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REVIEW

Human-mediated migration of plants, their pathogens and parasites

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Abstract

The adoption of agriculture in several parts of the world during the early Neolithic period led to a fundamental change in human migration. By introducing newly domesticated crops into new environments, pathogens and parasites were also inadvertently transferred from their regions of origin and underwent a considerable population growth. In the newly settled regions, some pests of indigenous plants adapted to new crops by host switching. This review is limited to three basic migration events and mainly to agricultural crops of the temperate zone: (1) the migration of the first farmers from SE Asia to Europe, (2) European expansion from the 16th century onward, (3) modern globalization since the 20th century. Molecular analyses offer the opportunity to study the evolutionary history of pest populations, their origin and dynamics and their spread around the world. Cereals' rusts and powdery mildew, storage insects were the first to spread with wheat species, barley, and pulses from the Levant across Eurasia. The Columbian exchange of crops to and from the Americas brought entirely new pests to Europe while old world pathogens spread to the Americas and subsequently to all other regions colonized by Europeans. Modern globalization further facilitated the spread of pathogens and insects worldwide, as previously inconceivable amounts of agricultural products, business travelers, and maybe tourists have elevated global accessibility. This is illustrated by case studies based on fungi and insects. In the near future, pests will have colonized all crops in all countries where they can exist according to their agro-climatic requirements.

Keywords Blast · Cereals · Potato · Maize · Rusts · Insects

Introduction

Migration is a fundamental characteristic of humanity, one that underwent significant changes when humans adopted agriculture independently in multiple regions worldwide ("centres of origin") starting around 12,000 years ago. Farmers are sedentary and depend on their land to generate sufficient food for themselves and their communities. In the early stages of human history, agricultural communities were forced to migrate because of various factors such as presumably diminishing productivity of soils, epidemics of plant pathogens or locally unsustainable increase in human population size, leading some communities to search for new land (Bocquet-Appel 2011). As a result, farming spread from small regions of origin to vast areas, resulting in the colonisation of entire continents in the course of a few thousands of years. The first of such migrations, the migration of Neolithic farmers from the Levant coast to Europe, has been extensively researched (Shennan 2018).

The center of origin of a crop is generally also its center of deep genetic diversity, as suggested by the Russian botanist N.I. Vavilov as early as the 1920s (Vavilov and Dorofeyev 1992) and nowadays, that notion has been for the most part confirmed by genomic data. Likewise, diversity of a pathogen should follow the same patterns as those of its hosts and very often, but not always, the center of origin of a pathogen corresponds to that of its host (Zaffarano et al. 2006). However, human migration has often redistributed pathogen variation resulting in profound alterations of their shallow genetic diversity structure and on their population dynamics. Most hemibiotrophic and necrotrophic pathogens have a restricted mobility because they are rain-splash dispersed over small distances and undergo a long-distance transport only via seed or plant transport meaning human migration or trade. Biotrophic,

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wind-borne pathogens, however, may cross whole continents within one growth period. Short-term gene flow for these pathogens is of tremendous impact and resistance breeding and agricultural practices speed up pathogens' evolution to the point that often it becomes impossible to track the pathogen back to its origin.

The relationship between plants and their pests is driven by natural coevolution. Due to long-term host-pathogen interactions, hosts develop resistance mechanisms which in turn exert a strong selection pressure on pathogens to adapt. Such coevolutionary relationships usually have evolved in specific regional ecosystems that were separated by geographic barriers (Santini et al. 2018). When crops are moved to new regions, sudden epidemics may occur due to a lack of coevolution, especially if (1) their associated pathogens and parasites have no natural counterparts, (2) crops are naive to newly encountered pathogens and pests, (3) migrated pathogens could adapt to new, naive hosts, e.g., through a host switch mechanism. During the last 200 years, the number of plant diseases has increased almost exponentially, most of them arising from human-mediated alien pathogen introductions (Santini et al. 2018).

A human activity intrinsically linked to agricultural production is trade. Since the development of agriculture, regional trade routes became established and have been used repeatedly at different times. Highly valuable goods, as well as agricultural products and crops started to be transported between the continents. This began around 8000 BCE (before common era) with the spread of agriculture from SW Asia to Europe, intensified throughout the Middle Ages within Eurasia ("silk road") and further expanded after the discovery of the Americas in the 16th century. While, in the early times, crops were simply taken by the people who were migrating, later on also trade itself became important to society. More recently, during the 20th century, massive and fast long-distance movement of commodities was driven by cheaper transport technologies (container ships, cargo planes), by free-trade agreements currently controlled by the World Trade Organization (WTO), and by the internationalization or scaling up of the breeding business in agricultural and horticultural crops. This allowed pathogens to move into new areas of the world within hours by plane or weeks by ship.

Today, foreign crops are used for food supply in most countries (Khoury et al. 2016) and about 69% of national food supplies worldwide come from non-indigenous crops. In many areas of the world, including northern Europe, all or almost all of the cultivated crops are nonnative. Likewise, the pathogens and pests affecting nonnative cultivated crops are likely to have been imported from the areas of origin of these crops. Considering that three crops, namely rice from Southeast Asia, maize from Mesoamerica and wheat from the Middle East, are now globally grown and make up an estimated 42.5% of the worldwide food calory supply (FAO 2016), it is intuitive that global human-mediated massive movement of these crops must have resulted in the parallel massive movement of the pests affecting these crops. While crop movement is inextricably associated with human activities, given the limited competitive fitness of cultivated crops in nature, the movement of their pathogens is in part human-mediated and in part occurs naturally among cultivated fields.

While human diseases that track human migration have been intensively researched in the past decades (e.g., Wolfe et al. 2007; Houldcroft et al. 2017; Spyrou et al. 2019), the impact of human migration on crops and on their parasites and pathogens has been less studied. In archaeological sites, cultivated crops have been found mostly as charred seeds, making the identification of their pathogens extremely difficult. In former times, we were left often with marginal clues regarding the nature and importance of pests and pathogens of plants in the past. Nowadays, DNA barcoding (see glossary) unequivocally identify pathogens; multilocus DNA genotyping, haplotype networks and molecular phylogeny allows for the reconstruction of relationships/similarities among strains from different continents, countries, fields providing clues on likely migration routes of these pathogens.

Modern population genomics, mostly employing selection-neutral DNA markers and sequences, allow us to understand the diversity and population structure of pathogens, and to draw inferences on the isolation and/or connectivity of their populations and on their probable center of origin. As for agricultural crops, pathogen populations characterized by the highest deep genetic diversity (not to be confused with shallow genotypic diversity) are expected to be found in the center(s) of origin where speciation occurred and the history of a species is longest. Coalescent analysis can be employed for comparative studies of the time of divergence of cultivated crops from their wild progenitors and the time of divergence of pathogens associated with wild plants from their descendants associated with cultivated crops (Stukenbrock and McDonald 2008).

In this review, we will concentrate on migrations of agricultural crops and of their pathogens and parasites (Table 1) associated with three important periods in human history: (1) the ancient spreading of agriculture from SW Asia to Europe; (2) the expansion of Europeans to the rest of the world in the Modern Era, and (3) the contemporary globalization of our planet. In this paper, we follow the "Glossary of phytosanitary terms" of the FAO-IPPC, in which a pest is described as "any species, strain or

Table 1 Origin and gradual dispersal of fungal pathogens (yellow) and insects (red) mentioned in this review

Time frame	Origin	Dispersal		
Pathogen		Primary	Secondary	Tertiary
Domestication:				
Zymoseptoria tritici	SW Asia	Europe	America	Australia
Puccinia spp.	SW Asia	Europe	America	South Africa, Australia
Claviceps purpurea	SW Asia	Europe	World	
Sitophilus granarius	Israel	Egypt	Europe	World
Tenebroides mauritanicus	Africa/S-Europe	Europe	America	World
Columbian exchange:				
Ustilago maydis	Mexico	South America	North America	Europe
Setosphaeria turcica	Mexico	USA	Europe, Africa	China
Synchytrium endobioticum	Andean region	Europe	North America	World
Phytophthora infestans	Andean region	North America	Europe	World
Leptinotarsa decemlineata	Mexico	USA	Europe	East Asia
From Europe to the rest of the world:				
Rhynchosporium commune	Scandinavia	North America	South Africa	Australia
Ostrinia nubilalis	Europe	North America	North Africa, Türkiye, Iran	
Globalization:				
Phoma lingam	USA	Europe	Canada	Australia
Magnaporthe oryzae Triticum	Brazil	Bangladesh	Sambia	
Diabrotica virgifera virgifera	Mexico	USA	Europe	
Spodoptera frugiperda	South America	USA	Western Africa	India, China, Australia

biotype of plant, animal, or pathogenic agent, injurious to plants or plant products", a pathogen as "microorganism causing disease" and a parasite as "organism which lives on or in a larger organism, feeding upon it" (FAO-IPPC 2016).

Migration of crops, pathogens and parasites to Europe

First farmers out of SW Asia

Early farming began 10,000–9000 BCE in the Fertile Crescent, a region encompassing today's Israel, Jordan, Lebanon, Syria, South-East Turkey, northern Iraq and western Iran. The earliest sizeable migration event associated with the spread of agriculture occurred in Anatolia at about 8300 BCE (Bellwood 2005). Starting from Anatolia, farming reached southeastern Europe via the Aegean sea and Greece (Shennan 2018) routes in about 6500 BCE. It took about 1000 more years for farming to reach Central Europe and, finally, around 2000 BCE, farming had spread to most of southern Scandinavia (Balter 2012; Skoglund et al. 2014). Recent genetic and genomic studies of ancient DNA from human remains have shown that farming was most likely introduced to Europe by migration of early Anatolian farmers that replaced and intermixed with the indigenous hunter-gatherers (Bramanti et al. 2009; Brandt et al. 2013; Lazaridis et al. 2014; Skoglund et al. 2014; Haak et al. 2015). These early farmers brought with them an assortment of cultivated plants often referred to as a "crop agriculture complex" comprising many of the "founder plants" such as barley, emmer, einkorn, lentil, pea, linseed, chickpea and bitter vetch.

Early crops and their fungal pathogens

The coexistence of wild relatives of crops and their indigenous pests in the crops' center of origin is an important evolutionary feature, because some diseases, still important to today's agriculture, are likely to have co-migrated with their hosts during the spread of agriculture (Table 2). Likewise, disease resistances to pathogens in wild progenitors of our crops is likely to be the result of a coevolutionary process between hosts and pathogens.

These pathogens have certainly challenged farmers since the first plant domestication events, and early farming practices must have shaped their evolution. Because agriculture fostered genetic homogeneity within individual crops, higher plant densities and overall lower plant species diversity, pathogen populations underwent rapid adaptive evolution, becoming more virulent and host-specialized on cultivated crops compared to populations of the same pathogen that remained on wild undomesticated

Table 2 Some pathogens occurring on wild cereals in the Fertile Crescent (Lenne and Wood 1991; Fetch et al. 2003; Schneider et al. 2008; Nevo et al. 2013)

Wild progenitor	Disease common name	Pathogen
Hordeum spontaneum	Powdery mildew	*Blumeria graminis*
	Leaf rust	*Puccinia hordei*
	Net blotch	*Pyrenophora teres*
	Septoria speckled leaf blotch	*Septoria passerini*
Hordeum bulbosum	Stem rust	*P. graminis*
Triticum dicoccoides	Powdery mildew	*B. graminis*
	Leaf rust	*P. triticina*
	Yellow rust	*P. striiformis* f. sp. *tritici*
	Stem rust	*P. graminis* f. sp. *tritici*
Avena sterilis	Crown rust	*P. coronata*
Aegilops, Agropyron, Triticum spp.	Leaf rust, yellow rust, stem rust, powdery mildew	*Puccinia* spp. *B. graminis*
Hordeum murinum, Agropyron repens	Ramularia leaf spot	*Ramularia collo-cygni*

plants (Stukenbrock and McDonald 2008). A good example of such adaptive evolution is provided by powdery mildews on barley (*Blumeria graminis* f. sp. *hordei*), as shown by the high race complexity of these fungi on cultivated barley in Germany compared to the low race complexity of the same fungus found on wild barley (*Hordeum spontaneum*) in Turkey (Loewer and Braun 1996). Modern resistance breeding strategies have further contributed to increase the complexity of races of powdery mildews and rusts.

