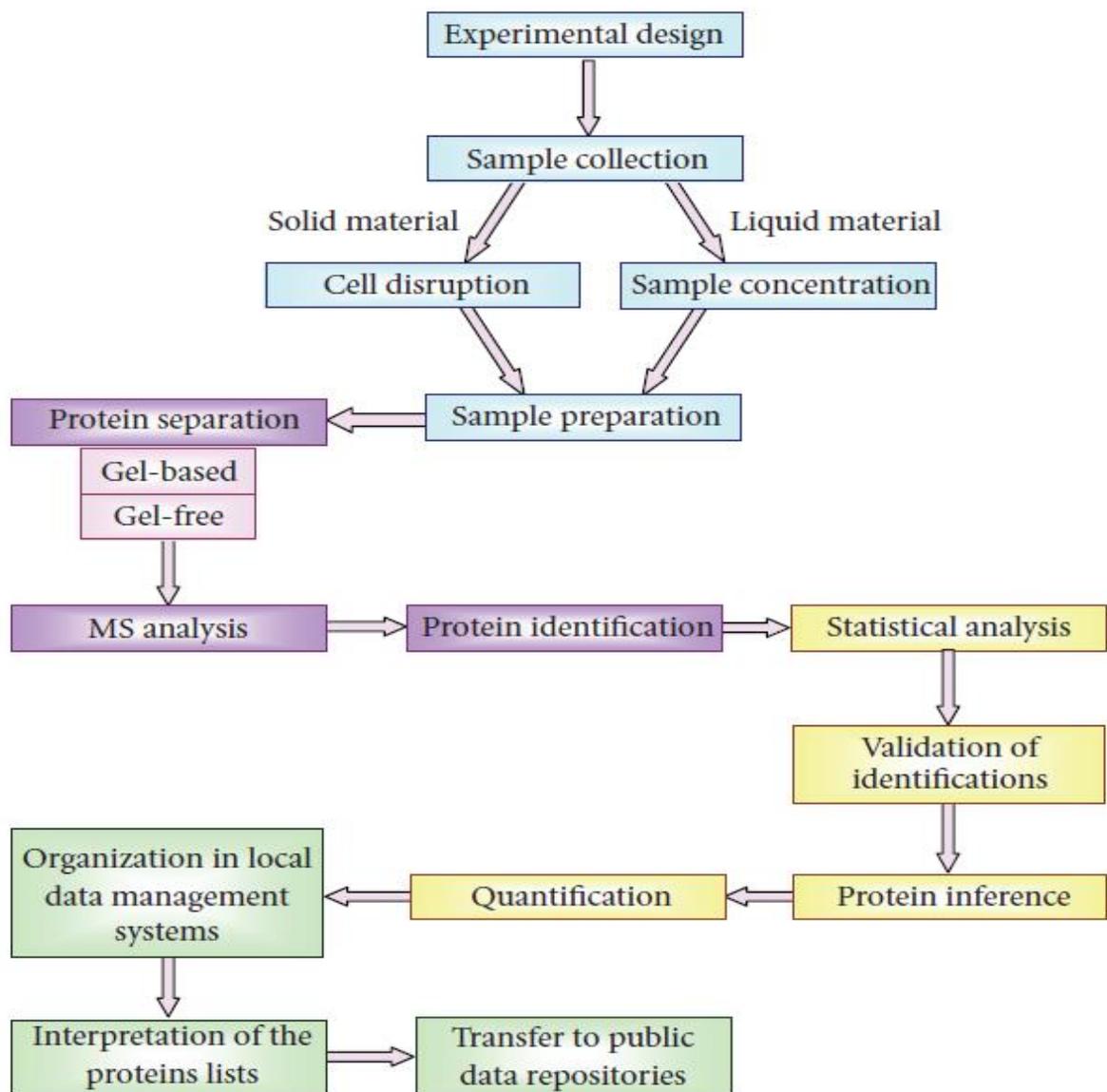


Figure 9 Schematic overview of the work flow in a fungal proteomic approach (González-Fernández 2010).

As indicated by the name, 2-DE consists of two dimensions: First dimension electrophoresis in which proteins are separated according to their isoelectric points (pIs) using isoelectric focusing (IEF) technique. Second dimension electrophoresis in which proteins are separated according to their molecular weight using sodium dodecyl sulfate polyacrylamide gel electrophoresis (SDS-PAGE). The proteins under investigation can then be detected by different staining techniques like colloidal Coomassie blue, zinc-imidazole staining, silver staining and fluorescence-based detection (Rabilloud et al., 2009; Görg et al., 2004).

