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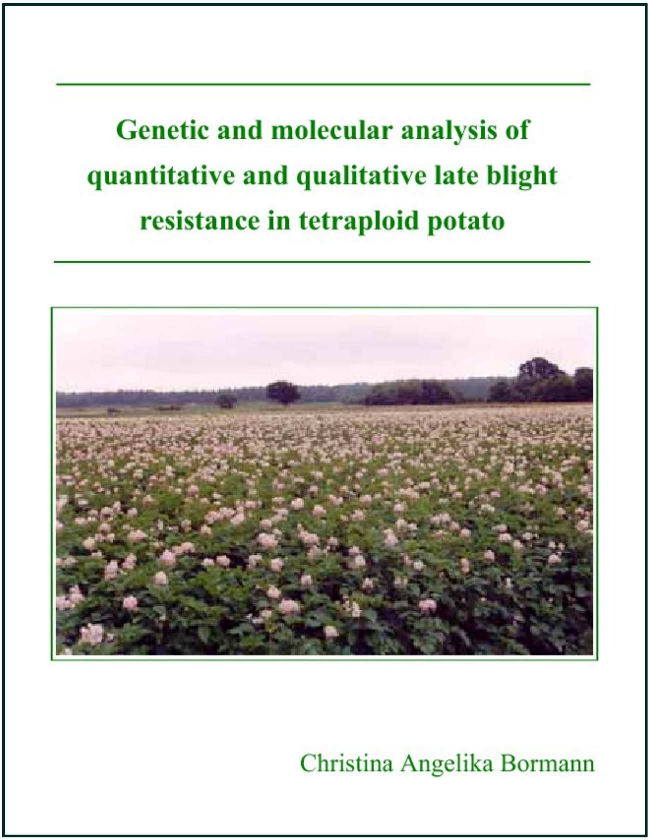
Genetic and molecular analysis of quantitative and qualitative late blight resistance in tetraploid potato



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Chapter 1 • Introduction

1.1 The potato

Importance:

The potato is a very important food crop ranking fourth in world food production after maize, rice, and wheat (Table 1.1). In Europe, it is even on the second place and in Germany it ranks third. The nutritive value of potato is very high [Hawkes 1990], especially containing the minerals potassium, iron, magnesium, and the vitamins B1, B2, and C. Tubers contain only 0.1% fat and their proteins are of high quality [Centrale Marketing Gesellschaft der deutschen Agrarwirtschaft mbH homepage: http://www.agrarnet.de /984.php]. All these properties make the potato an important food crop.

Table 1.1. **Production of major crops in the world, Europe and Germany.** Mean of 1998-2002.

Crop	Production [million metric tons]	Crop	Production [million metric tons]
WORLD:		EUROPE:	
maize	606,436	wheat	191,338
rice	593,508	**potato**	**138,086**
wheat	586,088	barley	85,900
potato	**310,070**	maize	71,175
cassava	176,527	rye	19,308
sweet potato	138,420	oat	16,655
barley	135,227	rice	3,186
sorghum	58,321	millet	935
yams	38,031	sorghum	713
millet	27,273	sweet potato	60
oat	25,825	yams	2
rye	21,033		
GERMANY:			
wheat	21,016		
barley	12,468		
potato	**12,169**		
rye	4,411		
maize	3,321		
oat	1,175		

[FAOSTAT Statistical database of the Food and Agricultural Organization of the United Nations: http://apps.fao.org/default.htm].

Origin:

The potato originates from the central Andes of Peru and Bolivia. The first domesticated potato was probably *Solanum stenotomum* Juz. et Buk., a diploid potato which originated from *S. leptophyes* Bitt., grown in Northern Bolivia in the area between Lake Titicaca and Lake Poopó about 10,000 to 7,000 years ago [Hawkes 1990].