Wild progenitors are still a rich source of resistance genes. Nevo et al. (2013) found that wild emmer (*T. dicoccoides*) populations in Israel were characterized by the presence of resistance to several leaf diseases, including leaf rust, yellow rust, stem rust, and powdery mildew. Similarly, wild *Aegilops* species are a source of resistance to leaf rust, yellow rust, stem rust, powdery mildew, and to various parasites including cereal cyst nematodes, root knot nematodes, Hessian fly and greenbugs (Schneider et al. 2008), further suggesting that these pathogens and parasites may have evolved in close contact with the progenitors and the relatives of our domesticated wheats. For leaf rust (*Puccinia triticina*) and stem rust (*P. graminis* f. sp. *tritici*) even their alternate hosts grow in the same region (Dawson et al. 2015; Sun et al. 2021). In a natural habitat in Israel, a *forma specialis* of leaf rust was newly described on *Aegilops speltoides*, the putative donor of the wheat B genome (Yehuda et al. 2004). This new *forma specialis*, called *P. triticina* f. sp. *speltoides*, is now assumed to be the progenitor of modern wheat leaf rust, thus providing an interesting example of host-pathogen coevolution in the Fertile Crescent following the wheat evolution (Kolmer et al. 2019).

A nice example is provided by the comparative studies on the evolution of *Mycosphaerella graminicola* (anamorph *Zymoseptoria tritici*) causing Septoria tritici blotch in wheat and the evolution of wheat itself. A worldwide study has shown that *M. graminicola* populations from Israel display the greatest genetic diversity, suggesting a middle eastern origin of this pathogen (Stukenbrock et al. 2011). Interestingly, it has been determined that *M. graminicola* diverged from a grass-infecting *Mycosphaerella* species, discovered in NW Iran, about 10,000 to 12,000 years ago, a time estimate that closely matches that of the early wheat domesticates einkorn and emmer. The spread of wheat growing to all temperate regions of the world increased exponentially the populations of both host and the pathogen, and the constant selection of unique wheat varieties in different ages and world regions combined with a strong host preference for wheat developed by *M. graminicola* (Stukenbrock et al. 2007) transformed this fungus into a fast-evolving pathogen with unique evolutionary patterns (Stukenbrock et al. 2011). In a follow-up study, Feurtey et al. (2023) could show that global diversity patterns of the pathogen match the history of wheat cultivation with a single expansion event from the center of origin, Europe as a bridgehead of distribution and several bottlenecks during the human-mediated transport to other continents. A similar example is provided by the evolution of powdery mildews that are highly specialized on their respective cereal hosts (Wyand and Brown 2003).

Storage beetles and flies accompanied the spread of agriculture

While there are practically no archaeological findings of prehistoric pathogens, insects with a stiff front pair of wings called elytra can still be found in archaeological sites (Panagiotakopulu and Buckland 2018). Among them, storage parasites are most frequently detected. The first such finding is that of a granary (or wheat) weevil in Israel from the pre-pottery Neolithic C era (PPNC, Table 3). We can assume that these storage pests were an inevitable consequence of a blooming agriculture, given that storage of agricultural products is a fundamental prerequisite for an agrarian society (Garfinkel et al. 2009).

Granary weevil and cadelle are convincing examples of organisms likely to have closely tracked the movement of

Table 3 Earliest findings of insect pests in the Neolithic (Panagiotakopulu and Buckland 2018)

Site	Geographic area	Chronology (cal BCE)	Archaeological period
Granary weevil (*Sitophilus granarius*)			
Atlit-Yam	Israel	6200	Pre-pottery Neolithic C
Haçilar	Asiatic Turkey	6400	
Dispilio	Greece	5700	Middle Neolithic
Plaussig u.a.	Germany	5250	Linearbandkeramik (LBK)
Göttingen	Germany	4935–4800	LBK
Cadelle (*Tenebroides mauritanicus*)			
Plaussig	Germany	5250	LBK
Erkelenz-Kückhoven	Germany	5057	LBK

crops by plant domestication, migration, and trade, because they either cannot fly or cannot cross larger distances. Furthermore, they cannot survive harsh winters outdoors. The granary weevil (*Sitophilus granarius*) feeds on grains of wheat, barley, rye and oat. The female lays eggs inside a grain and seals it afterwards making the entry hole in the seed virtually undetectable. The beetle probably originated in rodents' nests in the Fertile Crescent (Panagiotakopulu and Buckland 2018) and later its spread was greatly facilitated by the storage of grains in granaries. Besides the very early finds reported in Table 3 and some mention in Sumerian cuneiform tablets, finds in Egyptian pharaonic tombs (2900–2150 BCE), stables in Amarna (14th century BCE), linearbandkeramik (LBK) settlements in Northern Europe and Roman settlements throughout Europe are known (Patterson 2019). Today, this pest is considered cosmopolitan although it clearly evolved in the Fertile Crescent. Similarly, the cadelle beetle (*Tenebroides mauritanicus*) and parasites of pulse crops are dating back to the 6th and 7th millennia BCE (Antolín and Schäfer 2020). The availability of new habitats and substrates resulted in a rapid adaptation of these insects, which soon became inextricably associated with crops both in the field and in storage. As agriculture spread to new areas, so did the crop-associated pests becoming a worldwide threat.

Late comers from the East: rye and ergot

The presumed ancestor of cultivated rye (*Secale cereale* ssp. *cereale*), *S. cereale* ssp. *vavilovii*, today lives in a large area from the Levant to Afghanistan. Rye was collected in SW Asia as early as the Mesolithic and was probably cultivated by the early pre-pottery Neolithic (PPNA), however, later archaeological finds are scarce and controversial. Rye was first transported to Europe as a weed, as early as the LBK phase, around 4400 BCE (Behre 1992). By the late Bronze Age, weedy rye had spread throughout the eastern and central parts of Europe and had already developed domestication traits such as reduced brittleness, relatively large grains, and a coordination of growing time with other cereals. Neolithic samples in Europe always contained only single grains of rye, which were mixed with other cereals (Behre 1992) supporting the idea of rye being a weed at that time. In Ukraine, Crimea and Georgia, rye cultivation was a standard practice already by the 6th/5th century BCE while the very first indication of rye cultivation in Central Europe dates back as far as 800–600 BCE (Behre 1992). Furthermore, numerous finds of cultivated rye, dated to 100 CE (common era), have been reported from Roman garrisons in the Netherlands, Great Britain, Germany, Switzerland, Austria and Poland (Behre 1992). By the early Middle Ages, rye was the major staple crop from Central and Northern Europe till Siberia.

An important disease of rye is ergot caused by the fungus *Claviceps purpurea*. It preferentially infects open-pollinated grasses, because the florets are wide open to trap pollen and the spores are carried by wind and rain or insects. Infection takes preferentially place on the unfertilized stigma. They germinate, mimic pollen tube growth, and form a purple-black fungal mass, the sclerotium, in the ovule instead of a grain. The sclerotium contains numerous alkaloids that are toxic to humans and animals. Since the fungus can infect several hundred grasses, including all cereals, and can still be observed in many wild grasses today, ergot is probably an ancient disease that may have already occurred in the Fertile Crescent. Thus, it is likely that this may be the disease mentioned on a writing tablet of the Assyrians around 600 BCE as a "noxious pustule in the ear of grain" (van Dongen and de Groot 1995). The Roman historian Lucretius (98–55 BC) named the human disease caused by the toxic alkaloids *Ignis sacer*, i.e., Holy Fire, a name that becomes widely used in the Middle Ages that is called today "ergotism". In the Middle Ages, large ergot epidemics were recorded from the 8th to 11th century (Wozniak 2020). In addition to these written records, which are often ambiguous and cannot be properly attributed, there are finds of ergot sclerotia in archaeological sites that provide undoubted evidence of the spread of the disease. The earliest European find is from emmer (*Triticum turgidum* ssp. *dicoccum*) remains in a settlement of the Lengyel culture near Krakow/Poland, which followed the Linear Pottery Culture, and was dated 3430 BCE (Aaronson 1989). This shows that ergot probably came to Europe early on together with the first crops and was able to spread not only on rye but also on wheat, barley and, of course, various grasses. Further notable finds date back to 1000 BCE to 900 CE and the disease persists to this day.

European expansion

The term “Columbian exchange” was coined by the US historian Alfred W. Crosby in 1972 and used as a book title (Crosby 1972). The term was used to refer to the biological exchanges set in motion by the voyages of Christopher Columbus in 1492. However, its meaning has been expanded to include all of the first modern oceanic European maritime voyages, starting with the discoveries of the Atlantic archipelagos of Madeira and Azores by the Portuguese in 1419 and 1427, respectively, and continuing with the circumnavigation of the West African coast around 1434 (WIKIPEDIA: Age of discovery). These first expeditions were the beginning of numerous naval explorations across the Atlantic, Indian, and Pacific oceans, later followed by land expeditions on all foreign continents continued till the late 19th century (WIKIPEDIA: Age of discovery). Before Columbus’ first voyage to the Caribbean, the calabash gourd (*Lagenaria siceraria*) and the coconut (*Cocos nucifera*) were the only plant species present in both the Old and the New World, while sweet potato (*Ipomoea batatas*) was grown both in the Americas and Polynesia (Merrill 1954, cited after Gibbs et al. 2008). All other crops were grown only in restricted regions neighboring the regions where they originated.

Starting with Columbus’ journey, a large number of cultivated plants were dispersed by the maritime trade around the globe and a lot of pathogens and parasites with them. This is also the first documented example in world’s history of a migration of plants and their pathogens that was not driven by migrating people searching for new agricultural land, but by the discovery of new lands by individual parties resulting in the subsequent colonization of newly discovered lands and in overseas trade. Later, it was European settlers who brought their crops (along with their weeds, pathogens and parasites) to the New World, redirecting the migration path.

Columbian exchange to Europe

Spread of maize and of its fungal diseases into Europe

Sedentary agriculture in the Americas started at about 9000–8000 BCE with the domestication in Mesoamerica of crops such as maize (corn), beans, and squash and the domestication of crops such as potato and tomato in the Andean region (Piperno et al. 2009). The migration of maize outside of Mexico within Mesoamerica started at about 5500 BCE, and by 3000 BCE the crop was known all the way to Peru and Brazil (Raymond and DeBoer 2006). The cultivation of maize appeared much later to the North, and the first records of this crop date back to 1000 BCE in New Mexico and Texas. All of these early migrations were related to the movement of indigenous people via pre-Columbian trade routes (Bedoya et al. 2017).

Maize came to Europe following at least two different routes (Dubreuil et al. 2006). The maize that Columbus brought from the Caribbean belonged to the race group ‘Tropical Flint’ a race group that, being adapted to hot climates and short-day conditions, could only be grown in Europe in Andalusia, southern Italy, and Anatolia. Much more important was the later import of the ‘Northern Flint’. This race group was widely grown in pre-Columbian times along the east coast of North America from the St. Laurent Bay down to the Florida panhandle, thus being adapted to short growing seasons and severe environmental conditions (Dubreuil et al. 2006). Northern Flint became the prevalent race grown in most of the European continent. Several Spanish, Portuguese and French expeditions to Northeastern America took place in the early 16th century (Rebourg et al. 2003) and it is likely the ‘Northern Flint’ maize may have been brought back to Europe during the return journeys of such expeditions (Rebourg et al. 2003). Based on genetic data, Mir et al. (2013) concluded that American Northern Flints were introduced to Europe several times, thus explaining the relatively high genetic diversity in Europe compared to Africa and Asia. There were three ways in which maize diseases were spread in the novel regions. First, some diseases, such as smut, must have been introduced with the first shipments from overseas. Second, maize pests from other plants made a host switch to maize, e.g., the European corn borer, *Ostrinia nubilalis*. Third, other pathogens and pests were later imported from their areas of origin.

