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# DNA FROM HERBARIUM SPECIMENS SETTLES A CONTROVERSY ABOUT ORIGINS OF THE EUROPEAN POTATO[1]

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Landrace potato cultivars are native to two areas in South America: the high Andes from eastern Venezuela to northern Argentina and the lowlands of south-central Chile. Potato first appeared outside of South America in Europe in 1567 and rapidly diffused worldwide. Two competing hypotheses suggested the origin of the "European" potato from the Andes or from lowland Chile, but the Andean origin has been widely accepted over the last 60 years. All modern potato cultivars predominantly have Chilean germplasm, explained as originating from breeding with Chilean landraces subsequent to the late blight epidemics beginning in 1845 in the UK. The Andean origin has been questioned recently through examination of landraces in India and the Canary Islands, but this evidence is inferential. Through a plastid DNA deletion marker from historical herbarium specimens, we report that the Andean potato predominated in the 1700s, but the Chilean potato was introduced into Europe as early as 1811 and became predominant long before the late blight epidemics in the UK. Our results provide the first direct evidence of these events and change the history of introduction of the European potato. They shed new light on the value of past breeding efforts to recreate the European potato from Andean forms and highlight the value of herbarium specimens in investigating origins of crop plants.

**Key words:** crop origins; cultivated potato; Solanaceae; *Solanum tuberosum*.

The Solanaceae contain many domesticated species including several economically important crops. The genus *Solanum* L., which contains an estimated 1500 species (Bohs, 2007), includes three major food crops: potato (*S. tuberosum* L.), tomato (*S. lycopersicum* L.) and eggplant (*S. melongena* L.), as well as other minor foods, medicines, and ornamentals.

Potatoes were domesticated in the Andes of southern Peru about 10 000 years ago. They had a monophyletic origin from a wild species of the *Solanum brevicaule* complex in Peru (Spooner et al., 2005a; Spooner and Hetterscheid, 2006). Landrace potato cultivars are highly diverse, containing diploids ($2n = 2x = 24$), triploids ($2n = 3x = 36$), tetraploids ($2n = 4x = 48$), and pentaploids ($2n = 5x = 60$) (Huamán and Spooner, 2002). The taxonomy of cultivated potatoes is controversial; with anywhere from one to 20 species recognized (Huamán and Spooner, 2002), but all form a common gene pool (Spooner et al., 2005a). The tetraploid cytotypes are the highest yielding; they are the sole cytotype of modern cultivars and are widely distributed in two regions in South America: the high Andes from Venezuela to Argentina (Andean landraces) and to the south in the lowlands of south-central Chile in Chiloé Island, including the immediately adjacent Chilean lowlands and other islands to the Chonos Archipelago (Chilean landraces) (Huamán and Spooner, 2002). Despite these altitudinal differences, their tuberization response is a factor of daylength, not altitudes. As a result, the Andean landraces tuberize poorly in the latitudes of much of Europe, but the Chilean landraces tuberize well there (Glendinning, 1983).

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***The potato outside of its home in South America and its acceptance in Europe***—The first record of cultivated potato outside South America was in the Canary Islands in 1567 (Hawkes and Francisco-Ortega, 1993; Ríos et al., 2007), and shortly thereafter in continental Spain in 1573 (Hawkes, 1990; Hawkes and Francisco-Ortega, 1992; Romans, 2005). The first botanical description was made by Bauhin in 1596 although the source of the plant was not known (Hawkes, 1990). The potato then spread throughout Europe and worldwide and is here referred to as the "European" potato. It was slow to be adopted as a major food crop until about 100 years later, and in some European countries it was rejected as an acceptable food well into the late 1700s. For example, in eastern France although its acceptance was rapid as early as 1600, many public demonstrations were necessary to show that potatoes were a safe food before widespread acceptance throughout the country (Zuckerman, 1998). In 1771 a high prize was offered by the French Academy of Besançon for the discovery of a new food that would replace cereals in case of famine. Antoine-Augustin Parmentier promoted potatoes, and Louis XVI gave him land to plant them as his prize (Stuart, 1937). At the beginning of the 19th century, the French National Society of Agriculture documented a collection of about 120 potato varieties (Stuart, 1937).

