"What a Painfully Interesting Subject": Charles Darwin's Studies of Potato Late Blight

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Charles Darwin's famous voyage on the HMS Beagle led him around the world on a collecting journey that culminated in his theory of evolution. In 1835, the Beagle traveled to the island of Chiloé, and there, Darwin discovered and sent potatoes back to England. Darwin's interest in the potato and potato late blight spanned four decades. He used the potato to investigate questions of what a species is, understand its ravages by a plant pathogen, and investigate ideas on clonal versus sexual reproduction on species fitness. Darwin's letters reveal his thoughts on free trade, population growth and food security during the Irish famine. Darwin was involved in the first research to find resistance to late blight and personally funded a breeding program in Ireland. Here, we discuss Darwin's studies on potato late blight and its relevance today in studies of global migrations of the pathogen and development of durable resistance.

Keywords: Darwin, Phytophthora infestans, evolution, Irish famine, plant disease

Potato late blight a remerging plant disease threat

Potato late blight caused by *Phytophthora infestans*, a member of the Oomycota, was responsible for the plant disease that led to famine in Ireland of 1845 (Berkeley 1846). The pathogen is still wreaking havoc on potatoes and tomatoes in the United States and many areas of the world and is considered a threat to global food security (Hu et al. 2012, Fry et al. 2015). To control late blight, fungicides are applied at a higher rate than on any other food crop at global costs exceeding $1 billion.

Phytophthora infestans is considered a serious threat to food security and is a reemerging disease for several reasons. The pathogen has a polycyclic life cycle, and aerial sporangia can be dispersed over distances of many kilometers and therefore easily spread (Fry et al. 2015). The pathogen can also be transported in infected tubers, tomato fruit, and infected transplants (Hu et al. 2012). Fungicide-resistant strains of the pathogen emerged shortly after the release of the phenyamide fungicide metalaxyl in the 1980s (Fry et al. 2015). In addition, the monoculture of highly susceptible potato varieties in the United States has exacerbated disease. R-gene based resistance in potato has been deployed and has been unsuccessful; the pathogen genome is plastic, and a suite of effector proteins have evolved to evade host-plant R-gene-mediated resistance derived from *Solanum demissum*.

Late blight, the Darwins, and food security

Potato late blight was reportedly first observed on potatoes in the United States in 1843 in areas around the ports of Philadelphia and New York and spread within the eastern United States for several years before it was reported in Europe in 1845 (Bourke 1964). Potato harvests in 1843 in New York, Pennsylvania, Connecticut, and New Jersey were reportedly destroyed "due to a rot that seized them before they were taken from the ground" and became "an extremely offensive putrid mass" (US House of Representatives 1844). J. E. Teschemacher, curator of botany of the Boston Natural History Society, believed a fungus caused the disease and published a report in 1845; others supported the idea of spontaneous generation, and debate ensued (Teschemacher 1845). The germ theory had not been developed at that time, and the potato blight outbreaks provided a dramatic case study to debate the theory (Berkeley 1846). By 1845, epidemics were severe on both continents, and naturalists and botanists were scrambling to understand the cause and manage the consequences (Lindley 1845).

When late blight emerged in England, Charles Darwin was living in Down House, Down Kent (figures 1b and 1c), with his wife Emma, raising a family, conducting research, writing, and growing potatoes. Darwin wrote to John Henslow, his Cambridge mentor in 1845 at the onset of the disease in Britain, "My Dear Henslow, I have to thank you for several printed notices about the potatoes etc etc. What a painfully interesting subject it is; I have just returned home & have looked over my potatoes & find the crop small, a

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Figure 1. (a) A reproduction of a frontispiece by R. T. Pritchett in Darwin (1890), from the first Murray illustrated edition of the **Journal of Researches.** ***The illustration shows the*** **HMS Beagle** ***in the Straits of Magellan at Monte Sarmiento. (b) Darwin's study at Down House, where he wrote his many books and letters. (c) Darwin's bronze statue at the Royal Botanic Gardens, in Kew, England. Many of Darwin's plant samples were identified there by Hooker.***

good many having rotted in the ground, but the rest well. I am drying sand today in the oven to store with the greatest care in baskets, my seed-potatoes" (Darwin C 1845a).

The painful subject to which Darwin refers is the initial outbreak of the potato late blight in Europe and the British Isles. As farmers and peasants suffered, scientists were debating. The debate was about the very nature of disease in plants, the source of the blight, how the vitality of potatoes could be restored, and the variation in populations of *Solanum tuberosum* planted in the UK.