One interesting aspect to explore is that of the relationship between the many pathogens and pests of maize that are also found on the native and wild teosinte, the maize progenitor that is fully interfertile with maize. In some cases, genetic evidence suggests that highly diverse pathogen populations in Mexico must have originated there, but, in most cases, it is unclear whether teosinte or maize may have been the original host of pests and pathogens shared by both plant species. Even though resistance genes for several maize diseases, including northern corn leaf blight, southern corn leaf blight, and gray leaf spot, have been detected in teosinte (de Lange et al. 2014), it is unclear whether these may also be present in corn. Although our limited knowledge prevents us from determining the host of origin of such diseases, it does indicate that teosinte has been coping with infection by many of the same pathogens infecting corn, and presents a fine example of a wild host representing a source or a reservoir of infection for a cultivated crop.

The corn smut fungus, *Ustilago maydis*, highly specialized on teosintes and maize, provides instead a good example of a pathogen likely to have evolved on the wild host before jumping to the cultivated one. Molecular analyses have shown that this species evolved from its sister species *U. bouriquetti* 10–25 million years prior to the domestication of maize (Munkacsi et al. 2007). The species first jumped onto maize in its native range presumably at the time maize became domesticated and grown on larger acreages, then it spread worldwide following the international trade of maize by humans (Munkacsi et al. 2008). This is obviously reminiscent of what happened in the Fertile Crescent with other cereals' pests. The relationship between humans and the spread of maize and its pests is strongly supported by various lines of scientific evidence. In particular, the times of evolutionary splitting of populations of the pathogen, for instance between populations on teosinte and those on maize or between those in Mexico and those in the USA, match the times when maize was domesticated and when corn spread northwards, respectively, thus providing strong evidence of the direct effect of humans on the evolution and spread of the smut pathogen (Munkacsi et al. 2008). The jump on maize resulted in a DNA bottleneck, probably due to a founder effect related to the emergence of the first genotypes adapted to maize. Further bottlenecks may have been caused by the long-distance human transport of the pathogen together with maize and followed by subsequent isolation of allopatric pathogen populations and by the adaptation of different fungal genotypes to different world regions (Kellner et al. 2014). This is a fine example of the adaptive selection of pathogens that are adapted to different world regions, but that tend to maintain uniformity of their adaptive genes within a region, a strategy that confers a fitness advantage to these genotypes regionally.

The most common fungus infecting teosinte in the Guatemalan Highlands is *Setosphaeria turcica* (teleomorph: *Exserohilum turcicum*) causing northern corn leaf blight (NCLB), nowadays, one of the most important fungal diseases of maize in the subtropical and temperate regions. A population-genetic analysis of *Setosphaeria* isolates revealed that genetic diversity of the fungus was higher in Mexican populations compared to those from Kenya, China, and Europe, suggesting that *S. turcica* originated in Mexico and only recently invaded Europe (Borchardt et al. 1998). This was confirmed by recent full-genome sequencing of isolates from North America, Europe, and Africa (Vidal-Villarejo et al. 2023). *S. turcica* provides an additional example of local genotypic adaptation of invasive pathogens. The first European reports on NCLB were from Italy and SW-France in 1876 and 1900, respectively (Vidal-Villarejo et al. 2023). The disease was first found in the warmer regions of southern Europe, but starting in 1995 the fungus expanded its range throughout all of the maize cultivation regions in NW Europe. Today it is one of the most common leaf diseases in maize. A recent study on the population structure of European isolates has illustrated that Europe has been colonized rapidly by at least three clonal lineages of *S. turcica,* with the dominance of a single mating type (Vidal-Villarejo et al. 2023). However, an additional fourth cluster, diverse and genetically recombining, was also identified, and this group bears strong genetic similarities with two North American isolates. This more diverse cluster points to a North American origin of the pathogen because there is no evidence of sexual reproduction ongoing in Europe. Its movement by humans to Europe was followed by the dominance of new clonal lineages tracking the cultivation of the crop in NW Europe. Accordingly, estimates of divergence times of all clusters ranged between 816 and 360 years ago, before the first reports of *S. turcica* in Europe but consistent with the times of early European maize cultivation. In contrast, individual lineages within the less diverse clusters emerged less than 40 years ago being caused by a simple increase in population size due to the expansion of the NW European maize cultivation area rather than with a history of rapid selection (Vidal-Villarejo et al. 2023).

Potato and its pests

Potato with its pathogens and parasites are an ideal example of human-assisted migration, given that they all originated in the Americas and could only have come to Europe through human transport of infected tubers. Tetraploid potato species occur in two distinct regions of South America: in the high Andes, from Venezuela to Argentina (Andean landraces, *Andigenum* group) and, with a distinct distribution gap of about 600 km, in south-central Chile (Chilean landraces, *Chilotanum* group). The cultivated landraces from Chile are derived from the Andean landraces and probably originated by crossing with another wild species from Bolivia or Argentina. Potato domestication in the Andes started at approx. 7000 to 5000 BCE (Fuentes et al. 2019). There were several introductions of both Andean and Chilean landraces to Europe, but Chilean landraces were better adapted to local conditions because of their long-day character, and by 1811 they had become the sole source of European varieties (Rodríguez et al. 2010). This is also shown by studies on chloroplast DNA, where a Chilean origin could be proven in 99% of today's European varieties (Ríos et al. 2007). It should also be noted that the establishment of potato as a mainstream and widespread staple food in Europe did not occur until the 18th/19th century.

Late blight of potato caused by the oomycete *Phytophthora infestans* is today the most important potato and tomato disease worldwide. The pathogen is an obligate biotroph and can only survive on living host tissue including the tubers. When two mating types (A1, A2) are available in the same host, a sexual cycle is possible leading to long-living oospores, but the most prominent reproduction is clonal by asexually produced sporangia. These can spread locally by air movements spanning several kilometers (Ristaino 2021), but interregional or intercontinental long-distance transport is only possible by the transport of infected tubers or other plant material. Peru and other South American locations, where the close relative *P. andina* has been detected, and Mexico, where genetic diversity is higher and where sexual reproduction occurs frequently, have both been suggested as the birthplace of the pathogen, without a clear winner (Lucas 2017).

The history of *P. infestans* is an example that includes multiple introduction events by the shipment of infected seed tubers, bridgehead effects, and admixture events. The disease was first detected in 1843 near the ports of New York, Philadelphia and in the surrounding US states (Fig. 1). The first European report occurred in 1844 in the West Flanders town of Kortrijk, 9 km from the French border, where new potatoes from North and South America were imported to advance potato breeding. However, the first symptoms were not taken seriously (Zadoks 2008). A year later, when Flanders researchers replanted some infected tubers, these became the cause of Europe’s first and largest late blight epidemic. By August 1845, the disease had arrived on farms around Paris. A “devastating disease” in potatoes was also firstly reported in Ireland on August 23, 1845. The outbreak destroyed, through September and October alone, the whole potato crop in Ireland. The disease re-appeared in two subsequent years and lasted in total about 5 years resulting in death by starvation related health issues of an estimated 1.5 million Irish people. At the same time, one million Irish people emigrated, mainly to the USA and Canada (Drenth et al. 1993), to escape the famine. By 1845, *P. infestans* had spread over western Europe, reaching the Netherlands, Belgium, France, Denmark, the German Empire, and Switzerland. Yield losses across the countries above ranged between 22 and 65% (Zadoks 2008), but the effects on society were not as dramatic as in Ireland, because cereals supplemented the staple diet of most Europeans from the mainland.

Molecular analyses of isolates from potato leaves preserved in herbaria dating to that period showed that a uniform strain was the cause of the devastating epidemic (Yoshida et al. 2014). The strain is now called FAM-1 (from famine) and its mitochondrial haplotype is called Herb-1 (from herbarium, Saville and Ristaino 2021). This strain was genotyped all over the world, and its most recent

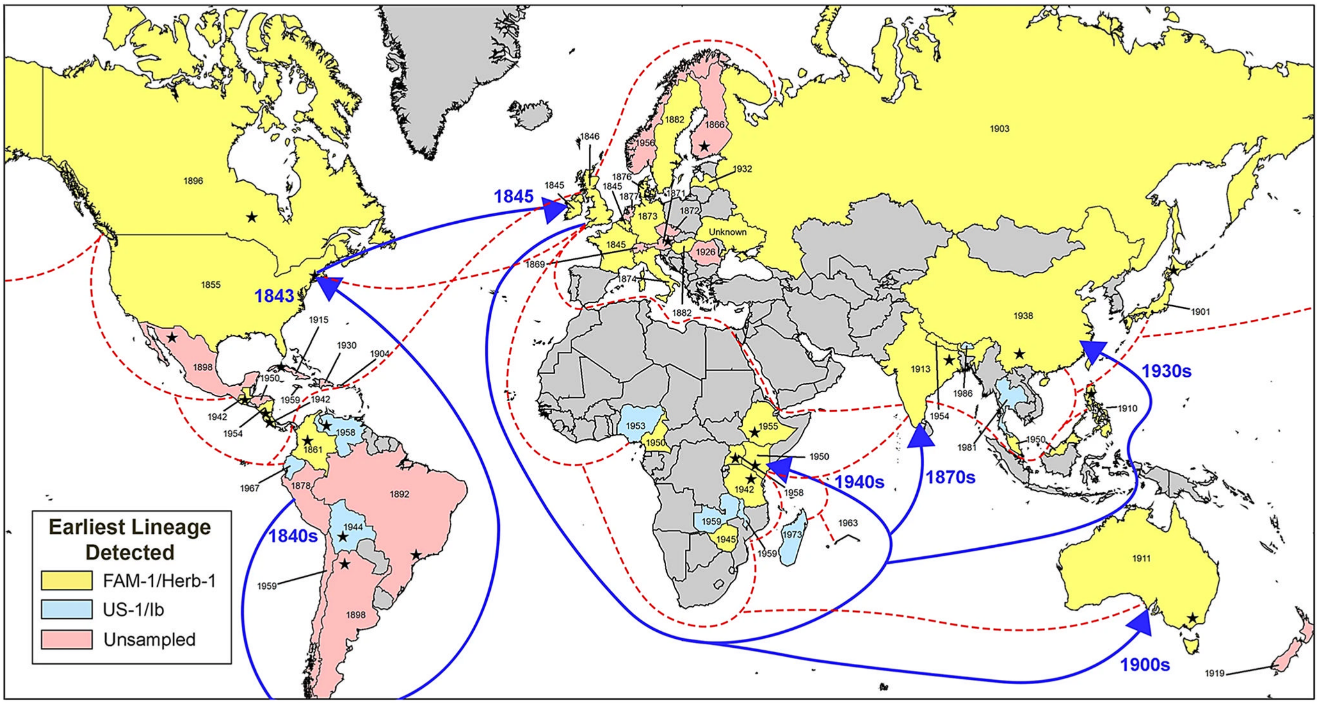

Fig. 1 Global map of early outbreaks of late blight caused by *Phytophthora infestans*. Years within each country indicate the date of the earliest known specimen, stars the approximate location. Dotted lines indicate representative trade routes of the British Empire circa 1932. Arrows indicate the most likely migration path taken by the FAM-1 lineage (Saville and Ristaino 2021, open access)

finding was in Malaysia in 1987 (Saville and Ristaino 2021). The analyses of historic samples illustrate that FAM-1 was “likely spread during global colonization from Europe” throughout the world within 140 years (Saville and Ristaino 2021, Fig. 1). European sailors, missionaries and colonists disseminated potatoes across the world and the authorities propagated potato growing in the colonies as cheap and nutritious crop also for the native people. Later outbreaks of *P. infestans* can be correlated with the main trading routes of the British Empire (Fig. 1). Thanks to the movement of new seed tubers from Europe, *Phytophthora* spread to such remote areas like Tasmania (1907), New Zealand (1919), Madagascar (1973). The real origin of FAM-1, however, is still unclear (Ristaino 2002).

Using DNA genotyping, individual strains can be monitored as they spread globally through human activities. The FAM-1 genotype was replaced by the US-1 genotype during the 1950s. US-1 also spread all over the whole world except for Australia. Interestingly, a greater subclonal variation was found within FAM-1 than in the US-1 genotype (Saville and Ristaino 2021). US-1 was probably dominant in Europe since the 1940s and it was still the predominant lineage in Great Britain in 1978–1982 (Yoshida et al. 2014). The use of the fungicide Metalaxyl strongly limited the incidence of US-1, which is sensitive to this fungicide, and facilitated the emergence of Metalaxyl-tolerant strains (Goodwin et al. 1998).