In Italy and Germany potatoes were cultivated in small gardens by 1601. A famine in Prussia effectively stimulated potato cultivation; however, in some regions of Italy acceptance of potato was slow. For example, in Naples, a boat load of potatoes was rejected by the residents in 1770 during a famine (Stuart, 1937; Zuckerman, 1998). In Sweden, by 1764 a royal edict was issued to encourage potato cultivation (Stuart, 1937). In 1850, Nicholas I of Russia forced people to plant potatoes, establishing its cultivation there (Zuckerman, 1998). In England, potatoes started to gain importance as a crop by 1662 when The Royal Society recommended planting them to prevent famine, and by 1830 potatoes were well established as a field crop (Stuart, 1937). In Scotland, potatoes were mostly grown in gardens before 1760 (Stuart, 1937), and in Ireland potatoes started to be considered as a field crop in 1640 thanks to English immigrants (Zuckerman, 1998) (Fig. 1).

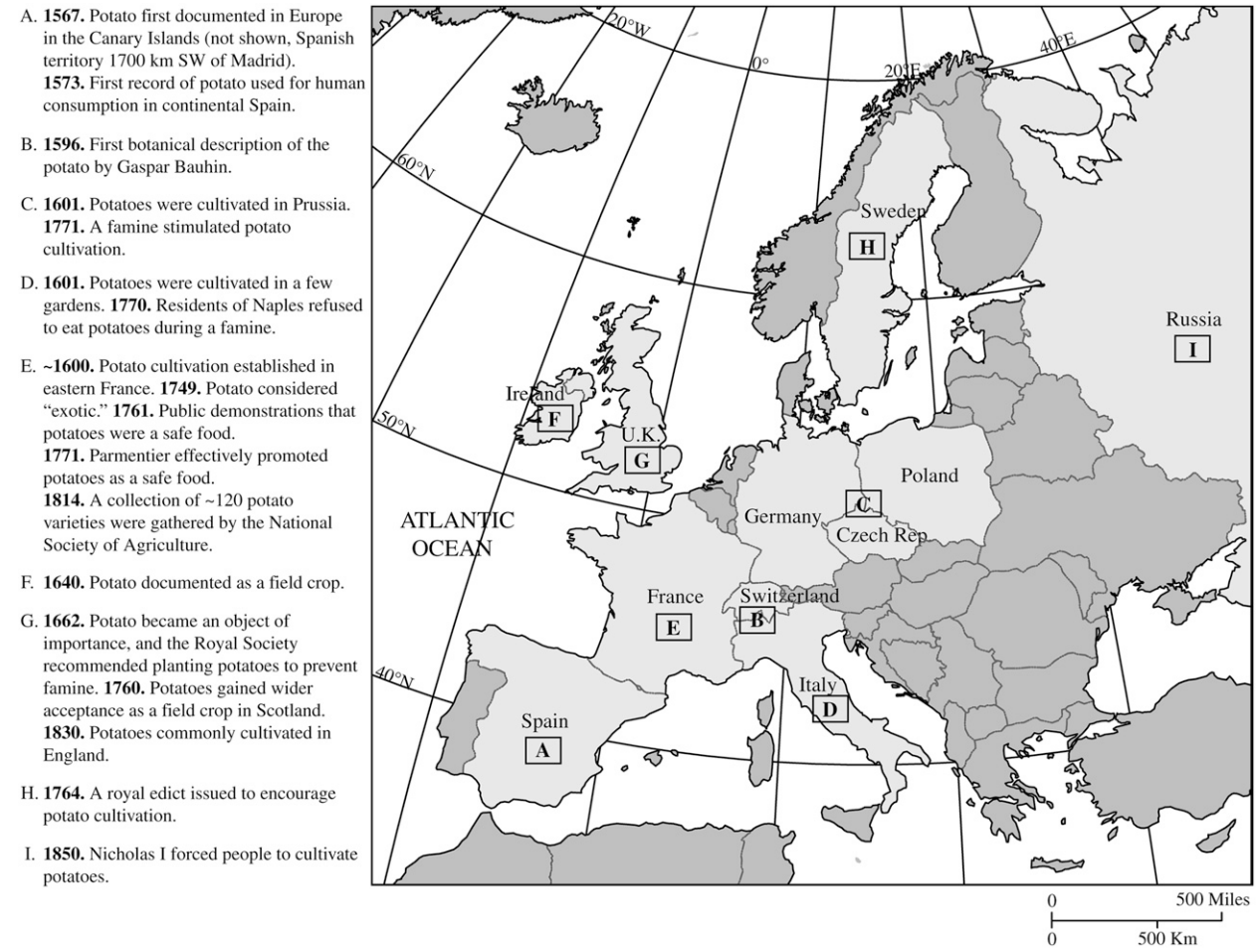


Fig. 1. Important dates and places that document the introduction and acceptance of potato outside of its original home in South America.