In the same letter, Darwin (1845a) said,

I think it is a very good suggestion of yours, about gentlefolk not buying potatoes & I will follow it for one. The poor people, wherever I have been, seem to be in great alarm: my labourer here has not above a few weeks consumption & those not sound; as he complains to me, it is a dreadful addition to the evil, flour being so dear: some time ago this same man told me, that when flour rose, his family consumed 15 pence more of his 12 s earnings per week on this one article. This would be nearly as bad, as if for one of us, we had to pay an additional 50 or 100 £ for our

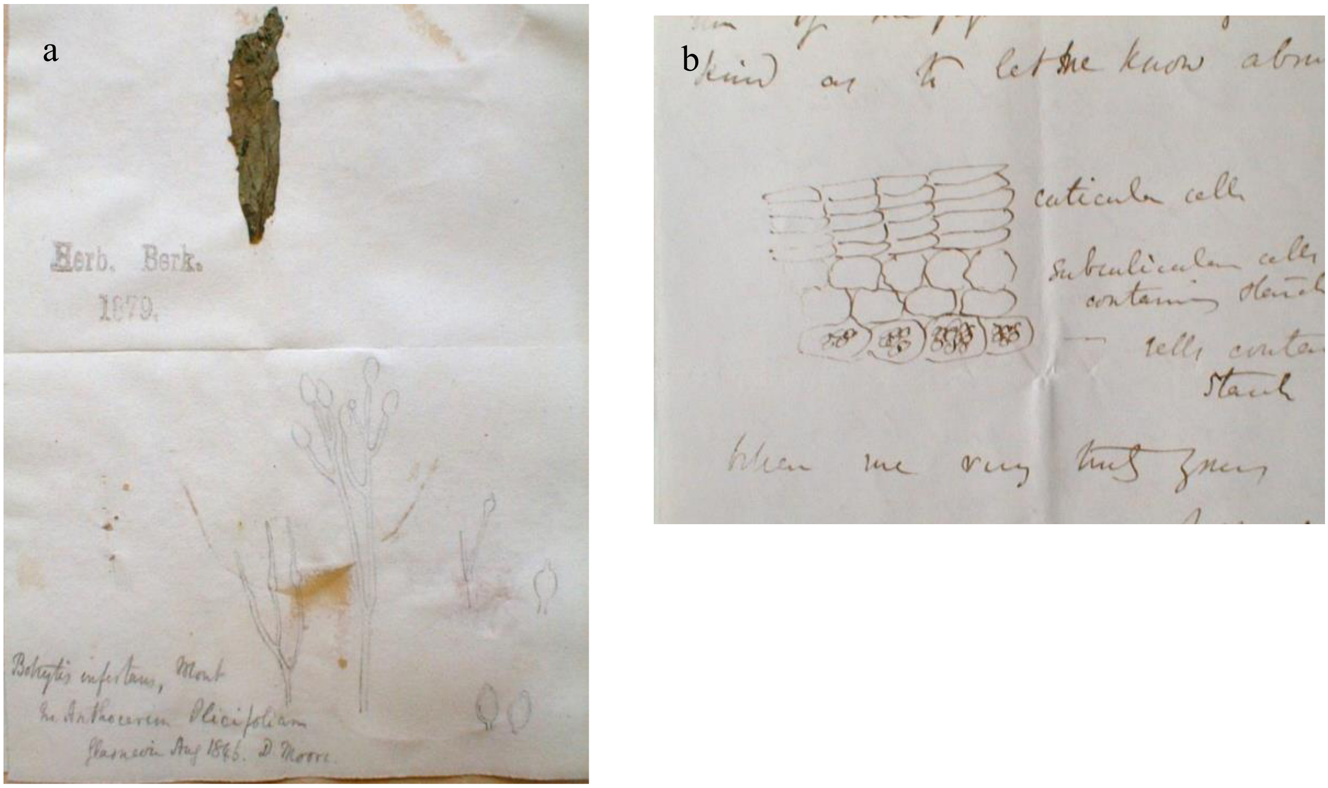

Figure 2. M. J. Berkeley's drawings of* Botrytis infestans*, including (a) the asexual sporangia and sporangiophores of the pathogen drawn on a specimen label and (b) a cross-section drawing of an infection of the potato tuber by the pathogen.

> bread: how soon in that case, would those infamous corn laws be swept away.

Darwin's comments were set in a social and political context of rich and poor. The Irish famine disaster led to the repeal of the Corn Laws that had put high tariffs on imported grain. Darwin supported free trade. Darwin's concern about the rising cost of flour led him to an experiment with making potato flour, and when he purchased additional land, he "told [his] agent to arrange allotments to every laborer." The need for more allotments indicates the threat that late blight posed to food security of the rural poor who lacked their own land to grow crops. An expansion of the allotment system in England was under heated debate. In agreeing with Henslow, Darwin said that "gentle folks" should avoid eating potatoes so that the lower classes might have a larger supply of the carbohydrate-rich crop—natural selection at several levels, indeed. Darwin's wife, Emma, told their cook to stop preparing potatoes, and she gave bread tickets to the poor so they could make purchases at the village bakery, thereby helping ease the hunger at their back door (Desmond and Moore 1991). Meanwhile, Darwin began thinking about using potato tubers he had collected on the *Beagle* voyage in South America (figure 1a) for replenishing the diseased stock.