In the 16th century when the Spanish conquistadores came into contact with cultivated potatoes, they were widely distributed throughout the Andes from Columbia to Peru and in Southern Chile. One of the first records from the Spanish was by Juan de Catellanos (Elegías):

The houses (of the Indians) were all stocked with maize, beans and truffles (= potatoes), spherical roots which are sown and produce a stem with its branches and leaves, and some flowers, although few, of a soft purple colour; and to the roots of this same plant, which is about 3 palms high (= 60 cm), they are attached under the earth, and are the size of an egg more or less, some round and some elongated; they are white and purple and yellow, floury roots of good flavour, a delicacy to the Indians and a dainty dish even for the Spaniards [cited from Hawkes 1990].

Fig. 1.1. **Potato harvesting in ancient Peru at the time of the Spanish conquest** [manuscript of Felipe Guamán Poma de Ayala (1583-1613): from Hawkes 1990]**.**

The first introduction of the potato into Europe was in Spain about 1570. A second introduction probably occurred between 1588 and 1593 in England, and from there it spread over Western Europe. In the early 17th century the first potatoes were introduced from England to North America. British missionaries then introduced them to Asia and Africa at the end of the 17th century. In Eastern Europe potatoes were grown in the late 18th to early 19th century [Hawkes 1990]. The worldwide distribution of the cultivated potato today is shown in Figure 1.2.

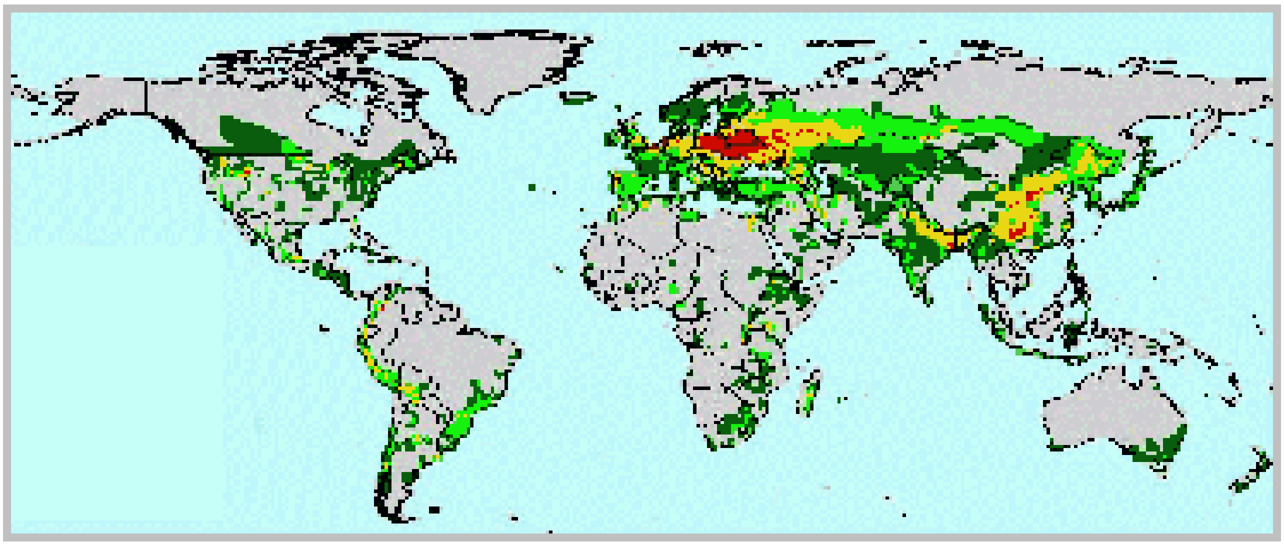

Fig. 1.2. **Production of potatoes in the world** (from green indicating low to red indicating high potato production). [World Potato Atlas: CIP (Centro Internacional de las Papas), Peru, 1999-2002, www.cipotato.org].

When potatoes were first brought to Europe, the plant was regarded as a botanical curiosity and not as a food crop. This was probably due to the formation of small tubers under long day conditions, since the introduced potato originated from short day conditions. Nevertheless the potatoes produced fruits in the old world, containing seed of sexually produced progeny. Gardeners might have (unconsciously) selected those new plants with better adaptation to long days, which probably resulted in earlier formation of larger tubers. The increased yield might have led to the recognition of the potato as a food crop at the end of the 18th century. The potato was adopted soon as an important crop in Europe especially for poor people, because the yield on marginal soils was much higher than for wheat and barley and the nutritive value is high [Brown 1993, CIP homepage: www.cipotato.org, Hawkes 1990].