***Hypothesis about the origin of the European potato***—The origin of the European potato has been the subject of long controversy. Russian investigators (Juzepczuk and Bukasov, 1929) first proposed that the European potato was introduced from tetraploid landraces from Chile, while British investigators (Salaman, 1937; Salaman and Hawkes, 1949) suggested that it came from the Andes and persisted until the potato late blight epidemics beginning in the UK in 1845, after which it was replaced with Chilean germplasm through introductions and breeding efforts. Potato landraces from the high Andes and from lowland Chile can be distinguished, although sometimes with difficulty, by the following five traits: (1) cytoplasmic sterility factors: hybrids of Chilean landraces as females with Andean landraces as males have male sterility, but the reciprocal cross is fertile (Grun, 1979); (2) morphology, with the Chilean landraces having wider leaflets held more outward from the plant and other minor morphological differences (Huamán and Spooner, 2002); (3) the Chilean landraces tuberize under long days, the Andean landraces under short days (Glendinning, 1975); (4) a suite of microsatellite markers (Spooner et al., 2005b); and (5) a 241-bp deletion in the *trn*V-UAC/*ndh*C intergenic region of the plastid DNA molecule, which is absent in 94% (or 95%) of the Andean tetraploid landraces and present in 86% (or 81%) of the tetraploid Chilean landraces, depending on the studies of Hosaka (2004) or Spooner et al., (2007). This plastid deletion is associated with specific mitochondrial DNA types not found in Andean germplasm (Kawagoe and Kikuta, 1991; Hosaka, 1995; Lössl et al., 1999).

The Chilean origin hypothesis was proposed because of similarities of Chilean landraces to modern European cultivars with respect to morphology and tuberization under long days (traits 2 and 3 described earlier). Alternatively, the Andean origin hypothesis suggests that these two traits in European potato evolved rapidly from Andean landraces to a Chilean-type potato through selection following import to Europe. It further proposed that the late blight epidemics beginning in the United Kingdom in 1845 killed the Andean forms that later were replaced by breeding and introductions with the Chilean landraces.

The Andean origin hypothesis has been generally accepted over the last 60 years (Swaminathan, 1958; Simmonds, 1964, 1995; Glendinning, 1975; Hawkes, 1990; Hawkes and Francisco-Ortega, 1992; Hancock, 2004). It was supported, in part, by the identity of putative long-remnant landrace introductions of potato in India (Swaminathan, 1958) and in the Canary Islands (Hawkes and Francisco-Ortega, 1992) as Andean potatoes. However, the Indian landraces were shown to be of Chilean origin (Spooner et al., 2005b) and the Canary Island landraces as of Andean and Chilean origins (Ríos et al., 2007). These unexpected results stimulated our present reexamination of the origin of the European potato.