A proteomic study by Liu et al., (2009), investigated the influence of RB gene (resistant gene against *Phytophthora infestans*). Two potato genotypes Katahdin and transgenic potato Katahdin which is carrying the RB gene representing susceptible and resistant genotypes respectively were tested. After inoculating both genotypes with *P. infestans* total leaf proteins of both genotypes were extracted. The results showed 12 proteins in relative abundance were different after comparing the genotypes. Five proteins (Ribulose biphosphate carboxylase small chain 2A, Ribulose biphosphate carboxylase/oxygenase activase, Cytosolic ascorbate peroxidase, Oxygen-evolving enhancer protein 1 and Quinone oxidoreductase-like protein) were suggested to play important roles in photosynthesis and stress responses.

Lim et al., (2012) suggested that the fractionation strategy using differential centrifugation to separate the pellet (cell wall fraction) and the supernatant (cytoplasmic fraction) from potato leaf tissues can be used for successful construction of a protein profile in potato leaf tissues to study potato leaf physiology, biochemical aspects of abiotic stress and potato-pathogen interactions.

An approach by Kato et al. (2012) to investigate the role of nitric oxide in plants, they performed a proteomic analysis of S-nitrosylated proteins in potato leaves and tubers using biotin switch assay optimized for potato tissues and nano liquid chromatography combined with MS. They treated potato leaves and tubers with glutathione (GSH) and S-nitrosoglutathione (GSNO) as NO donors Fig.10 and were able to identify 80 S-nitrosylated proteins. They suggested that part of those proteins are Redox-related proteins, Defense-related proteins, Photosynthetic-involved proteins and metabolic enzymes.

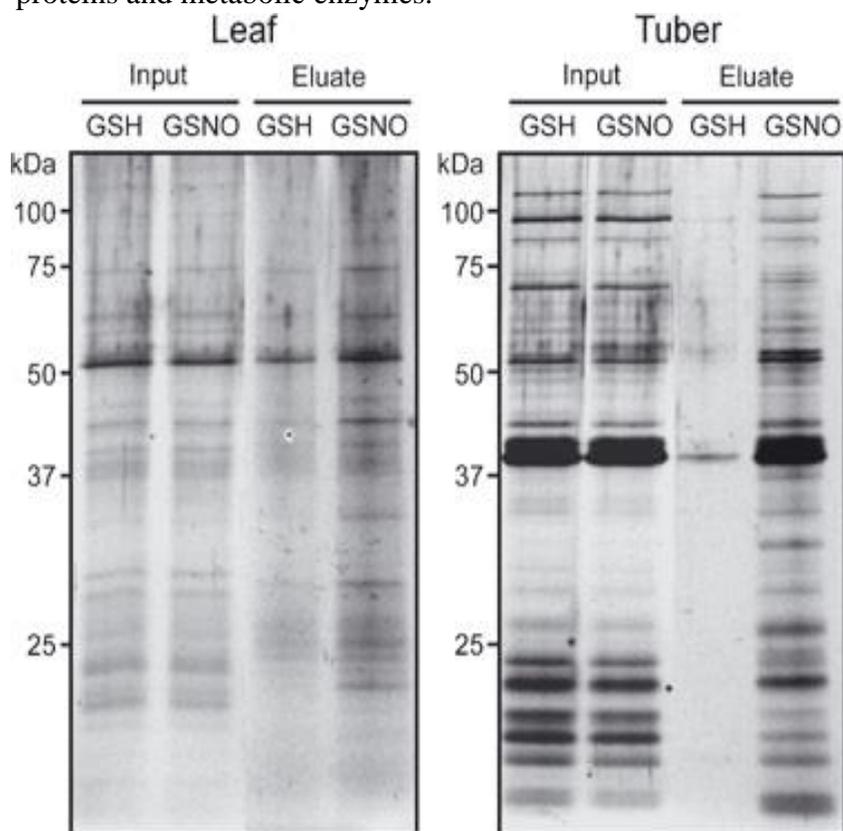


Figure 10 Purification of S-nitrosylated proteins in GSNO-treated extracts from potato leaves and tubers. Leaf (A) and tuber (B) proteins (5 mg) were treated with 0.5 mM GSH or GSNO, and subjected to biotin switch method. Biotinylated proteins were purified by affinity chromatography using neutravidin-agarose. Proteins before purification (input) and eluates were separated by SDS-PAGE and visualized by silver staining. Numbers on the left of the panels indicate the position of the protein-markers in kDa.