A crucial migration of *P. infestans* with far-reaching consequences occurred between Mexico and Europe in the early 1980s. Prior to that migration, the A1 mating type was the only one occurring worldwide outside of Mexico. Given that only one mating type was present worldwide, no sexual recombination was possible for the pathogen outside of Mexico. In Switzerland, the A2 mating type was dated to 1981 (Hohl and Iselin 1984), in the former German Democratic Republic A2 was detected in 1980 and in the Netherlands and the UK A2 was dated to 1981 (Drenth et al. 1993). The most likely explanation for the arrival of the A2 mating type was the shipping of infected potato tubers from Mexico to Europe. By the early 1990s, the A2 type was detected in all potato-growing countries in Europe. As a result of sexual recombination between isolates with different mating types, at least 25 fungal genotypes were identified in Europe in 2022 (EuroBlight 2023). There is a 1:1 distribution of both mating types, as expected for a random-mating population. Currently, the range of virulence in European isolates resembles the highly diverse population structure in central Mexico (Drenth et al. 1993).

The A2 mating type is now present across the whole globe, and A2 isolates have sported a remarkable propensity for intercontinental human-mediated migration (Naveed et al. 2017). In 2009 and 2010, a new race of the pathogen caused the first severe outbreak in tomato in the Indian State of Karnaka, leading to losses up to 100% (Chowdappa et al. 2013). All analyzed isolates had identical DNA fingerprints matching the fingerprints of the lineage EU13_A2 (also known as Blue_13) known in Europe since 2004 and likely to have been transported to India on seed potato tubers from Europe. A total of 375 tons of potatoes were imported from the UK during 2005–2006 and 125 tons were imported from the Netherlands in 2006–2007: the EU13_A2 lineage was dominant in both countries at that time (EuroBlight 2023). EU13_A2 was also detected in south-western China one year after the first European description and dominated the population in that region in the 2005–2009 period (Guha Roy et al. 2021). Today, EU13_A2 has been reported in Bangladesh, Nepal, Pakistan, and Myanmar and appears to be slowly replacing the US-1 lineage in East Africa (Naveed et al. 2017).

Besides pathogen transport on infected potato seed tubers, long-distance pathogen migration is also possible via the movement of infected tomato plants. This pathway led to a 2009 pandemic in the USA caused by the wide distribution of strain US-22 via infected tomato plants from a single national supplier (Fry et al. 2013).

Potato wart disease, caused by *Synchytrium endobioticum,* is a classic example of a disease that can only have been spread long-distance by human-mediated migration. This soilborne biotrophic chytrid fungus, in fact, has no long-distance natural dispersal mechanisms, and infection of new tubers relies on soilborne resting propagules, called sporangia or sori (Obidiegwu et al. 2014). The pathogen is believed to have originated in the Andean region where it co-evolved with its solanaceous hosts (van de Vossenberg et al. 2022). To date, no molecular analyses of *Synchytrium* have included South American populations of the pathogen. However, all five monogenic resistances known today (*Sen1*-*Sen5*) were recently found in several wild potato species including *Solanum tuberosum* ssp. *andigena*, a potential progenitor of cultivated potato (Prodhomme et al. 2020). A long-distance transport is only possible by internally infected tubers or seed tubers with adhering infested soil particles. Mitochondrial genomic variation of *S. endobioticum* revealed that the pathogen was introduced to Europe at least three times (van de Vossenberg et al. 2018).

Outside South America, the disease was first found in England as early as 1876 or 1878 according to non-scientific reports (Obidiegwu et al. 2014, Fig. 2). At that time, potatoes had already been cultivated in Europe for about 150 years. Other early individual appearances occurred in today’s Czech Republic in 1888 and in Finland in 1893 (Stachewicz 1989). The first scientific report of the disease was made in 1896 by the Hungarian phytopathologist K. Schilberszky on tubers that were grown locally from seed tubers imported from England

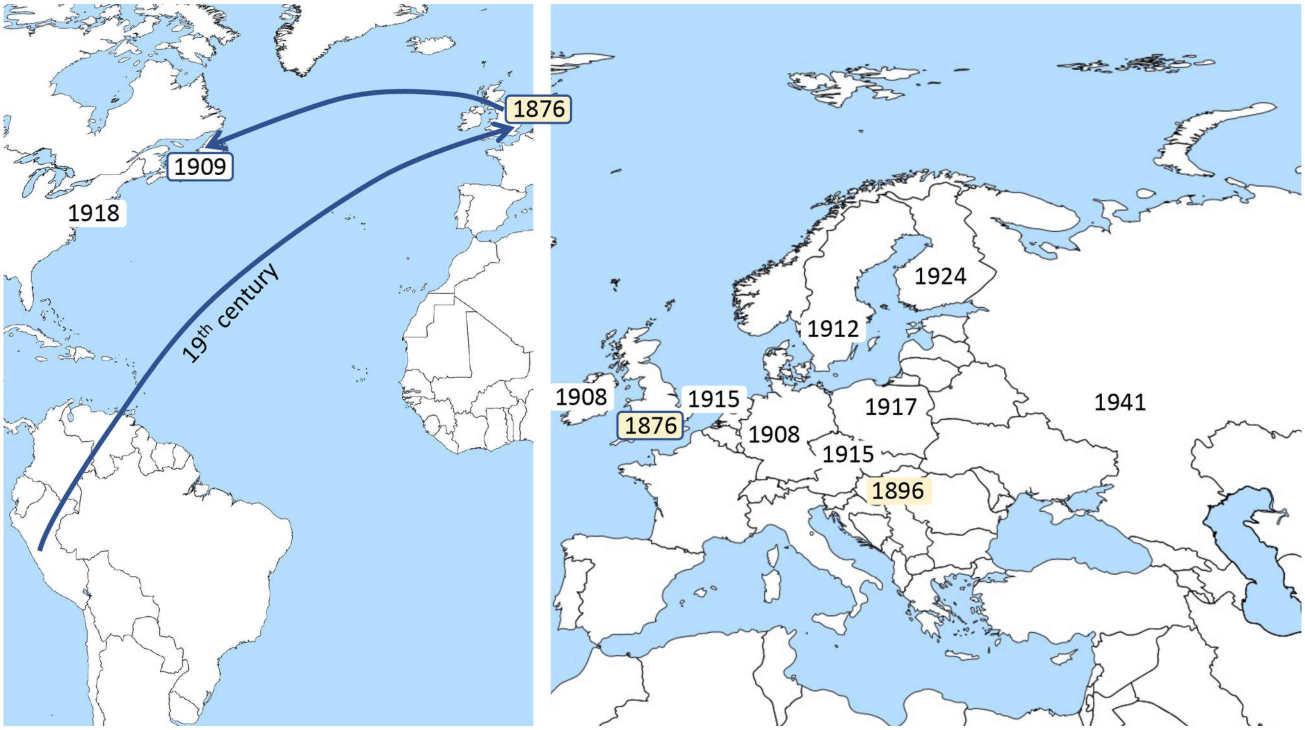

Fig. 2 Early distribution of the potato wart disease; colors represent the century (data from Hampson 1993; Obidiegwu et al. 2014; Stachewicz 1989; Map WIKIMEDIA COMMONS: Cbrittain10, CC BY-SA 3.0)

(Hampson 1993). At that time, England had already established a successful potato breeding and exported elite cultivars as seed potatoes in several parts of the world.

The disease was most likely introduced to England after the great potato famine (1845–1849) caused by *P. infestans* when South American potatoes were imported to find disease resistances to *P. infestans* (Obidiegwu et al. 2014). The disease spread rapidly through Northern and Eastern Europe during the beginning of the 20th century (Fig. 2) and Orton and Field (1910) as early has 1910 had called wart a "dangerous European disease" and feared the introduction to the USA. Thousands of outbreaks were reported in England and Germany between 1919 and 1923 (Hampson 1993). The shortage of seed potato during the First World War led to the import of British potato from infested fields to new regions and during the Second World War German troops are believed to have brought potato wart to the former USSR (Hampson 1979).

In 1909, the disease was brought by human migration from England or Scotland to the island of Newfoundland, at that time not yet a part of Canada (Hampson 1993). Unsubstantiated hypotheses suggested that immigrating miners brought infected potato tubers in their bundles (Obidiegwu et al. 2014). A very detailed analysis of the spread of the disease in Newfoundland showed that the distribution within the island was clearly related to human transport on the sea and through roads or rail (Hampson 1993). The first phytosanitary measures were applied in 1910 to prevent the spread of the disease to mainland Canada (Potato Canker Act, Newfoundland, enacted 1911). In 1912, a ban of potato imports from the United Kingdom to Canada and the USA was passed by the legislature. Unfortunately legislative measures did not take into account that potato wart occurs both in agricultural fields and in private gardens where potatoes are grown. Thus, the first report of wart in the USA came from small garden plots in 27 communities in Pennsylvania in 1918 (Obidiegwu et al. 2014). Today, potato wart has been reported from nearly every potato-growing country (EPPO Global database 2023a), including most of Central, Northern and Eastern Europe, Türkiye, South Africa and, since 2005, even China and New Zealand. However, the distribution within a country is fragmented due to strict regulatory strategies.

Another potato pest coming from America is the Colorado potato beetle (CPB, *Leptinotarsa decemlineata*, meaning "ten-striped lightfoot" in Latin). This beetle originated in Mexico, where it still feeds on wild relatives of potato like *Solanum rostratum* (Grapputo et al. 2005). The CPB and its larvae feed on the leaves, and they can detoxify even high concentrations of solanine. CPB can eat entire potato fields bare within a short period of time. Additionally, other solanaceous crops, especially tomato, bell pepper, tobacco can also be attacked. The beetles are poor fliers, but they can use high winds for long-distance migration (Grapputo et al. 2005).

CPB was first detected in the USA along the Nebraska and Iowa border in 1811, most likely on wild *S. rostratum* plants (Izzo et al. 2018). The transition to potato as CPB's primary host occurred during the first commercial potato growing of the 19th century. In 1859, the first mass reproduction of the beetle was observed in Nebraska. In 1865, CPB crossed the Mississippi River and broke into Illinois; by 1870, it had established in Indiana, Ohio, Pennsylvania, Massachusetts and New York State (Izzo et al. 2018). By 1874 it had reached the Atlantic Coast (Jacques and Fasulo 2020). It reached Europe from the US East coast at the end of the 19th century presumably by ship transports. It was first sighted in 1877 in the docks of Liverpool, in Rotterdam and at two German locations (Mülheim/Rhein, Torgau) (WIKIPEDIA: Kartoffelkäfer). Considerable efforts were immediately put in place to contain the infestation and at least the first invasion in the UK was not successful (WIKIPEDIA: Colorado potato beetle). In 1887 and 1914, however, new, larger infestations appeared in Europe. In 1922, the beetle became established near a USA military base in Bordeaux and destroyed all potato stocks in an area of 250 km^2 (Fig. 3). The CPB has no natural predators in Europe and therefore it can reproduce unhindered under suitable weather conditions. Analysis of mitochondrial (mtDNA) and nuclear DNA (nDNA) have revealed that beetles from a single successful founder event invaded Europe (Grapputo et al. 2005, Fig. 3). Only one mtDNA haplotype (out of 20 known haplotypes found in North America) is present in Europe: the same haplotype is also the dominant one in Idaho, possibly suggesting Idaho may be the source for the European population. Alternatively, several introductions of the same haplotype might have occurred. This is supported by the considerable nuclear genetic variation found in Europe, albeit at a lower level than that observed the USA. High migration rates were detected within Europe: this may