Potato species and its wild relatives:

The potato has a large number of wild relatives (> 200 species). They are widely distributed throughout the American continent – from South-West USA over Central America to almost every country in South America. There are two centers of diversity, one in Central Mexico and another one in the high Andes from Peru over Bolivia to North-West Argentina. The wild potato species are distributed over a wide range of ecosystems and are adapted to a range of extremes such as temperature and humidity. Morphologically, wild potatoes resemble a small version of the cultivated potato and most of the wild potatoes (73%) are diploid (2n = 24), but also tetraploids (4n = 48) and hexaploids (6n = 72) occur [Hawkes 1990].

Seven potato species of different ploidy level are cultivated – from diploid (2n = 24: *S. ajanhuiri* Juz. et Buk., *S. phureja* Juz. et Buk., and *S. stenotomum*), triploid (3n = 36: *S. chaucha* Juz. et Buk. and *S. juzepczukii* Buk.), tetraploid (4n = 48: *S. tuberosum* L.), to pentaploid (2n = 60: *S. curtilobum* Juz. et. Buk.). The most important cultivated species is the tetraploid *S. tuberosum*. Its subspecies *tuberosum* is distributed worldwide. The subspecies *andigena* is cultivated in the Andes of South America. Besides the diploid *S. phureja*, which is cultivated from Peru to Ecuador, Columbia, and Venezuela, all the other diploid, triploid, and pentaploid potatoes are only found in the high Andes from central Peru to central Bolivia. All cultivated species occur in a high diversity of flower colors and tuber shapes and colors. The only exception is *S. tuberosum* spp. *tuberosum*, which has a low diversity compared to the other cultivated species [Hawkes 1990].

1.2 *Phytophthora infestans* Mont.: the cause of late blight

Biology of *P. infestans*:

The oomycete *P. infestans* is the cause of late blight in potatoes, tomatoes, and some other members of the family Solanaceae [Agrios 1997]. Oomycetes have been previously grouped with fungi such as ascomycetes and basidiomycetes due to the similar filamentous growth. However, based on data about metabolism, cell wall composition, and rRNA sequence, oomycetes are taxonomically closely related to diatoms and brown algae (Figure 1.3) [Judelson 1997].

The life cycle of *P. infestans* is demonstrated in Figure 1.4. The nucleus of this organism is diploid at each step in its life cycle except in the gametangia where haploid nuclei are formed. The late blight disease develops from the asexual cycle. It begins when sporangia land on the plant tissue and release biflagellated zoospores. The zoospore encysts

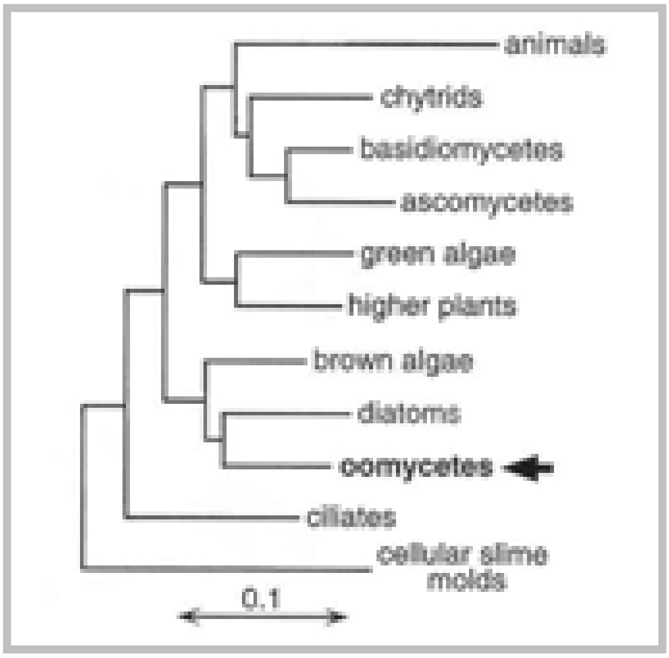

Fig. 1.3. **Phylogeny based on small-subunit rRNA sequence similarities.** The horizontal bar indicates the distance representing 10 changes per 100 nucleotide positions [Judelson 1997].