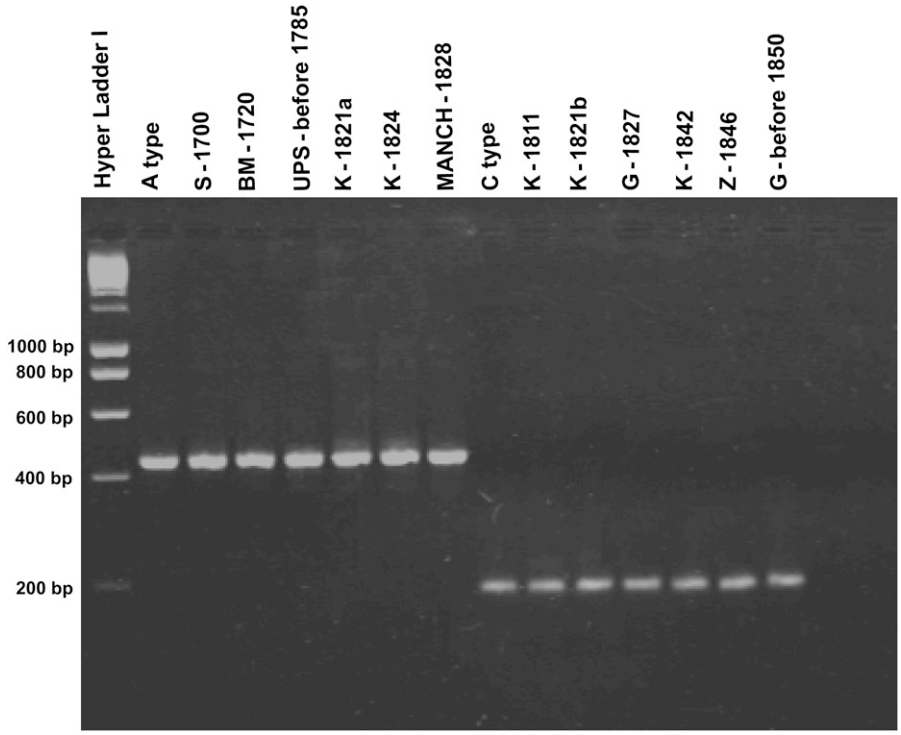


Fig. 2. Amplified PCR products of the plastid *trn*V-UAC/*ndh*C intergenic spacer region of 12 pre-1850 *Solanum tuberosum* specimens. The labels indicate the herbarium code and year of collection. The first seven lines show the Andean type of plastid DNA, and the last seven show the Chilean type. See Appendix S1 in Supplemental Data in online version of article for further details of these collections.

All data bearing upon the origin of the European potato have been inferential. The purpose of our study is to present the first direct evidence of the introduction of potato to Europe from either the high Andes or lowland Chile, through an examination of the plastid 241-bp deletion marker from historical (1700–1910) herbarium specimens.

## MATERIALS AND METHODS

***Plastid DNA isolation and PCR***—Total genomic DNA was isolated from leaves of 64 herbarium specimens dated between 1600 and 1910 (Appendix S1, see Supplemental Data with online version of this article). Approximately 0.5 $cm^2$ of tissue was ground in sterile 1.5 mL tubes using sterilized micropestles, with the addition of 150 μL of extraction buffer 1 (0.35 M sorbitol, 0.1 M Tris HCl PH 7.6, 0.005 M EDTA pH 8.0, and 0.02 M sodium bisulphite), 150 μL of CTAB extraction buffer 2 (0.2 M Tris HCl pH 7.6, 0.05 M EDTA pH 7.5, 2.0 M NaCl, and 2% CTAB), 60 μL 5% of sarkosyl (*N*-lauryl sarcosine), and 10 μL of 10 mg/mL RNAse A. After 15 min incubation at 65°C, the solution was placed in the purple filter columns from a Nucleo Spin Plant DNA extraction kit (Macherey-Nagel, Bethlehem, Pennsylvania, USA) and centrifuged at 11 000 rpm for 5 min. Then 350 μL of ice cold 100% ethanol was added to the supernatant before incubation on ice for 5 min. The solution was then poured into the green filter columns from the Nucleo Spin Plant DNA extraction kit and centrifuged at 11 000 rpm for 1 min. The membrane was washed twice with 500 μL of 70% ethanol and centrifuged for 1 min. The DNA was eluted in the preheated (70°C) elution buffer from the extraction kit. A pair of primers in the *trn*V-UAC/*ndh*C intergenic spacer region (H1-F: 5′ AAG TTT ACT CAC GGC AAT CG 3′ and H1-R: 5′ GGA GGG GTT TTT CTT GGT TG 3′) was used based on previous reports (Hosaka, 2002). PCR reactions were performed in a 10 μL volume containing 100 mM Tris-HCl, (Promega, Madison, Wisconsin, USA), 2.5 mM $MgCl_2$ (Promega), 0.25 mM of each dNTP (Promega), 0.5 μM of each primer (forward and reverse, UW- Biotechnology Center, Madison, WI), 0.25 units of *Taq* polymerase (Promega), and 10 ng of genomic DNA. A modified PCR protocol with the addition of 1% PVP and 1% BSA was also assayed to obtain amplification for samples that did not produce any PCR product. PCR was carried out in a MyCycler thermal cycler (Bio-Rad, Hercules, California, USA), set to the following program: 1 cycle of 3 min at 94°C; 40 cycles of 30 s at 94°C, 30 s at 55°C, 1 min at 72°C; and one final cycle at 72°C for 5 min. The amplification products were run on a 3% agarose gel and stained with ethidium bromide 0.5 $\mu g \cdot mL^{-1}$ and viewed with ultraviolet light. Negative controls (master mix and nontemplate DNA) were used. All positive controls were manipulated separately from the herbarium samples to avoid contamination using the same master mix. All PCR reactions were repeated twice.