Miles J. Berkeley decisively changed the battlefield over the potato blight when he convincingly argued that the agent of the disease was not the weather, as other prominent naturalists such as John Lindley believed, nor the soil, ill humors, immoral people, or bad potatoes but rather a plant pathogenic organism (Berkeley 1846). Berkeley and Darwin were collaborators. In 1840, Berkeley described and published on some of Darwin's fungal specimens collected on his *Beagle* voyage (Berkeley 1840). Berkeley used the name *Botrytis infestans* for the pathogen, a name given by Montagne in France. Berkeley observed and sketched infected tubers and minute sporangia on diseased tissue and confirmed that the pathogen caused the disease (figures 2a and 2b). The pathogen was renamed *Phytophthora infestans* in 1876 by Anton DeBary (1876). DeBary's work was funded by the Agricultural Society in London in 1874, much to the dismay of Hooker, who wrote to Darwin that this was an insult to Berkeley and his 30 years of work on the disease (Hooker 1874). Neither scientist could offer a cure for the disease. The Agricultural Society awarded a prize that stimulated the submission of 94 essays on the disease in 1873.

Darwin's collections of potatoes

Darwin's role in famine "relief" began years earlier with his plant collections during his voyage on the *HMS Beagle*. In Chile, on the Island of Chiloé, in the lower Cordilleras, and in Ecuador, on the Galapagos Islands, he collected potatoes and other wild solanaceous species that were shipped back to England to John Henslow at Cambridge University (Darwin C 1835, 1846). Darwin also wrote about potatoes