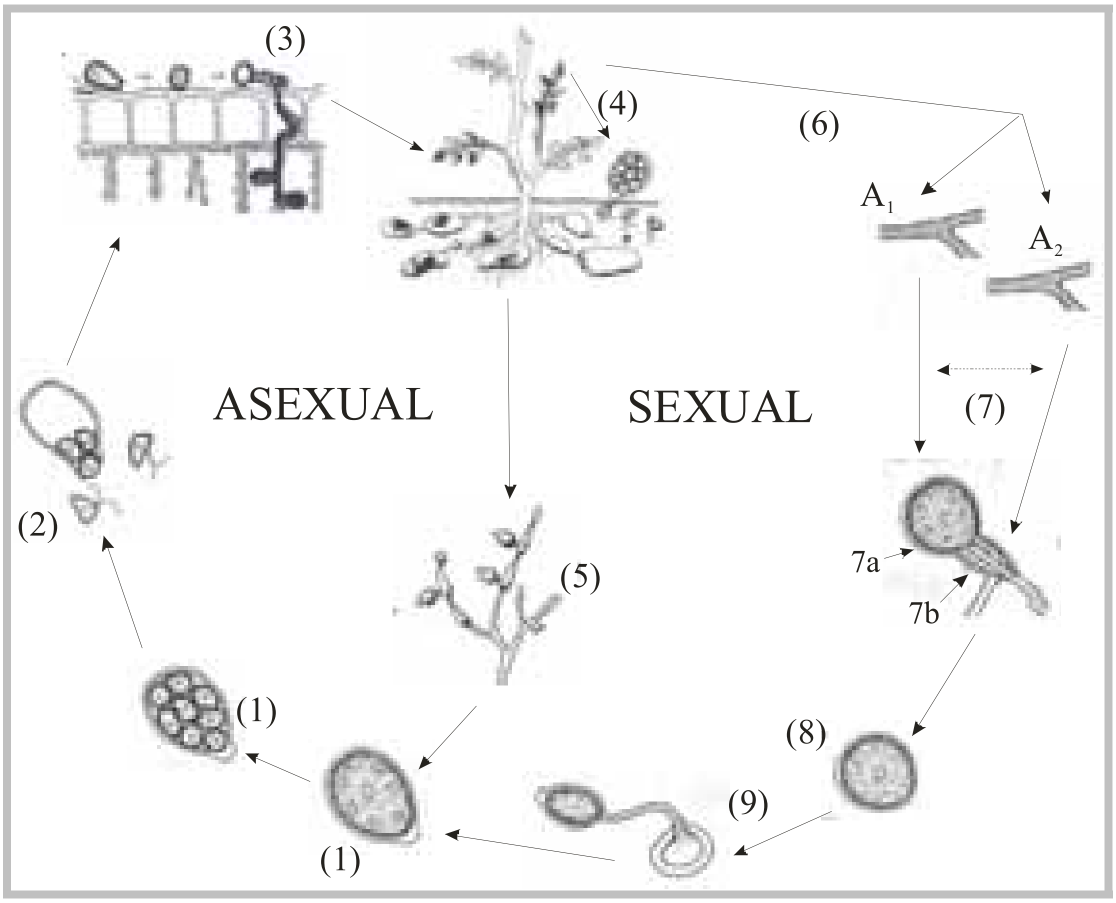

Fig. 1.4. **Life cycle of *P. infestans*** [modified after Agrios 1997 and Judelson 1997]**.**
(1) Sporangium. (2) Release of biflagellated zoospores. (3) Zoospore infecting the plant tissue and feeding via haustoria. (4) Distribution of sporangia. (5) Sporangiophore with sporangia. (6) A_1 and A_2 mating type. (7) Interaction between the mating types by hormones and formation of oogonia (7a) and antheridia (7b). (8) Oospore. (9) Germinating oospore. More details about the life cycle can be found in the text.