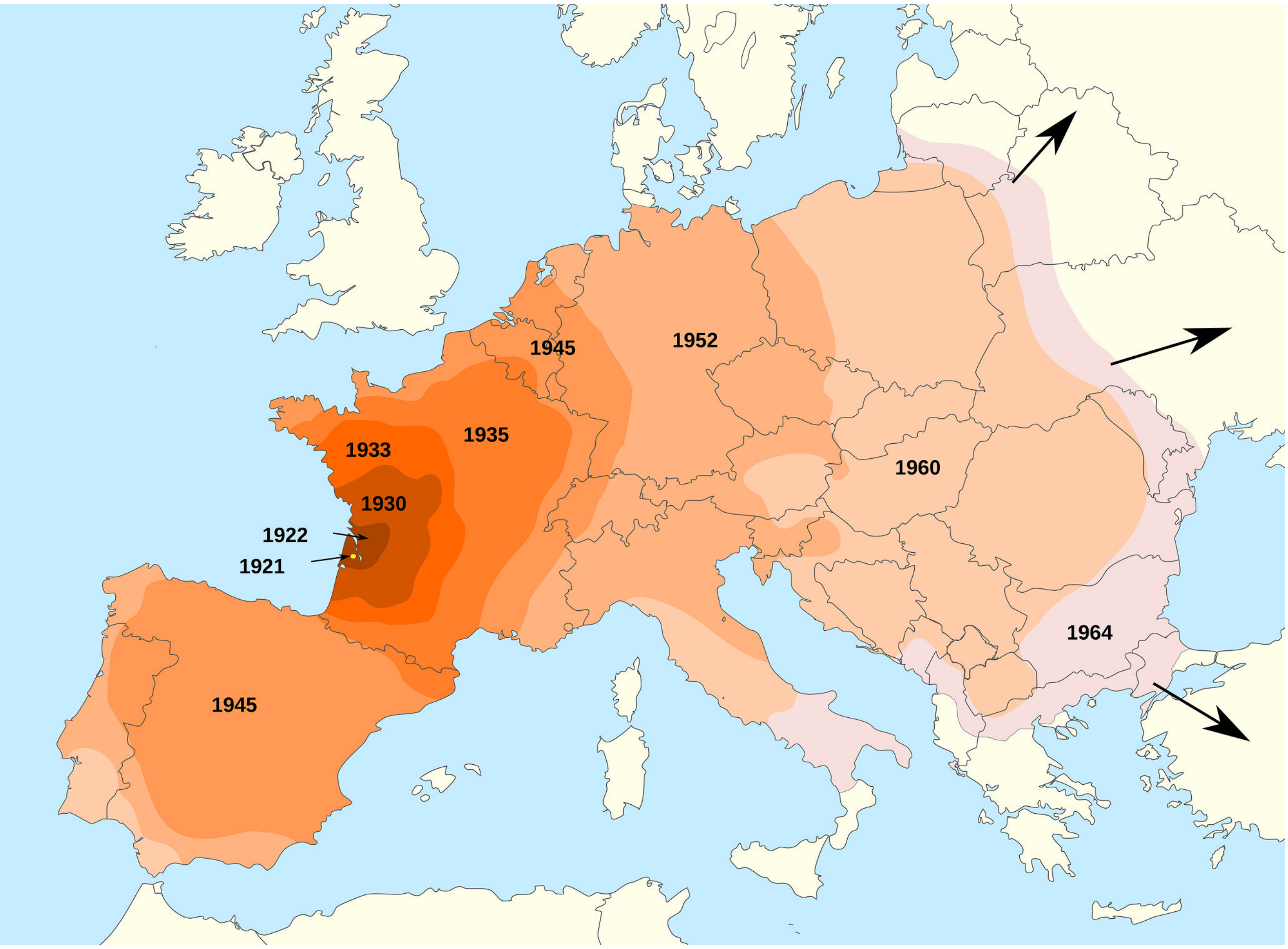

Fig 3 Expansion of the Colorado potato beetle in Europe 1921–1964 (WIKIMEDIA COMMONS: Doryphore - expansion en Europe.svg/ Spedona, CC-BY-SA 4.0; data retrieved from Johnson 1969, p. 410)

be the result of the intensive commercial trade within Eurasia. In Finland, a country recently invaded by the CPB, for example, several accidentally introduced beetles were found in lettuce from supermarkets and restaurants (Grapputo et al. 2005).

Earlier invasions in northern Europe were not successful, but this might change due to warmer temperatures. Northern Russia has also been successfully invaded by the CPB. Currently, the beetle is spreading eastwards through Central Asia towards Siberia (Grapputo et al. 2005). European populations were reported to have arrived in western China between 1979–1993 (Liu et al. 2012). The beetle reached Xinjang by 1993, and became established at least in three distinct regions (Yang et al. 2021). Yang et al. (2021) detected low genetic variation in western China, a region colonized by CBP from northeastern Kazakhstan, but very high diversity was detected in eastern China, a region that may have been colonized by CPB from southern Siberia. Thus, CBP was able to colonize with human help the vast area of northern Eurasia within about 100 years and is nowadays distributed on the whole northern hemisphere (EPPO Global Database 2023b).

From Europe to the rest of the world

The effects that the Columbian exchange and the further European maritime travels had on plants and their parasites and pathogens cannot be overestimated. The Europeans did not only import crops from the Americas, including maize, potato, red pepper, tomato, but settlers also took their own crops, including wheat, rye, barley, outside of Europe. This process occurred progressively, as Europeans explored and often conquered new lands. For example, papaya ring spot virus (PRSV) originated from Old World viruses of cucurbits between 1600 BCE and 250 BCE (Gibbs et al. 2020). However, the origin of papaya is in tropical Southern Mexico and Central America. Around 1550 CE, the Spaniards took papaya seeds to the Philippines, and from there to Malacca, India, and finally to Naples in 1626 CE, so that now papaya is commonly grown in all (sub)tropical regions of the world. In each region where papaya and the cucurbit-derived PRSV accidentally came into contact, "papaya ringspot disease" developed (Gibbs et al. 2020). This disease is thus a fine an example of a disease that was directly born out of the Columbian exchange. Similarly, the Americas and Australia where originally free from diseases of small-grain cereals, just because there is no natural occurrence of progenitors or direct relatives of small grain cereals in these continents. Due to the intensive interaction between European countries and their colonies, Europe often served as a bridgehead for further global dissemination of pathogens and pests.

Spread of a European-derived pathogen associated with agriculture

The versatility of pathogens is immense. When agriculture extended from its areas of origin following human migration, vast areas of former uncultivated regions became arable farmland, and this provided ideal conditions for parasites and pathogens associated with the crop to increase their population size. Eventually, some native pests of weeds performed a host switch in the newly cultivated regions and invaded foreign crops. This happened in Europe with at least *Rhynchosporium commune* causing scald in barley, other *Hordeum* species and *Bromus diandru*. Later on, this disease spread across the whole world wherever barley is grown.

R. commune is a haploid fungal pathogen. Molecular analyses of 1600 isolates from all over the world has shown that the center of origin is not the Fertile Crescent (Zaffarano et al. 2006), but most probably Scandinavia. This hypothesis is supported by the fact that Scandinavian populations had: (1) the largest effective population size, (2) the highest allelic richness, (3) the greatest richness of private alleles, (4) while being the largest source of migrants to the rest of the world, compared to any other population (Linde et al. 2009, Fig. 4). The Near Eastern populations in the region where barley is originary did not show any of these features. Furthermore, the effective population size in countries neighboring Scandinavia was shown to be about four times smaller than that in Scandinavia and effective population size further decreases as one approaches the Near East (Fig. 4). The origin of *R. commune* as a barley pathogen was estimated to date back to 1600–800 CE (Zaffarano et al. 2008). This fits well with the time frame when sedentary agriculture first occurred in Scandinavia, 3000–1000 BCE (Skoglund et al. 2014). During this period, the pathogen might have jumped from a wild grass to cultivated barley providing strong evidence that man-made agriculture has led to the evolution of new pathogens by bringing naive cultivated crops together with pathogens from other parts of the world.

Nowadays, this pathogen can be found worldwide. Because *R. communis* is rain splash-dispersed and moves mainly within a field, each long-distance migration must be facilitated by humans, either by moving the host plant to neighboring regions (short-distance migration) or through seed-borne inoculum that is inadvertently sent along during shipment (long-distance migration). The latter is supported by the presence of latent seed infections without symptoms. Estimates of the number of migrants showed specific routes of the fungus around the globe (Fig. 4). Barley was brought to South Africa by the Dutch about 350 years ago, to California by Spanish missionaries about 250 years ago,

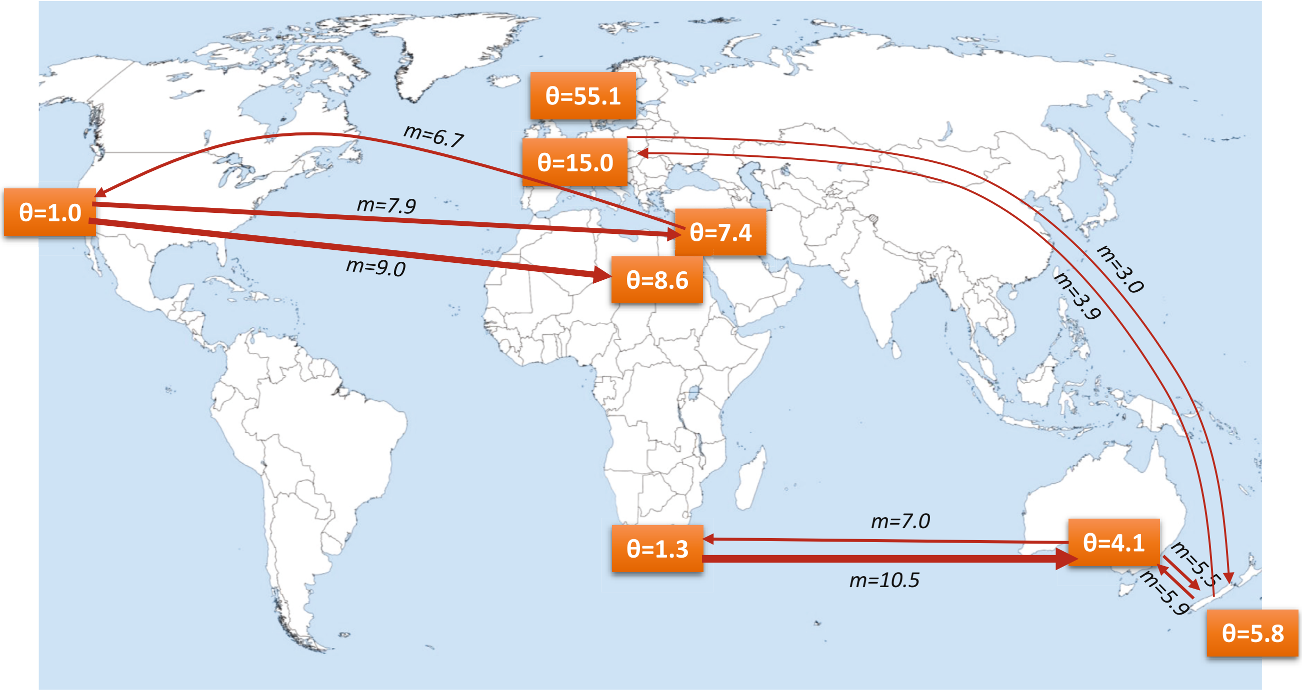

Fig. 4 Effective population size (θ) and estimated number of migrants (*m*) of *Rhynchosporium commune* populations from four continents (data from Linde et al. 2009, map: WIKIMEDIA COMMONS: Petr Dlouhý, public domain)

and to New Zealand by the British about 150 years ago (Linde et al. 2009). The low effective population size (Fig. 4), low genotypic diversity and low allele richness in these regions indicate more recent founder effects and coalescent genealogies have shown that a population expansion occurred during the last 250 years (Zaffarano et al. 2009). This coincides with the period when barley was introduced to continents outside of Europe and with the further increase of barley acreage by intensive agriculture.

Although the shorter migration from Australia to New Zealand could alternatively be explained by prevailing air currents, other long-distance exchanges of migrants were most likely mediated by humans, e.g., by the exchange of breeding material between South Africa and Australia, New Zealand and Europe as well as between California and the Middle East and NE Africa (Linde et al. 2009). This is consistent with the hypothesis, that the pathogen moved from its center of origin only recently and consists now of multiple founder populations that are reproductively isolated from one another due to geographic distance, given that only restricted long-distance movement occurs (Zaffarano et al. 2009).