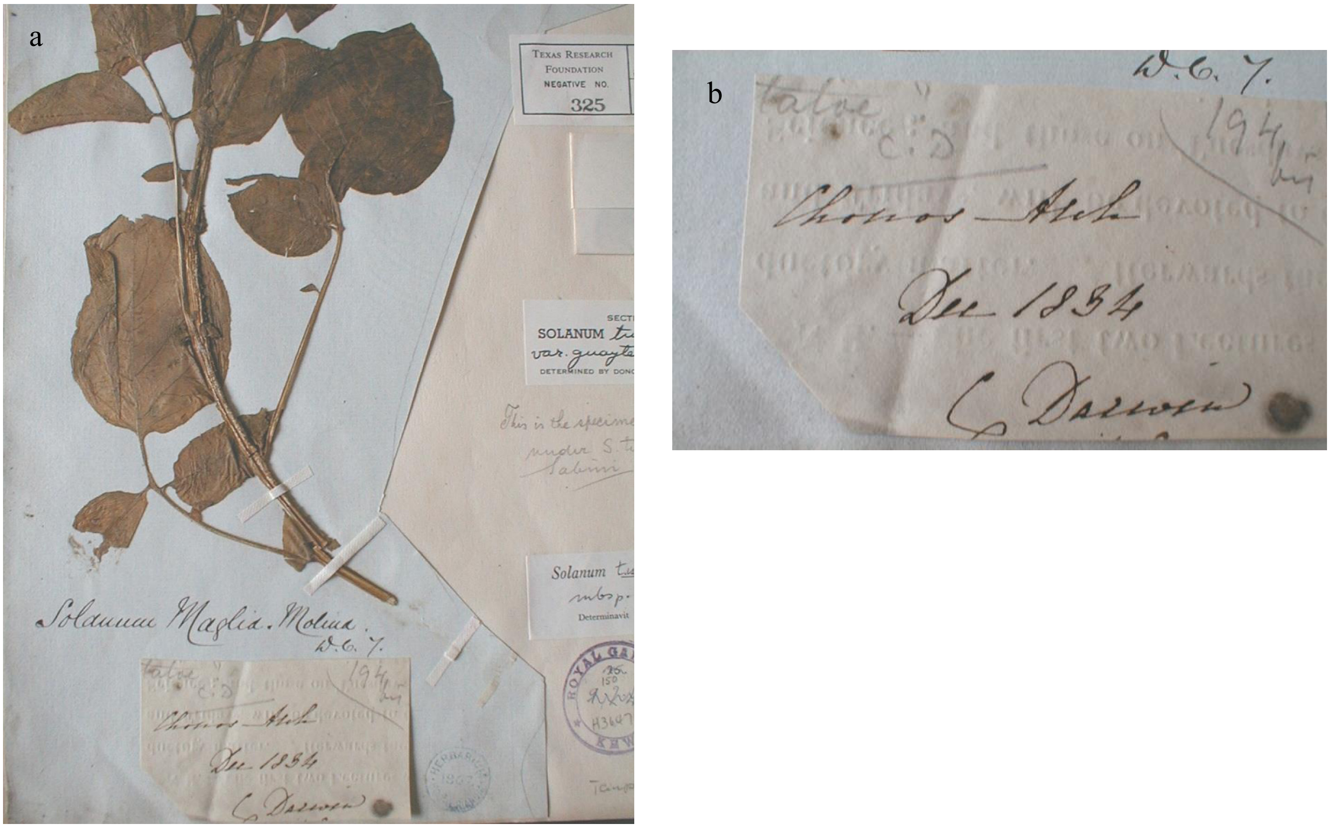

Figure 3. Specimens of (a)* Solanum maglia *collected by Charles Darwin in South Chile in the Chonos Archipelagos and stored in the Royal Botanic Garden, in Kew, England. Renamed* Solanum tuberosum L. *subsp.* tuberosum *Hawkes var guaytecarum (Bitt.) Hawkes. (b) The expanded specimen label.

many times in his journals, indicating that the crew "stocked up on game and potatoes" (Desmond and Moore 1991). In fact, Fitzroy, the captain of the *HMS Beagle*, believed that in addition to the indigenous people, the procurement of wild potatoes was one of the highlights of the trip (Desmond and Moore 1991).

Darwin wrote to his sister, "We left the Island of Chiloé a week since; for which place a succession of gales compelled us to bear up. We staid some days in order to refresh the men. Pigs & potatoes are as plentiful as in Ireland. With the exception of this weighty advantage, Chiloé, from its climate is a miserable hole" (Darwin C 1834). Here, Darwin once again makes reference to the use of potatoes (and pigs) as a food source for the both the crew and people of Chiloé.

On Chiloé, Darwin considered the diversity of potatoes and collected them in their native state. He wrote to Henslow in April 1835, "In the Mendoza bag, there are seeds or berries of what appears to be a small Potatoe plant with a whitish flower. They grow many leagues from where any habitation could ever have existed, owing to the absence of water. Amongst the Chonos dried plants, you will see a fine specimen of the wild Potatoe, growing under a most opposite climate & unquestionably a true wild Potatoe. It must be a distinct species from that of the lower Cordilleras one" (Darwin C 1835). Darwin noted the variation and diversity of potato in the wild state, perhaps assembling information that would become useful as he developed his ideas on the evolution of potato and other species (Darwin C 1839 p. 347).

There is no mention of potato disease in the regions Darwin visited during his voyage in his writings. Darwin was aware of plant ailments, and he identified rust in Brazil and collected a specimen of wheat stem rust on the north bank of the Rio Plata (Henslow 1844, Darwin 1844). He sent the sample to Henslow, who reported on the specimen later in an article that appeared in the *Gardeners' Chronicle* (Henslow 1844). Berkeley (1840) had identified the rust in Darwin's specimen as *Puccinia graminis*. Other evidence in his handwritten notebooks of observations of fungi were made (Porter 1987).

Darwin collected several specimens that he labeled and referred to as *Solanum maglia* from the Chonos Archipelago (figure 3) and true potato seed from the Cordilleras in Chile. He wrote to Henslow from London in 1837, urging Henslow to identify the potatoes: "Pray take in hand as soon as your lectures are over, the potato from the Chonos" (Darwin C 1837a). Later that year, he continued to inquire about the potato specimens with Henslow: "To examine the

Figure 4. (a) A potato field trial with potato landraces on the island of Chiloé (trial of J. Solano and I. Acuno, INRA, Chile). (b) A native woman from Chiloé Island selling "papas nativas," or primitive landrace potatoes, at the farmers market on Chiloé Island.

Potatoe from Chonos would not take you long, & it is probable you already know the name of some insignificant little plants" (Darwin C 1837b). The first author found one dried specimen (labeled 194bis) from Darwin's Chonos potato (figures 3a and 3b) in the Herbarium of the Royal Botanic Gardens at Kew, and another was located in the Cambridge University Herbarium. The *S. maglia* from Chiloé is now recognized as *S. tuberosum* (Spooner DM at al. 2012). Darwin also collected many plant species that were sent to Henslow, Hooker, and others for identification (Porter 1980, 1986, 1987).

Darwin on the origins of the potato

Darwin (1839) wrote in his *Journal of Researches* that "Humboldt, in his Essay on the Kingdom of New Spain, has given a most interesting discussion of the common potato. He believes that the plant described by Molina, under the name of *maglia*, is the original stock of this useful vegetable, and that it grows in Chile in its native soil" (p. 347). Darwin speculated on the "endemism" of potatoes in the region and their center of origin in South Chile. He also cited Humboldt's writings on the movement of potato by native Indians "to Peru, Quito, New Granada, and the whole of the Cordillera, from 40° south to 5° north" and mentioned that "previous to the Spanish conquest, it was unknown to Mexico." "Among the Chonos Islands, a wild potato grows in abundance, which in general habit is even more closely similar to the cultivated kind than is the *maglia* of Molina" (Darwin C 1839, p. 348).