3 OBJECTIVES

- Establishing an artificial inoculation system for two potato genotypes with strains of *Alternaria* spp. (*Alternaria alternata* and *Alternaria solani*).
- Photographic documentation of early symptom development.
- Investigating the morphological and histological reactions of potato leaf tissue to the inoculation with *Alternaria* spp.
- Identify the proteomic changes of potato leaves in response to the infection by *Alternaria* spp.

4 RESEARCH HYPOTHESES

- The typical symptoms of potato after early blight infection can be visually identified (AI).
- Different responses of the genotypes to the infection of each fungal strain represented in distinct symptoms and morphological abnormalities are expected.
- The level of resistance/susceptibility of potato genotypes can be evaluated based on the result of the screening assay.
- Observable modification of the protein abundance of the genotypes as a response to the infection should occur.
- Differentially abundant proteins in susceptible compared to resistant genotypes can be used to develop biomarkers.

5 MATERIALS AND METHODS

5.1 Plant and fungal material

Seed tubers of commercial potato varieties Bintje (Early medium-maturity) and Norvarno (Late maturity) respectively, will be requested from Denmark as they are characterized by their low and high resistance to early blight (*Alternaria alternata* and *Alternaria solani*) respectively (Abuley et al., 2017).

Pure isolates of different races of *A. alternata* and *A. solani* will be requested from DSMZ (Deutsche Sammlung von Mikroorganismen und Zellkulturen). The isolates will be stored at 5°C (Ravikumar et al., 2016) until the time of inoculum preparation. Furthermore, isolates will be collected from potato breeders (cooperation with Prof. T. Debener).

The potato seed tubers will be sterilized with 1% sodium hypochlorite for 5 min and washed 3 times with sterilized distilled water (SDW), then planted in plastic pots (30 cm diameter, one tuber per pot) filled with peat moss and grown in greenhouse under standard cultivation conditions for potato.

5.2 Inoculation with *A. alternata* and *A. solani*

For inoculum preparation, sporulation will be induced by maintaining the isolates on potato dextrose agar (PDA) medium at 23-25°C for 6 days with 16hL/8hD photoperiod. Conidia will be obtained by washing the PDA plates of different isolates (SDW), the suspension will be collected in test tubes and adjusted to 10^6 conidia ml^{-1} using haemocytometer.

Four plants 45days old of each of each variety will be grown in greenhouse using the recommended cultivation protocols. The plants will be inoculated by spraying the spore suspension then covered with plastic bags moisturized with SDW on the interior layer to maintain sufficient humidity thus improve the fungal growth. Experiments will include variation of the following factors: inoculum density, physical growth conditions, additional wounding, and testing different plant organs for inoculation.

The degree of aggressiveness for the different isolates will be assessed using the scale for evaluation of the damage produced by *Alternaria solani* in potato greenhouse and field plants (Rodríguez et al., 2007).

The control plants will be treated with SDW under the same cultivation conditions.

Late blight and insects will be controlled using the recommended protocols to make sure that, early blight will be the only mean of infection.

Establishing the inoculation protocol will be the basis of a screening assay in which a larger number of 10-12 genotypes will be tested for their reaction to *Alternaria* leaf spot.

5.3 Morphological and histological analysis

Morphological identification of typical early blight symptoms on the tested genotypes will be assessed and photographs of the plants will be taken in daily bases for later documentation.

Two sets of leaf tissue samples will be taken from the inoculated and control plants, the samples will be taken on different intervals (6, 12, 24, 36, 48 and 72 h) for the histological analysis. The samples will be discolored in chloral-hydrated solution (2.5 g/ml) and stained with trypan blue (0.05%) then adjusted to slides for examination by differential interference contrast microscopy (Dita et al., 2007).

5.4 Proteomic analysis

The second part of the samples taken after inoculation will be processed by phenolic leaf protein extraction and methanol precipitation followed by two dimensional electrophoresis (isoelectric focusing and SDS-polyacrylamide gel electrophoresis), gel images analysis and mass spectrometry. The exact extraction and purification protocol and the kits that will be used later to be determined according to the available resources. However, it will be similar to the protocol described by Carpentier et al. (2005) and Liu and Dennis (2009).

Relevant time points and the genotypes will be identified in the experiments described under 5.3.

6 CALENDAR OF RESEARCH ACTIVITIES

Activity	Semester			
	Winter 2017/18	Summer 2018	Winter 2018/19	Summer
Literature review				
Planting and inoculation				
Morphological and histological analysis				
Protein analysis				
Quantitative gel				
Mass spectrometry and protein identification				
Statistical analysis				
Thesis writing				

7 Reference

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