and produces a germ tube. The germ tube can penetrate the leaf tissue directly or it enters through stomata. The mycelium then grows between the cells and forms haustoria, which enter the host cell, enabling a biotrophic feeding relationship with the plant cell. The mycelium continues to spread through the fresh tissue, while the infected cells die off. Besides the germination of the zoospore a direct germination of sporangia is also possible. After the infection new sporangiophores emerge from the stomata of the leaves, which produce a large number of sporangia. If the conditions are favorable (cool and moist weather) new sporangia can form within 2.5 to 4 days. Hence, many asexual generations and new infections can occur in one growing season. Newly formed sporangia are washed from the leaves into the soil by rain. The zoospores then germinate and enter the tubers through lenticels or wounds and the disease develops. *P. infestans* over winters in the tubers and new disease cycles start in spring developing from left tubers in the field or from infected seed tubers [Agrios 1997, Judelson 1997].

P. infestans has an A_1 and A_2 mating type and is therefore heterothallic. The two mating types do not differ by dimorphic sexual forms, but rather by hormone production and response. Oogonia (female gametangia) and antheridia (male gametangia) are formed in response to the hormones. Within the mating zone vegetative growth is inhibited. *P. infestans* isolates are generally bisexual, but they preferentially form antheridia or oogonia depending on their mating partner. Haploid nuclei are formed in the gametangia, which are fused in a diploid oospore. From the germinating oospore progeny of the A_1 or A_2 mating type develop [Judelson 1997]. The oospores can survive in the soil for longer periods than sporangia. Under experimental conditions it has been shown that oospores remained infectious for 4 years [Flier et al. 2002].

The symptoms of late blight occur first as water-soaked spots on the leaves. Under moist weather conditions those spots enlarge to brown, blighted areas with diffuse borders. At the edge of the lesions a white downy fungal growth (3-5 mm) appears on the abaxial surface of the leaf. When the disease continues, the leaves soon die off and all aboveground parts of the plant can rot off. Symptoms of late blight on potato leaves can be seen in Figure 1.5. If the weather becomes dry, the oomycete stops its growth, but when it is moist again it can continue its development. Infected tubers first have purple or brownish spots that consist of water-soaked, dark to reddish brown tissue, which extends 5 to 15 mm into the tuber flesh. If the disease develops further, the infected tissue gets hard, dry, and sunken [Agrios 1997].

Fig. 1.5. **Symptoms of late blight on potato leaves** [Windeby, Germany, July 2003].

Importance of late blight for potato cultivation:

Late blight is one of the most devastating diseases in potato cultivation. It can destroy a whole field within a few days, if the conditions are favorable. The first well documented outbreak of late blight in Europe was the so called Irish potato famine from 1845 to 1851. The pathogen, which was previously unknown to the European farmers, could easily spread due to the narrow genetic base of the potato cultivars grown, which did not show any natural resistance to late blight. This outbreak had a large impact on the population of Ireland, who at that time was economically dependent on English landlords. The tenancy they had to pay to their landlords was the crop they produced on the land. Only potatoes were not part of this tenancy and thus were the major food for the Irish population. Due to the late blight epidemic, all potato fields were destroyed leading to the starvation of one million people and 1.5 million Irish left their country (from 8 million inhabitants) (Figure 1.6) [Brown 1993, CIP homepage, www.cipotato.org].

Today, potato cultivation is heavily dependent on fungicide control, but the economic importance of late blight is still severe. It has been estimated that late blight leads to a loss of 10% to 15% of the global annual potato production. This crop loss plus the application of fungicides leads to an economic value of US$ 3 billion [Turkensteen & Flier 2002]. The control of late blight has become more and more difficult since the 1980s. This is due to the replacement of the old late blight lineage US-1 (A_1 mating type only), which was spread worldwide, by a new more aggressive *P. infestans* population (A_1 and A_2 mating types).