Wild *Solanum* species are still grown by native people in Chile and referred to as *papas nativas* on Chiloé today (figure 4a). The potato is now known to be indigenous in the Andes and was introduced outside the Andean region four centuries ago by Spanish colonists (Spooner DM et al. 2014). A single monophyletic origin of potatoes from wild species has been documented in southern Peru and northwest Bolivia (Spooner A et al. 2005). DNA from herbarium specimens was used to determine that the Andean potato grown in Europe in the 1700s was replaced by the Chilean potato as early as 1811, before the late blight epidemics in the United Kingdom, discounting alternative hypotheses that the European potato originated from high Andean populations farther north (Ames and Spooner 2008).

Darwin considered whether potatoes in Chile were of recent or ancestral origin, saying, "So very close is the resemblance with the cultivated species, that it is necessary to show that they have not been imported. The simple fact that their growth on the islands, and even small rocks, throughout the Chonos Archipelago, which has never been inhabited, and very seldom visited, is an argument of some weight." Darwin learned that native peoples knew of the potato and their "being well acquainted with the plant" suggested that this was evidence of their ancestral origin in the region: "The simple fact of their being known and named by distinct races, over a space of 400 to 500 miles on a most unfrequented and scarcely known coast, almost proves their native existence" (Darwin C 1839, p. 348).

Henslow examined the dried specimens that Darwin brought back and said that "they are the same as those described by Mr. Sabine in Valparaiso but they form a variety which by some botanists has been considered as specifically distinct" (Darwin C 1839, p. 348). Here, Darwin is challenging a strictly creationist view and believed distinct species of potatoes evolved in the region. He described the variation in species of potatoes in Chile and their evolution in different habitats and climatic regions, stating, “It is remarkable that the same plant should be found on the sterile mountains of central Chile, where a drop of rain does not fall for more than six months, and within the damp forests of the southern islands. From what we know of the habit of the potato, this latter situation would appear more congenial than the former, as its birthplace” (Darwin C 1839, p. 348). Potatoes produce more food per unit of water than any other food crop (FAO 2008). Their drought resilience is currently being exploited as present-day farmers struggle with climate change (Khan et al. 2012).

Darwin’s potatoes studied during the famine

The potato seed and tubers, first sent by Darwin to Henslow in 1835, were grown and tubers sent to J. D. Hooker at Kew Gardens and to Darwin’s second cousin and former housemate at Cambridge, William Darwin Fox (Fox 1846). Darwin wrote to Fox in February of 1845 prior to the potato late blight outbreaks in the region, asking for a few of his potatoes to grow at his farm: “PS. I should like very much sometime a few of my potatoes & chiefly to get true seed from them & see whether they will sport or not readily” (Darwin C 1845b). In 1845, during the late blight outbreaks in the UK and Ireland, it was believed that “wild” or indigenous potatoes might possess resistance to the disease and were in high demand. There was a belief that by going back to the “motherland” of the host, one might be able to find resistance to the disease and rejuvenate the potato culture of Europe. Although several kinds of potato were grown in the British Isles, the diversity of types was quite local, and monoculture was rampant. The variety “Lumper” that was grown in Ireland at the time was popular among the rural poor and was very susceptible to the pathogen.

Potato late blight struck in Ireland and at Darwin’s farm in England in the fall of 1845. It was Darwin who was among the first to suggest growing potatoes from true seed, and he was cited by John Lindley (1846) in the *Gardeners’ Chronicle*. This idea, essentially the concept of hybrid vigor, harkens back to Darwin’s grandfather Erasmus Darwin’s studies that crossing would yield healthier plants (Darwin E 1800). Entangled in this discussion about the cause of decline of the potato was debate about the effects of clonal cultivation on the crop: Would crossing help counteract hereditary disease? Did extended propagation weaken plants and did plants have a defined lifespan like people? Might it be the case that perpetual cloning causes a breakdown in the “essence” of the potato (Lindley 1846)?

In 1846, Darwin wrote to Fox, “I see since I wrote to you that someone has urged the necessity of sending to South America for new seed” (Darwin C 1846). Fox tested Darwin’s potatoes for resistance to late blight in the field during the epidemics in England. Subsequently, Fox (1846) wrote the following in a letter to the *Gardeners’ Chronicle*:

> It has stuck me that the following fact may be of some value to some of your correspondents who talk about the necessity and desirability of getting potatoes anew from the original stock in South America. I have considerable quantity of this much-to be desired stock, obtained in the following manner. In the spring of 1835, Mr. Darwin collected some seeds from ripe tubers, in the Cordillera of central Chile, in a most unfrequented district, many miles from any inhabited spot, and where the plant was certainly in a state of nature. These vegetated under Professor Henslow’s care in 1836 or 1837, and in that year or 1838, Mr. Darwin gave a tuber to me. It was either three or four years before the potatoes from it became eatable.