Cereal rusts colonize the world

Wheat is affected by three species of rusts, yellow (stripe) rust (*Puccinia striiformis* f. sp. *tritici*), brown (leaf) rust (*P. triticina*), and stem rust (*P. graminis* f. sp. *tritici*), all of which originated in the Old World (Europe, Central Asia). The oldest stem rust spores have been found on wheat ears grown in Israel about 3300 years ago (Kislev 1982), but it is presumed these rusts may have originated much earlier on wild progenitors of wheat in SW Asia. Rusts have robust spores enabling long-distance transport by prevailing winds or by human transport, however, it is not easy to differentiate these two different routes. Regions within Eurasia are interconnected by windblown asexual spores. For intercontinental transport it is crucial that the survival of urediniospores may last for more than 2 weeks on clothes, vehicles, tools or luggage at ambient temperatures (GRDC 2016). Cereal rusts started spreading worldwide about 500 years ago with the transport of European cereal crops to the Americas, Australia, and South Africa.

Wheat stem rust (*Puccinia graminis* f. sp. *tritici*) was introduced to North America by European settlers who brought with them its intermediate (alternate) host, barberry (*Berberis vulgaris*). They valued this European shrub for its vitamin-rich berries, hard wood and as a hedge around home gardens. Over time, barberry became invasive and spread throughout the North American continent. When settlers began converting large areas of prairie to wheat fields ("wheat belt"), stem rust found its ideal conditions, i.e., a main host (wheat) that allowed it to multiply asexually *en masse* in the summer, and an intermediate host (barberry) that gave it a sexual phase in the spring.

The first epidemic was described in 1878 (Hamilton 1939), but the epidemics of 1904 and 1916 were massive (Roelfs 1978). Losses of US$10 million occurred in Minnesota, North and South Dakota alone. Stem rust destroyed more than 20% of the wheat crop several times in subsequent years between 1917 and 1935. In the worst epidemic of 1935, more than 50% of the wheat yield in North Dakota and Minnesota was lost to stem rust, and stem rust destroyed about 10–20% of the yield in multiple years to follow and as late as the 1950s (Leonard and Szabo 2005). In 1919, the USDA (United States Department of Agriculture) started a barberry eradication program which was implemented in 18 U.S. states, until it was permanently suspended in 1980. The program resulted in stem rust becoming a minor problem on wheat and other small grains in North America (Peterson et al. 2005). The first wheat stem rust outbreak was documented in South Africa in the Western Cape in 1726 according to Pretorius et al. (2007) while the first wheat growing was dating back to 1652 (Nhemachena and Kirsten 2017). Intercontinental movement of airborne spores from Asia or South Africa to Australia has also been hypothesized (Watson and de Sousa 1982), and it is possible that stem rust arrival and establishment on susceptible Australian native grasses may have predated the arrival of European settlers.

Nowadays, wheat leaf rust (*P. triticina*) is another cereal rust with a worldwide distribution. It was first reported in South Africa at the beginning of the 18th century (Pole Evans 1911), possibly as early as 1708–1710, but as of 1727 the rust had decimated the wheat crop. The early settlers had brought these rusts with them around 1680, when the first cereals were planted in the region (WIKIPEDIA: Geschichte Südafrikas). A large DNA-based study of the worldwide wheat leaf rust population has showed the presence of a close genetic relationship among leaf rust populations from different continents (Kolmer et al. 2019). The populations from North and South America are closely related with those from Europe, the Middle East, Central Asia and Russia. To date, a small number of identical genotypes persists in different continents. The authors speculate that North and South America might have received the fungus during the European colonization. Recent intercontinental migrations have also been detected: for example, a genotype that was first found in the mid-1990s in the USA and Canada made its way to South America (1999) and France (2000–2001 Kolmer et al. 2019).

Wheat yellow rust (stripe rust, *Puccinia striiformis* f. sp. *tritici*) is a pathogen that is notorious for its migratory spores. The disease first occurred in the USA around 1915 (Carleton 1915), most likely arriving on American soil with the shipments of European wheat cultivars in the early 1900s (Ali et al. 2014a, Fig. 5). In very susceptible cultivars, the fungus does not only infect the leaves, but also the heads and produces spores adhering to the seeds which become themselves infectious. The movement of infected seed thus can result in the movement of the pathogen. Initially, wheat yellow rust was significant only in areas with cool summer temperatures like NW Europe (for review Schwessinger 2017). However, the emergence of new races in the near-Himalayan region (e.g., ‘Warrior’, Ali et al. 2014b) and in Ethiopia (*PstS1*, *PstS2*, Schwessinger 2017), with varying adaptation to warmer climatic conditions, has allowed the pathogen to spread worldwide, including warmer regions (Fig. 5). Currently the disease is present as far as Australia, Middle East, Central Asia and South Africa, and is also reported from the warmer Southeastern USA (see Walter et al. 2016)

For leaf rust and especially yellow rust, Australia provides a giant laboratory for phytopathologists. Because no wheat, barley or their direct relatives are native to the region, these cereal pathogens have been introduced from outside. While leaf rust reached Australia as early as 1825 (McAlpine 1895, cited after Kolmer et al. 2019), yellow rust first appeared in eastern Australia as late as in 1979, and it was clearly a NW European race (Fig. 5). It is likely that some spores had entered the country adhering to clothing with tourists or businesspeople, despite harsh quarantine measures (Kolmer 2005). Molecular markers indicated that yellow rust isolates sampled across more than 30 years (1979 to 1991) all had the same genotype supporting the hypothesis that they were derived from a single introduction (Steele et al. 2001). A second invasion occurred in 2002 to Western Australia (Wellings et al. 2003), most probably by natural long-distance dispersal by prevailing winds from Africa (Fig. 5). DNA patterns of the new race were totally different from already existing races in Australia (Wellings et al. 2003).

The journey of the European corn borer (*Ostrinia nubilalis*) to North America

In the USA, the parasite *Ostrinia nubilalis* is called the “European corn borer (ECB)” because of its European origin. First detected by Jacob Hübner in 1796 in Hungary and Austria without noting the host plant (Caffrey and Worthley 1927), the European corn borer is described as a polyphagous insect that is native to Europe, Northern Africa, and Western Asia (Willett and Harrison 1999). Around 1835, it was firstly recorded in Europe as a seriously damaging insect in maize, hops, millet, hemp, and broomcorn (Caffrey and Worthley 1927). The latter crops might have been reservoirs of the insect prior to the maize introduction to Europe in the 16th century.

The corn borer came to North America probably on broomcorn (*Sorghum bicolor*) from Hungary or Italy

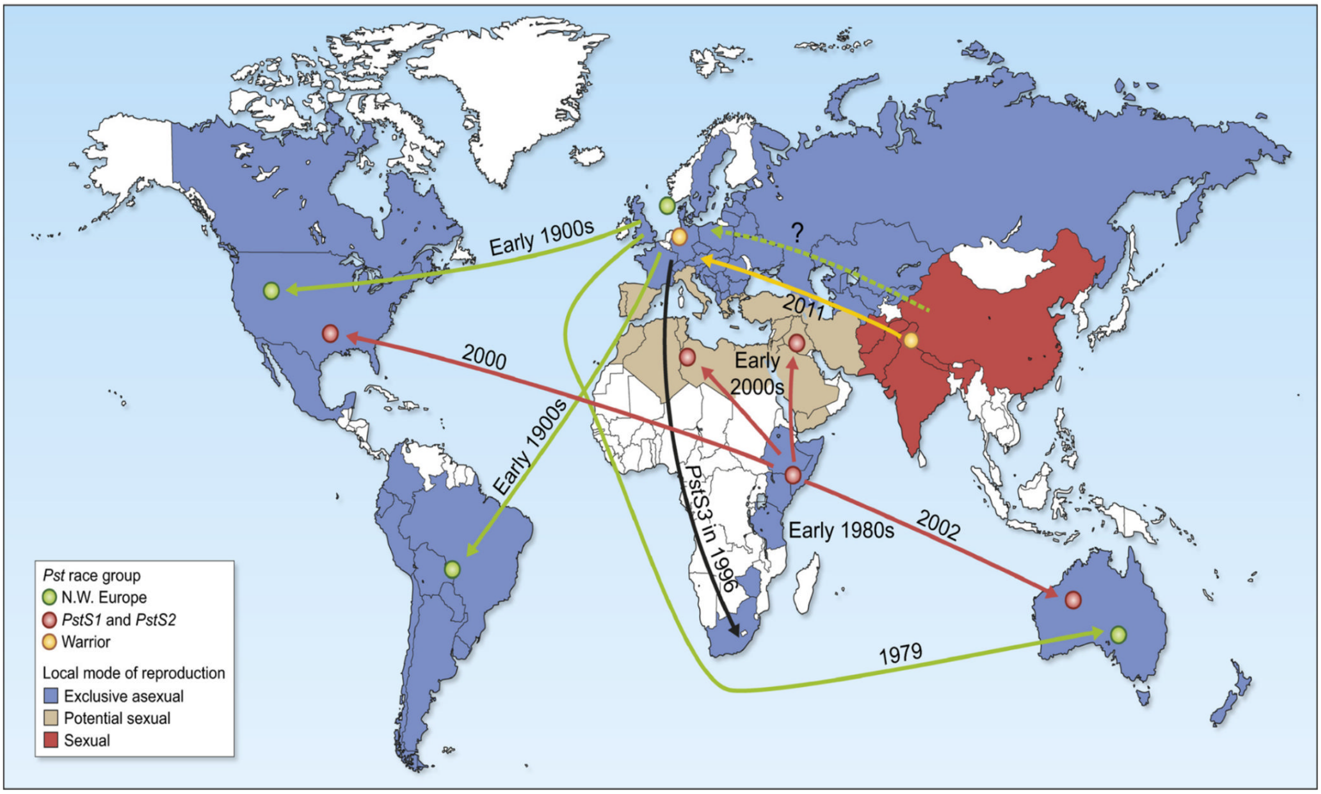

Fig. 5 Intercontinental migration of important yellow rust race groups and primary mode of reproduction (Schwessinger 2017, open access)

(Smith 1920) in 1909–1914, when at least 12,000 tons of the crop were imported. The first insects were recorded in 1917 near Boston (Fig. 6). Because the damage on plants had been observed prior to the identification of the European corn borer and the area of infestation was already sizeable, the date of its introduction was estimated to be circa 1910. During the 1920–1923 period, federal inspectors repeatedly found living larvae of the parasite in the upper part of broomcorn used at that time for manufacturing ordinary house brooms (Caffrey and Worthley 1927). Its spread across North America has been well documented (Caffrey and Worthley 1927; Hudon and LeRoux 1986, Fig. 6). As judged by the insect's diversity, ECB seems to have been introduced into North America several times (Willett and Harrison 1999). Today, ECB thrives in all maize-growing areas east of the Rocky Mountains with considerable losses for farmers and being a main incentive for growing of genetically modified maize.