***Plastid DNA sequencing***—For DNA sequencing, DNA bands from 14 accessions were cut and purified from the gel using a Zymoclean Gel DNA Recovery Kit (Zymo Research, Orange, California, USA). The purified plastid DNA molecules were cloned into a pGEM-T Easy Vector system (Promega). Plasmid DNA was purified from transformed *E. coli* JM109 using the Wizard Plus SV Minipreps DNA purification System (Promega,). Sequencing reactions consisted of 1 μL of BigDye Terminator v. 3.1 mix (Applied Biosystems, Foster City, California, USA), 1.5ul of dilution buffer (Applied Biosystems), 5–20 pmol of primer, and 0.2 μg of template DNA in a final reaction volume of 10 μL. The sequencing reaction was carried out in the MyCycler thermal cycler, set to the following program: 1 cycle of 3 min at 95°C; 40 cycles of 25 s at 96°C, 20 s at 50°C, 5 min at 60°C; and a final cycle at 72°C for 7 min. Excess dye terminators were removed using CleanSeq magnetic bead sequencing reaction clean up kit (Agencourt Biosciences, Beverly, Massachusetts, USA). The samples were resuspended off of the beads in 50 μL of double-distilled $H_2O$. Twenty μL of each sample was loaded into a 96-well PCR plate, and the plate loaded onto the sequencers according to the manufacturer's instructions. Samples were subjected to electrophoresis on an Applied Biosystems 3730xl automated DNA sequencing instrument, using 50-cm capillary arrays and POP-7 polymer. Data were analyzed with the program Sequencing Analysis version 3.7 PE-Biosystems version 3.7. Five clones were sequenced for each accession. PCR products of amplifications with and without additives were sequenced for verification purposes. DNA sequences were edited using the program Staden V.1.6.0 (Staden, 1996), and aligned manually. The sequence obtained for the accession of Andean type *Solanum tuberosum* was used as control because of the lack of the plastid deletion.

***Plastid DNA statistical interpretation***—As mentioned, Hosaka (2004) and Spooner et al. (2007) surveyed the presence or absence of the 241-bp plastid DNA deletion from landrace populations of *S. tuberosum* from the high Andes and from lowland Chile. We analyzed these data through logistic regression using the program SYSTAT 10 (SPSS, 2000) to calculate the probability that our determinations from European collections were from one of these two areas. The 314 tetraploid accessions of *S. tuberosum* from Hosaka (2004) and the 278 tetraploid accessions of *S. tuberosum* from Spooner et al. (2007) were assembled into two independent data sets and labeled as originating from the high Andes or from lowland Chile, concordant with their determinations of the 241-bp deletion.

## RESULTS

We gathered leaf samples from 64 herbarium specimens collected before 1910 from 11 European herbaria (Holmgren and Holmgren, 1998) [Appendix S1 in Supplemental Data in online version of article]. The plastid *trn*V-UAC/*ndh*C intergenic region was amplified for all but 15 of the 64 samples. Likely causes for amplification failures were DNA degradation in herbarium specimens caused by suboptimal drying and poor

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                10                                                  60                                                  120
A type          tagtttactcacggcaatcgtttaagcagatgaaagaaaaaacgcatatcaatggatccaatagatattgatttttgcaattgcagataaacaaaccaaccctttcggcattaatcttcgg
S-1700          ..........................................................................................................t.........
BM-1720         ..........................................................................................................t.........
UPS-Bef.1785    ..........................................................................................................t.........
K-1821a         ..........................................................................................................t.........
K-1824          a.........................................................................................................t.........
MANCH-1828      ..........................................................................t...............................t.........
C type          ........................**********************************************************************************************
K-1811          ........................**********************************************************************************************
K-1821b         ........................**********************************************************************************************
G-1827          ........................**********************************************************************************************
K-1842          ........................**********************************************************************************************
Z-1846          ........................**********************************************************************************************
G-Bef.1850      ........................**********************************************************************************************