Darwin’s tubers were grown by Fox:

> I had them growing last year among many other kinds; and they are a late variety, they had not ceased growing when the disease appeared in Cheshire. They fared exactly the same as the other kinds, having blotched in the leaf and a few tubers decayed. This year the haulm [stem] was destroyed totally in the same manner as all my potatoes were and on taking up the tubers I find about the same number diseased as in other kinds. I fear this decides the point as to the usefulness of procuring seed from even the fountain head—the wild stock itself. (Fox 1846)

Thus, Darwin’s collections of wild potatoes from Chile were crucial in some of the first trials for resistance to late blight done in England. Apparently, the potatoes from the Cordilleras and Chiloé that Fox tested were susceptible to blight. The first studies of the resistance of primitive Andean and Chilean landraces in their native landscape to late blight were only recently published (figure 4a; Perez et al. 2014, Solano et al. 2014). Some of these landraces possess significant levels of durable resistance that may be useful in potato breeding programs. It is valuable that they are still being grown by native island women from Chiloé (figure 4b). These women, keepers of the germplasm biodiversity, cultivate land races on Chiloé Island and sell their harvests in local markets.

The late blight outbreaks in the nineteenth century stimulated research to find resistance. John Lindley tested potatoes imported from Colombia, Peru, and Mexico for resistance to late blight in 1847 (Lindley 1848), saying, “Among the speculations that have been entertained respecting the Potato disease, one consisted in the belief that in order to secure against future ravages, it was necessary to bring the plant once more from its native country and begin over again the process of domesticating it.” Lindley, in 1846, tested potatoes from New Granada (modern-day Colombia) and golden-fleshed potatoes from Peru to evaluate their resistance to the late blight pathogen.

Figure 5. Potatoes grown at Down House in 2015. (a) Late blight symptoms on potatoes in the garden at Down House. (b) Historic potato varieties in the kitchen garden.

He reported that some of the Peruvian potatoes were diseased and some remained healthy, suggesting variation in resistance to the disease among South America potatoes. Detailed descriptions of the progression of symptoms were not given by Lindley, but this variation could have also been due to the presence of infected tubers among some of the potatoes from Peru (Lindley 1848). Lindley also tested potatoes from Toluca, Mexico, and named a new species, *Solanum demissum*, a dwarf plant that he grew in the Royal Horticultural Society Gardens (Lindley 1848). Lindley wrote that "the stems exhibited blotches in a worse degree than any other sort in the garden" and were susceptible to blight. *Solanum demissum* would later become the main source of resistance genes bred into potato (Glendenning 1983). Lindley, like Fox, also concluded that "neither renewal of seed, nor introduction from foreign countries could guarantee against the attacks." Ironically, neither Lindley, Fox, nor Darwin fully understood that the pathogen could survive in potato tubers and was likely introduced into Europe in the first place in infected tubers brought from the Americas.

Potato late blight still causes disease on Darwin's potatoes grown at Down House today (figure 5a). Darwin grew several kinds of potato on his farm, and all the varieties were susceptible to late blight. Heirloom varieties of potatoes are still grown at Down House, including the Belle de Fontenay, Ratte, and Pink Fir Apple (figure 5b). Darwin grew potatoes for food for his family and also studied their variation in morphological characters and reproduction. He also noted their susceptibility to potato blight and insect attack.

Potato late blight origins and archival plant specimens

At the same time that Darwin was contemplating improving the hybrid vigor of potatoes, Lindley, Berkeley, and later DeBary were debating whether fungi could cause plant disease and were trying to determine the source of the initial outbreaks. Berkeley and DeBary both believed the pathogen entered Europe from imported potatoes from South America and, like Darwin, suggested that resistance might be found there in the wild stock (Berkeley 1846, DeBary 1876). A vigorous nineteenth-century bat guano trade from Peru for use as fertilizer in addition to the trade of potatoes likely introduced the pathogen first into the United States and subsequently to Europe (US House of Representatives 1844). In the early twentieth century, Reddick (1939), Neiderhauser (1991), and others (Fry et al. 2015) would suggest that Mexico was the center of origin of the pathogen and the source of nineteenth-century outbreaks. New evidence for a South American disease origin has recently been published after researchers sequenced genomes from famine-era outbreaks (Martin et al. 2016).