Globalization in the 20th/21st century

Modern migration

The globalization of markets brings agricultural commodities thousands of kilometers away from where they were originally grown. In 2021 alone, there were 2.3 million merchant ships of which 973,743 ships were bulk carriers and 305,313 container ships trading internationally 11 billion tons of cargo (UNCTAD 2023). Global trade of agricultural products reached 482 million tons in 2022 (FAO 2023). Cereal exports are dominated by ten countries, notably the United States, Canada, France, India, Argentina, Ukraine, Germany, Australia, Russia, Italy with a total of 60% market share while among the main importers China, Japan and Mexico can be found. This means that pathogens and pests might be transported in large amounts from the Americas and Europe to Asia and vice versa together with the goods that are being traded. For example, two major tree pathogens, namely the chestnut blight fungus (*Cryphonectria parasitica*) and the Dutch elm disease fungus (*Ophiostoma ulmi*), were introduced to North America in the last century by transport of infected plant material from Asia (Milgroom et al. 1996) and from Asia via Europe (Brasier and Buck 2001), respectively. More recently, the Asian long-horned beetle (*Anaplophora glabripennis*) native to China and Korea was first detected in the USA in 1996 and soon afterwards in Canada (Hu et al. 2009). In Europe, the beetle was introduced from Asia in non-disinfected solid-wood packing material shipped to Austria in 2001 and has not yet been eradicated. As of 2022 it has been sighted in nine European countries, from France in the west, Italy in the south to

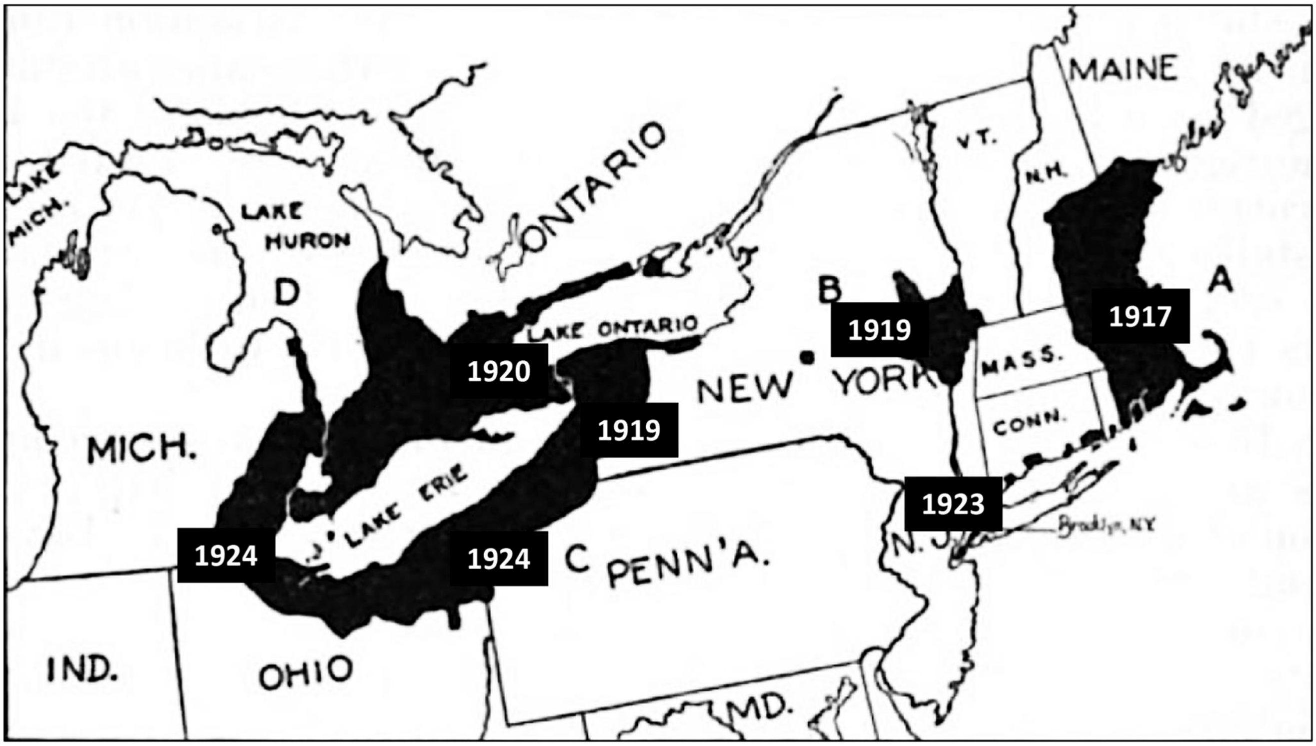

Fig. 6 Map of the first occurrence of European corn borer in North America by January 1, 1925 A. New England area, B. Eastern New York area, C. Lake Erie area, D. Canadian area (original map from: Caffrey and Worthley 1927, years were added)

Finland in the northeast (Kraus 2023). Likewise recent is the introduction of the Sudden Oak Death pathogen (*Phytophthora ramorum*) in Europe and in the USA through infected ornamental plants. While the center of origin of the pathogen is known to reside in the mountains of east and southeast Asia (Jung et al. 2021) its movement from Europe to North America has been proven thanks to population genetics analyses (Grünwald et al. 2012).

With international travel and commerce on an exponential rise, natural barriers to species spread are traversed. Insects can survive even in wheel bays of a Boeing 747B aircraft with minimum temperatures within the wheel bays ranging from +8 °C to +25 °C (Russell 1987). Mosquitos (*Culex quinquefasciatus*), house flies (*Musca domestica*), and flour beetles (*Tribolium confusum*) survived there to 84–99% on international flight routes for 6–9 h.

One additional pathway of long-distance introductions of both pest and pathogens is provided by the movement of troops during military operations. The strongest evidence supporting a military pathway for a pathogen is that of the conifer pathogen *Heterobasidion irregulare* transported from the Eastern USA to Italy by the 5th US Army division on green lumber used for crating and other military installations (Gonthier et al. 2004; Linzer et al. 2008). The introduction of several insects has also been shown to have been caused by the military while evidence about the military introduction of pathogens other than *Heterobasidion irregulare* seems circumstantial at best (Santini et al. 2023).

Within America, fresh products are shipped from Mexico, California, and Florida to the northern USA and Canada to supply people with vegetables and fruits. A second big player is the trade within the EU, where millions of tons of fresh products are transported every year from Spain, Italy, and the Netherlands to the rest of Europe. Germany alone imported 6.2 million tons of fresh fruit and 4.9 million tons of fresh vegetables in 2022 (DESTATIS 2023). Additionally, there are also significant trade relations between subtropical and tropical countries and the main hubs. Asparagus from Chile, grapes from South Africa or bananas from Costa Rica have long been part of everyday life in European industrial countries. And every fruit and every batch of vegetables can contain foreign pathogens and parasites. In the following section, we will present some examples of the global transportation of fungi and insects as a result of: (a) the extension of acreages of originally European crops to the whole temperate climate zone where novel pathogens may coexist (blackleg of rapeseed), (b) by grain trade (wheat blast), (c) by commerce (maize corn root worm), and, (d) potentially by tourism or business trips (fall army worm).

Case studies

Worldwide spread of rapeseed growing and of associated black leg disease

Rapeseed (*Brassica napus*) is an example of a relatively young crop that originated in Europe in the 14th century and spread throughout the northern hemisphere after the Second World War (Schröder-Lembke 1989). Accordingly, it is easy to follow how oilseed rape diseases and parasites did spread as a result of the increasing cultivation of oilseed rape. An example is provided by stem canker (blackleg) disease caused by the fungus *Leptosphaeria maculans* (anamorph *Plenodomus lingam*, syn. *Phoma lingam*).

Rapeseed is a cross between turnip rape (*Brassica rapa*) and cabbage (*B. oleracea*). While turnip rape is a millennia-old crop, rapeseed was firstly mentioned in the Netherlands in 1366 (Schröder-Lembke 1989) and it was only during the 18th century that its cultivation occurred at a larger scale. Rapeseed became a highly valuable oil crop for human nutrition from the mid-1970s onward caused by the elimination of anti-nutritional ingredients for humans and livestock (erucic acid and glucosinates, respectively) obtained through breeding. As a result, the interest in rapeseed cultivation exploded and the cultivation of this crop spread to Canada (as canola), Russia, India, China, and Australia.

The fungus *L. maculans* infects oilseed and vegetable brassicas. Although rapeseed is clearly a European crop, the pathogen seems to have evolved in the USA. Its first records are from early 1900s on cabbage in Wisconsin, USA (Henderson 1918). Today, it is a threat to *Brassica*-growing areas all over the world except for China, where no introduction has yet occurred, but where a sister species (*L. biglobosa*) thrives. The worldwide distribution of the pathogen most probably was caused by repeated worldwide seed transmission (Hall et al. 1996) especially when seed of susceptible cultivars were traded. In the newly colonized areas, it is possible to follow the rapid speed at which the pathogen spreads. Due to the increase of the area cultivated with *Brassica*, especially when highly susceptible varieties are used, and to the consequent build-up of infected plant residues in the soil, a rapid population build-up takes place often at a large geographic scale. For instance, in Canada, the first blackleg symptoms were recorded in 1975, and, within a few years, Central Saskatchewan was colonized followed by Manitoba and Ontario (Table 4). When the disease is established, ascospores from infected residues of rapeseed are the main source of infection.

An analysis of the worldwide population of *L. maculans* by microsatellite markers clustered the genotypes into distinct populations according to the major geographic regions (Dilmaghani et al. 2012). The origin of the pathogen in the USA was confirmed using Approximate Bayesian Computation (ABC) on the basis of multilocus genotyping and the authors speculate about a host shift from indigeneous crucifer weeds to *Brassica* hosts. Obviously, host shift speciation leads to the emergence of new pathogens followed in this case by independent introductions into Eastern Canada, Europe, and Australia.

Table 4 Spread of virulent isolates of blackleg disease in Canada (Gugel and Petrie 1992)

First occurrence	Province/State	Occurrence
1975	Central Saskatchewan	Three widely separated fields
1976–1977	Central Saskatchewan	Increase from 10 to 17% of fields
1978–1981	Central Saskatchewan	Tenfold increase in incidence
1982	Central Saskatchewan	Widespread epidemic, up to 56% yield loss
1986	Central Saskatchewan	65% of fields affected after severe outbreaks (1984, 1985)
1984	SW Manitoba	First occurrence
1985	SW to NW Manitoba	36% of fields surveyed
1988	SW to NW Manitoba	Prevalence 62% (SW), 31% (NW) of fields
1986–1987	Ontario	92% (1986), 100% (1987) of fields

From Brazil to the old world: wheat blast fungus

The wheat blast fungus *Magnaporthe oryzae* (also known as *M. oryzae* pathotype *Triticum* [MoT] or *Pyricularia graminis-tritici*) firstly described in 1985 in the state of Paraná/Brazil is likely to have originated through a host shift from a *Lolium* isolate to a wheat cultivar missing one of two resistance genes providing non-host resistance (Singh et al. 2021). The increase in population size by this isolate led to mutations that are lacking the corresponding avirulence gene, which is now infecting former non host resistant wheat varieties. The pathogen has spread to other wheat-growing areas of Brazil and, soon after 1990, it appeared in neighboring South American countries where it ended up occupying the entirety of wheat growing areas (Table 5) (Singh et al. 2021). A single finding of wheat blast in Kentucky/USA was most likely caused by the host jump from an endemic *Lolium*-infecting isolate to wheat and not by an introduction from South America (Farman et al. 2017). Nonetheless, in 2016, the pathogen arrived in southwestern Bangladesh (Islam et al. 2016) and in 2017 in Zambia (Latorre and Burbano 2021). In both countries, the fungus subsequently moved forward infecting wheat fields in more districts (Singh et al. 2021).

Table 5 First occurrence of wheat blast (Singh et al. 2021)

First occurrence	Country	Province/State
1985	Brazil	Paraná
1986–1990	Brazil	Central/Southern
1996	Bolivia	Santa Cruz
2002	Paraguay	Itapúa, Alto Paraná
2007	Argentina	Formosa
2016	Bangladesh	8 districts
2021	Bangladesh	23 districts
2017–2018	Zambia	1 district (Mpika)
2021	Zambia	4 districts

While the spread within countries and to neighboring countries might be caused by windborne inoculum, the outbreaks in Bangladesh and Zambia were caused by grain trade. Brazil is an important wheat exporter that between 2006 and 2017 delivered wheat or wheat-rye mixtures to no less than 65 countries (Ceresini et al. 2019). Imports of about 425,000 tons of wheat from Brazilian wheat blast epidemic areas were recorded to Bangladesh between 2008 and 2015 (Ceresini et al. 2019), thus providing the basis for an intercontinental transport. This migration path is substantiated by genomic analyses. Sequencing of >2500 genes and whole-genome SNP data showed that the Bangladesh isolates were genetically close to a Bolivian isolate B71 collected in 2012 (Gladieux et al. 2018). Wheat blast outbreaks in Zambia were also caused by isolates closely related to B71 (Latorre and Burbano 2021; Win et al. 2021). This introduction highlights the lack of international phytosanitary surveillance of grain lots, both by exporters and importers. Without a strict quarantine, the disease will continue to spread.