                                                                  180                                                 240
A type          aggcgaattacatattcatatccacaataaaagaattagtgagactccctttcttttgatatccccaatcttattgaattttggaagtcaactcatttcacgggcctggtgaaatgcaaa
S-1700          ............................................................................................................................
BM-1720         ............................................................................................................................
UPS-Bef.1785    ............................................................................................................................
K-1821a         ............................................................................................................................
K-1824          ............................................................................................................................
MANCH-1828      ............................................................................................................................
C type          ************************************************************************************************************************
K-1811          ************************************************************************************************************************
K-1821b         ************************************************************************************************************************
G-1827          ************************************************************************************************************************
K-1842          ************************************************************************************************************************
Z-1846          ************************************************************************************************************************
G-Bef.1850      ************************************************************************************************************************

                                                                  300                                                 360
A type          actacgaagaggaattcacatggatttaggaaaggcctgctgtatttgtgtacaagctaaagttttttgaaaaatgaatatctttggtcactttcattgtcaaataggcttttccttcgt
S-1700          ............................................................................................................................
BM-1720         ............................................................................................................................
UPS-Bef.1785    ............................................................................................................................
K-1821a         ............................................................................................................................
K-1824          ............................................................................................................................
MANCH-1828      ............................................................................................a...............
C type          *************************.............................................................................................
K-1811          *************************.............................................................................................
K-1821b         *************************.............................................................................................
G-1827          *************************.............................................................................................
K-1842          *************************.............................................................................................
Z-1846          *************************.............................................................................................
G-Bef.1850      *************************.............................................................................................