We used herbarium samples from the first US and EU outbreaks to shed light on the source of famine-era *P. infestans* (Ristaino et al. 2001, May and Ristaino 2004). It was previously suggested that the Ib mitochondrial lineage, originating from Mexico (Goodwin et al. 1994), caused famine-era outbreaks, but May and Ristaino (2004) used archival herbarium materials and documented a different lineage altogether (Ristaino et al. 2001). Multilocus sequence data from nuclear and mitochondrial loci were used to identify an Andean sister species of *P. infestans* that has been named *Phytophthora andina* (Gomez et al. 2007, Gomez et al. 2008, Oliva et al. 2010). The hybrid nature of this species that evolved in the Andean region of South America has been reported (Goss et al. 2011, Martin et al. 2016). US and European historic outbreaks were caused by the same lineage and share allelic diversity with South American *P. infestans* (Saville et al. 2016). In addition, *P. andina* occurs only in the Andean region and shares an ancestral haplotype lineage with famine-era *P. infestans* (Martin et al. 2016). Interestingly, basal lineages of *P. infestans* in Mexico occur on wild Solanaceous hosts and are more recent than famine-era and *P. andina* lineages, suggesting that the pathogen may have been introduced later on a wild host into Mexico (Martin et al. 2016). Thus, historic collections and studies on the diversity of wild *Solanum* hosts are still providing useful information on the evolutionary history of potato, *P. infestans*, and sister species of *Phytophthora*.

Darwin and Torbitt

Darwin was largely out of the picture on potato research through the 1850s. As he worked on *On the Variation of Animals and Plants under Domestication*" (Darwin C 1868), he returned again to the question of potato diversity. Extensive breeding programs were undertaken on seed-grown potatoes (Glendenning 1983). In an era before the mechanics of genetics were understood, experiments were conducted that would expand the knowledge of the genetics and breeding systems of *Solanum tuberosum*. Among those most closely involved with Darwin on this front was James Torbitt.

Charles Darwin's potatoes, collected from South America on the *Beagle* voyage, had played a role in early endeavors to find "blight-proof" potatoes. During the 1870s, plant reproduction captured his attention as well. Darwin's *The Variation of Animals and Plants under Domestication* was published first in 1868 (Darwin C 1868). Work on crossing experiments in support of his *The Effects of Cross and Self Fertilisation in the Vegetable Kingdom* had been underway since 1857 (Darwin C 1876). In these publications and elsewhere, Darwin focused attention on selection as a process by which specific characters could be introduced or enhanced. The potato was one example among many that he used (Darwin C 1868). In these publications, he cited himself on the geographical origin, and he recounted his experiments in growing 18 "kinds" in this garden. As others before him, he found little morphological variation in the foliage of these plants but found differences in flower size and color, in the form and position of the eyes, in their maturation rate, and in the form of the fruits. In *The Effects of Cross and Self Fertilisation in the Vegetable Kingdom*, he noted that plants grown from seed showed variation and that variation was sometimes found in clonally propagated plants and their tubers but at a lower rate. Darwin reviewed the literature on bud and stem grafting in potato by which intermediates and whole new strains were discovered. He also grew potatoes sent to him in 1879 from David Moore, curator of the Glasnevin Botanic Garden in Ireland, and noted differences in flower morphology and the attractiveness of potatoes to honey bees and even involved his children in the counts of honeybee attractiveness of plants at Down House (Nelson and Steward 1981). All of this was developed in the context of how selection could occur through the intervention of humans.

It is not surprising, then, that in 1876, James Torbitt, wine merchant, inventor, and potato breeder, began a correspondence with Darwin. Torbitt was interested in potato production in England, and in turning to Darwin for help and advice, he was turning to one of the foremost thinkers in England and to a formidable ally should he win him over (Evans et al. 1996). Torbitt was performing crosses to produce true seeds, not *seed potatoes* (pieces of tuber with buds attached that are used in vegetative propagation). The correspondence between the Darwin and Torbitt was expansive and includes 93 letters (Evans et al. 1996). Forty-eight other letters written by Darwin in support of Torbitt's undertaking include those to J. D. Hooker and various government officials (DeArce 2008). The correspondence between Darwin and Torbitt was reviewed elsewhere (DeArce 2008), and it is from this published account and review of original letters at Cambridge University Library that we gain an appreciation of Torbitt's potato-breeding program and Darwin's engagement in the vexing issue of late blight.

Torbitt came to work on his potato-breeding scheme in part because of his invention of a method to process the residue from potato starch production into a human food. His factory was moved from France to Belfast because of the Franco-Prussian War (1870–1871). In Belfast, his venture was "arrested by the potato disease" (Torbitt 1875). A seemingly practical man, he turned his attention to the potato plant and methods by which the disease might be eliminated or suppressed and thereby allow his commercial venture to succeed.

In Torbitt's first letter to Darwin in January of 1876 (Torbitt 1876a), he enclosed his article from *The Proceedings of Belfast Natural, Historical, and Philosophical Society*, an article that has not been located (DeArce 2008), but with this short letter he sparked a correspondence that would carry on until Darwin's death in 1882. A central question in that first letter was, "What is an individual?" This is a question that had hung in the air for 40 years (Lindley 1846). How does one think about potato culture when the potato had been propagated so long through clones? Later in 1876, Torbitt published a treatise on the blight with a promise of blight-free crops through propagation via seeds (Torbitt 1876b).