Notorious insects conquering the Atlantic: maize corn root worm and fall army worm

The story of the western corn rootworm (WCR, *Diabrotica virgifera virgifera*) in Europe is particularly remarkable. This insect, known in U.S. as the “billion-dollar beetle” because of the annual damage it causes, most probably originated in Mexico (Lombaert et al. 2018). Interestingly, it did not follow the early maize cultivation in North America around 1000 BCE but was a more recent invader. According to microsatellite data, WCR underwent a severe bottleneck in Mexico at about 900 CE: this bottleneck may have been caused by a host shift from another plant to maize. This time frame corresponds to the intensification of maize cultivation in the Southwest, Great Plains, and Eastern Woodlands of the USA beginning about 900–1000 CE (Lombaert et al. 2018). WCR arrived in the southwestern USA around 1500 CE, and the most recent WCR population in the Colorado/Great Plains region occurred in the first half of the 19th century (Lombaert et al. 2018). In the 1950s, WCR worked its way into the U.S. Corn Belt, causing the most damage in Iowa, Illinois, Indiana, Ohio, but also occurring in adjacent states (Lombaert et al. 2018). Thus, it appears that the moth followed the pattern of an invasive parasite going through a couple of rapid range expansions. Nevertheless, its enormous spread in the USA is man-made and promoted by non-rotated maize monoculture on vast areas of land (Gray et al. 2009), which only allowed the insect such mass reproduction that it became one of the worst pests of U.S. maize (Meinke et al. 2009).

WCR is currently invading European maize growing areas (Fig. 7). The moth was first detected near the Belgrade airport in 1992 (Bažok et al. 2021). This was thought to be associated with U.S. and NATO troops involved in military operations during the wars in Croatia and Bosnia, however, modelling the generational growth rates showed that the first successful introduction likely occurred much earlier, between 1979 and 1984 (Szalai et al. 2011). From its first detection, the beetle spread rapidly in approximately concentric circles, reaching Slovenia and eastern northern Italy as early as 1998, crossing the Alps and infesting maize stands in Switzerland and Austria in 2000 and reaching the Paris Basin in France by 2002. In Germany, the first beetle detections occurred by catches in pheromone traps in 2007 (Freier et al. 2015). Despite strict quarantine measures, WCR could not be stopped and today infests numerous regions in NW Europe.

Recent genetic studies of the insect have shown that WCR has been introduced from the northern USA at least four times independently to SE Europe, NW Italy, the UK, Paris-2 and Alsace (Ciosi et al. 2008, Fig. 7). Two additional outbreaks were caused by secondary migration within Europe: the UK population spread to Paris-1 and the population from SE Europe to the Friuli population in NE Italy. The Parisian, UK and Alsatian outbreaks are today extinct before they could spread due to strict pest control strategies. The SE European invasion was probably so successful because in the early phase of introduction no monitoring and quarantine measures were applied (Ciosi et al. 2008). Population genomics showed that mixing of independent invasions from North America to NW Italy and SE Europe already occurred in Veneto/Northern Italy (Bermond et al. 2012). The genetic variation here is much higher than in the original epidemics and several genetic signs of admixture can be detected. Such admixtures increase genetic variation, and this might be one cause that a similar degree of genetic variation was found both in Europe, where the pest is exotic, and in the northern USA, where the pest is native (Ciosi et al. 2008). Currently, all maize growing areas in Europe are affected, except for Portugal (Fig. 7). The cropping strategy had to be changed from one-sided maize monoculture for years to

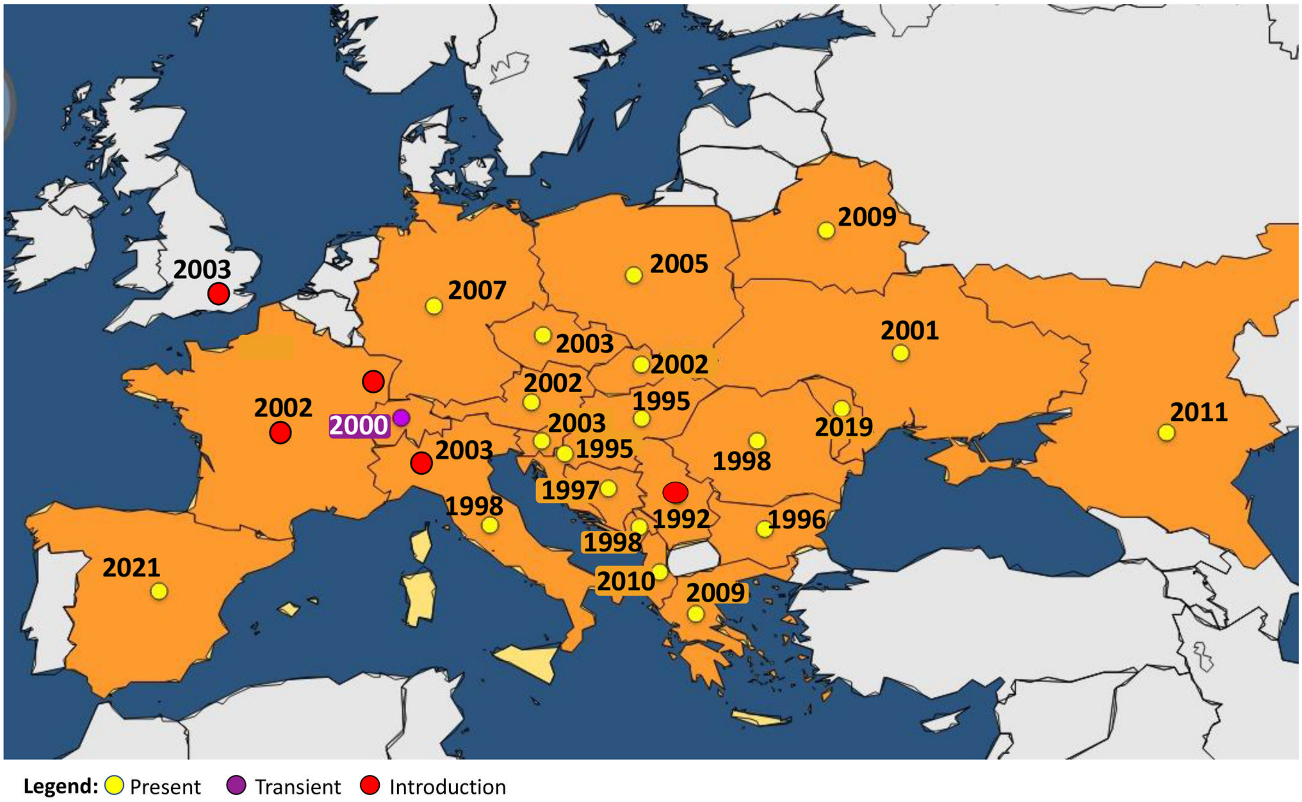

Fig. 7 Distribution of Western corn root worm in Europe with the first year of detection (EPPO Global Database 2023c, last updated: 2023-09-28), independent introductions after Ciosi et al. (2008)

a 2- to 3-year crop rotation. This is another example of how secondary non-native areas of infestations can themselves be sources of novel pathogen strains, in addition to novel strains coming from the area of origin of a pest.

Fall armyworm (FAW, *Spodoptera frugiperda*) is another perfect example of intercontinental spread of a pest through human transport and of the enormous damage these introductions can cause to agriculture in recipient countries. FAW is native to tropical and subtropical Americas and has been occasionally recorded in the USA (Wan et al. 2021). In January 2016, it was firstly detected in Western Africa (São Tomé, Nigeria, Benin, and Togo) and as of September 2018, it had invaded 46 African countries including Madagascar, the Seychelles, and Reunion archipelagos. By May 2018, the pest had reached southern India. FAW invaded China in December 2018 and is now (2021) present in 18 SE Asian countries. In January 2020, first records came from islands of the Torres strait (Australia) and within 4 months FAW had spread to 11 regions of Queensland, and each of three regions of the Northern Territory and Western Australia. The insect is highly polyphagous and has at least 353 host plants, very gluttonous, can survive in a wide range of habitats, has a large flight range, high fecundity, and rapidly develops resistances to insecticides and genetically modified *Bacillus thuringiensis* (Bt) constructs (Wan et al. 2021).

Molecular studies in the newly colonized regions confirm a foreign origin of the insects. By analyzing the nucleotide diversity within two genes Nagoshi et al. (2018) found a high genetic similarity within African FAW populations, consistent with a single invasion. The likely origin was identified as being in Florida and the Greater Antilles. A second subgroup could not be assigned to an origin (Nagoshi et al. 2018). Thanks to a molecular phylogenetic analysis, the more recent Indian invasion could be traced to FAW populations from Florida, Canada, Ghana, Nigeria and Uganda on maize (Kalleshwaraswamy et al. 2018). DNA sequences within the Indian population were identical to each other again pointing to a common ancestry of a small number of invasive beetles. The authors speculate on the invasion by agricultural commodities. FAWs that invaded China in 2018 were found to have a close relationship with African beetles by population-genomic analysis from *de novo* genome sequences and re-sequencing (Gui et al. 2022). Chinese populations were significantly different from American populations. Today (2023) fall army worm has additionally invaded Egypt, Jemen, Saudi Arabia, the Near East, Turkey, and all states of Australia except South Australia (EPPO Global Database 2023d).

The long-distance transport of the moths has to be associated with human transportation. Although FAW has been reported to move more than 400 km downwind within 8 h (Wolf et al. 1990), they cannot cross the Atlantic Ocean by themselves. Therefore, it is speculated that FAW entered western Africa in an aircraft either as adults or as eggs on parts of an airplane or in the cabin with passengers (Cock et al. 2017). In an early US study, the inspection of more than 9000 planes originating from South America and the Caribbean and landing the Miami airport, detected Lepidoptera eggs, with FAW as the most common species, in 0.86% of the total number inspected (Porter and Hughes 1950). The number of eggs on a single plane could be as large as 1000. It should be noted that the chances for adults surviving a direct flight in wheel bays or cargo holds are high (Russell 1987).

The future

Despite the emergence of multiple pandemics and of changing habits by consumers, who now prefer locally grown products, the tightly interconnected globalization we have created in the last decades cannot be reversed. As a result, the spread of pathogens and parasites around the world will only increase. A study of Bebber et al. (2014) analyzed 1901 pathogens and parasites and the distribution of their 168 host crops along varying agroclimatic conditions. The authors found that most countries already reported about 20% of the pathogens and parasites they could theoretically support ("saturation level") and according to them, this will rise dramatically due to climate change and still increasing international trade, soon leading to a "biotic homogenization". Countries like Australia, Germany, China, Italy, the UK, and Japan have already reached about 50% of their saturation level in 2000, while France, India, and the USA could be at the 60% threshold. It was predicted that the full saturation level will be reached as early as 2024 in the USA, while the other countries mentioned above may reach saturation by 2040.

Global climate change will exacerbate this situation by promoting thermophilic pathogens and especially insects on their way polewards (Bebber et al. 2013; Miedaner and Juroszek 2021a, b). This can lead to improved infection conditions, increased inoculum, increased pathogenicity and damage probability for these organisms (Chakraborty and Newton 2011). In contrast, significantly fewer pests will be inhibited by the higher temperatures. At most, increasing dry conditions during the growing season may reduce the load of fungal pathogens.

The only solution we have is international cooperation by an integrated research agenda with plant disease surveillance, geospatial analyses for monitoring, DNA-based sensors for detection of emerging plant diseases, population genomic surveillance, pathogen risk assessment and modeling to predict outbreaks with special emphasis on climate-driven diseases (Ristaino et al. 2021). Such systems have been initiated in the USA and Europe for potato late blight (EuroBlight, USABlight), for wheat rusts in Europe (RustWatch) and worldwide (Borlaug Global Rust Initiative) and must be developed further. The development of new pesticides or biocontrol agents and the selection of new host resistances with the help of international knowledge-based science are indispensable to control new pests and to restrict their negative impact on food security.

Glossary

Bottleneck (of populations)	Evolutionary event (e.g., migration) that drastically reduces size of whole populations
Bridgehead	When a continent/region acts as a point of entry for a pathogen, and subsequent spread arises from this source
DNA barcoding	Species identification by a short DNA fragment/ sequence from (a) specific gene(s)
Founder effect	Loss of genetic variation when a new population arises from only a limited number of individuals
Genetic drift	Random change in allele frequencies due to a small population size
Genotyping	Characterizing the genetic material by DNA techniques
Haplotype	Set of linked genetic determinants (markers, sequences) to characterize an individual, population or species
Phylogeny	Elaborating the evolutionary relationships in a group of individuals
Population expansion	Increase in population size

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