In his treatise, Torbitt outlined his case for propagating potatoes through growing plants from seed derived from crosses among cultivars (Torbitt 1876d). He discussed topics that had been part of the debates since the 1840s (Lindley

1846): Do clonally propagated plants eventually "wear out?" Do plants and their vegetative derived parts have a certain life expectancy? Torbitt cited the literature on grafting of fruit trees by Thomas Knight in 1801 (Knight 1801), reprinted it in his treatise, and cited literature on raising early potatoes from Asa Gray's article "Do varieties wear out, or tend to wear-out?" (Gray 1875).

In his first letters, Torbitt specifically wanted a public endorsement from Darwin. Darwin declined endorsement, which nonetheless happened because Torbitt sent Darwin's letter not only to the members of the legislature but also to the editors of the papers and to the land lords of Ulster! He also cited Darwin in his treatise (Torbitt 1876d). Subsequently, Torbitt apologized to Darwin, stating that the "last thing I would wish to do would be anything disagreeable to you" (Torbitt 1876c). Darwin agreed that his critique of Torbitt's work could be used privately. Behind the scenes, Darwin accepted Torbitt's apology and did take up Torbitt's case. He worked to promote Torbitt's program with influential scientists and government officials with the goal of providing funding for the on-going work of field tests and crossing potatoes.

In a letter to T. H. Farrer, Darwin asked Farrer to support government funding for the project and outlined Torbitt's case (Darwin C 1887): "Mr Torbitt's plan of overcoming the potato-disease seems to me by far the best which has ever been suggested" (Darwin C 1887). Darwin described the scenario, which reads like a case study for experimental evolution: "rearing a vast number of seedlings from cross-fertilized parents, exposing them to infection, ruthlessly destroying all that suffer, saving those which resist best, and repeating the process in successive seminal generation." He went on to indicate that not all plants of a species react the same way to pathogens or predators: "Therefore there is no great improbability in a new variety of potato arising which would resist the fungus completely" (Darwin C 1978). Curiously, his observation that the Colorado potato beetle differentially affects potatoes was not used. Torbitt crossed plants to produce more vigorous offspring, as Darwin demonstrated (Darwin C 1876). Despite Darwin's attempts to persuade, no government funding came forward. Darwin invested in the project and offered his personal funds; he convinced friends and family members to support the project and worked behind the scenes to solicit funds from other sources. Darwin wrote to Torbitt, "I have the pleasure to enclose a cheque for £90. I am extremely sorry that you cannot get your varieties sufficiently well known to ensure a large sale" (Darwin C 1881). Torbitt's project was in no way a small undertaking. Millions of seeds were harvested, distributed free of charge to many farmers and even members of the House of Lords, who planted, raised, and observed these plants' reaction to the potato late blight. Darwin grew Torbitt's varieties at Down House in 1881 and told Torbitt that his gardener reported that "these varieties were not attacked by the disease or only slightly but their yield was not good" (Darwin C 1882). By this time, Darwin was aging and wrote to Torbitt, "I have not strength sufficient to attend to the diseased varieties which you are so kind as to offer me. Those which you say that you will send shall be planted. It is very notable conduct of you to return the subscription, if trade continues to improve. As far as I am concerned, I am quite content to remain unpaid, as I gave the money for what I considered to be an excellent object" (Darwin C 1882). Torbitt in the initial stages also poured in his own money for the project. In fact, 8 years after Darwin's death, Torbitt was still promoting blight-resistant varieties and alluded to Darwin's approval in his advertisements: "TO CAPITALISTS—Means of obtaining the vastest profits ever yet realized. Matter approved of by one of the highest authorities in the world. Please communicate with James Torbitt, Belfast, Ireland." Others also began conventional breeding in potatoes for late blight resistance, and by this time, the late-maturing Scottish variety Champion was planted on over 80% of the land in England (Glendenning 1983).

Torbitt used a part of the Latin proverb on the title page of his treatise: *Cras credemus*, tomorrow we believe. The full quotation is *cras credemus hodie nihil*, tomorrow we believe but not today. Perhaps nothing can be more defining for a farmer or gardener than improving what will grow tomorrow. Looking at the tiny seed, it is difficult to believe that tomorrow one will have a crop. It also reflects a confidence and positive view that both Darwin and Torbitt held on the value of blight-resistant potatoes.

In 1845, Darwin (1845a) wrote to Henslow about potato blight, "What a painfully interesting subject it is." The disease rekindled Darwin's interest in potatoes and seems to have motivated Darwin from his first encounters with the plant in Chile until the end of his life. Potatoes are still grown at Down House, and the "painfully interesting" disease still affects potato there and globally and stimulates many investigations as scientists continue to work on the biology of this fascinating pathogen, understand its genetic diversity, and find durable resistance to the disease.

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