                                                                  420
A type          ataccttacttacctcgacctagcgaagcacaacaaaaaaaggtagtcttcttttttctgtattcaaccaagaaaaacccctcc
S-1700          ...................................................................................
BM-1720         ...................................................................................
UPS-Bef.1785    ...................................................................................
K-1821a         ...................................................................................
K-1824          ...................................................................................
MANCH-1828      ...................................................................................
C type          ...................................................................................
K-1811          ...................................................................................
K-1821b         ...................................................................................
G-1827          ...................................................................................
K-1842          ...................................................................................
Z-1846          ...................................................................................
G-Bef.1850      ...................................................................................
```

Fig. 3. Sequence of the plastid *trn*V-UAC/*ndh*C intergenic spacer region of the same 12 pre-1850 *Solanum tuberosum* specimens as in Fig. 2, compared with our sequence of one accession each of Andean *S. tuberosum* ("A-type") lacking a deletion, and Chilean *S. tuberosum* ("C-type") from Chile, possessing a 241-bp deletion. The nucleotides that are homologous to the sequence of the A type are indicated by periods, and deleted regions are indicated by asterisks.

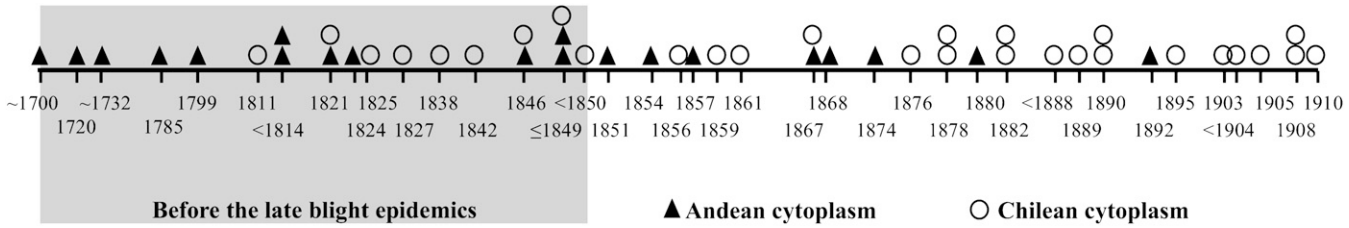


Fig. 4. Chronological summary of the 241-bp deletion in the *trn*V-UAC/*ndh*C intergenic spacer region of the plastid DNA of 49 herbarium specimens of *Solanum tuberosum* collected in Europe from the early 1700s to 1910, distinguishing germplasm originating from the high Andes or from lowland Chile. The gray box highlights those collected before the late blight epidemics that were well established in the UK by 1850.

preservation (Doyle and Dickson, 1987). Twenty-one of the 49 specimens that were amplified were collected before 1850, and 28 from 1850 to 1910. We sequenced DNA from the *trn*V-UAC/*ndh*C intergenic spacer region from 12 of these 49 specimens to sample whether the deletion is the same as that reported by Kawagoe and Kikuta (1991) (Figs. 2 and 3).

Logistic regression analysis of the 241-bp plastid deletion data obtained by Hosaka (2004) and Spooner et al. (2007) gave a 0.86 or 0.81 probability, respectively, of assigning a sample from Europe having the 241-bp deletion to Chile as its geographical location. It gave a 0.94 and 0.95 probability, respectively, of assigning a sample from Europe lacking the 241-bp deletion to the Andes. This analysis had significant $p$ values (0.0001) and high log likelihood estimates (−1.05228E+02, −1.23549E+02, respectively), supporting the diagnostic nature of this plastid deletion as a marker to discriminate the likely geographical sources of these introductions.

Our results show that the Andean potato (lacking the DNA plastid deletion) first appeared in Europe around 1700 and persisted until 1892, long after the late blight epidemics, while the Chilean potato (possessing the deletion) first appeared in Europe in 1811, long before the late blight epidemics and persisted until the present day, when over 99% of extant modern potato cultivars possess Chilean cytoplasm (Hosaka, 1993, 1995; Powell et al., 1993; Provan et al., 1999) (Fig. 4). This includes an extant cultivar Yam, released in 1836 before the late blight epidemics (Powell et al., 1993). Of the period from 1811 to 1850, 9 of the 16 specimens (56.3%) possessed Chilean cytoplasm (Fig. 4).

## DISCUSSION

Our results resolved the long-standing controversy about the origin of the European potato and stimulate a revision of the importance of late blight disease to the selection of Andean and Chilean landraces. Our evidence supports original introductions from the Andes, but refutes the idea that the late blight epidemics beginning in Europe in 1845 stimulated introductions of Chilean germplasm as breeding stock to combat this disease or eliminated the Andean potato, which persisted up until 1892. Chilean potatoes became predominant by at least 1811, fully 34 yr before the late blight epidemics (Fig. 4). The diagnostic nature of the 241-bp deletion is not absolute, but our conclusions are highly likely. It is possible that original frequencies of this deletion were higher or lower in historical times because of hybridization, lineage sorting, or founder effects.

There were always problems with the idea that Chilean potatoes were germplasm sources subsequent to the late blight epidemics. First, Chilean potatoes are not noted as sources of late blight resistance (Glendinning, 1975; Jansky, 2000). Second, plastids are not transferred in pollen in the Solanaceae (Corriveau and Coleman, 1988), so only crosses of Chilean potatoes as female with Andean potatoes as male would produce the over 99% of extant modern varieties having Chilean-type plastid DNA. However, this cross is hindered by the unilateral incompatibility of Chilean and Andean potatoes described (Grun, 1979).

Our results show the impact of understanding plant origins to practical breeding programs. Years of effort were put into creating "Neo-Tuberosum" populations through artificial selection of long-day adaptation from Andean potatoes. The goal was based on the unquestioned assumption that the European potato was solely of Andean origin and was mass selected for long daylength adaptation like the Chilean potato, but in the process of selection, many desirable characters for general adaptation, such as resistance to potato late blight, were lost (Simmonds, 1964; Plaisted, 1972; Glendinning, 1975). Our data, however, document that European potato germplasm was derived from high latitude Chilean forms of *Solanum tuberosum* in Europe long before the potato blight epidemics.

Our data also highlight the critical importance of herbarium specimens in investigating historical origins of crop plants. Literally all data sets addressing the origin of the European potato before this study (morphology of herbarium specimens, crossing behavior, molecular examination of extant putative remnant landrace populations in the Canary Islands, historical records) were ambiguous, contradictory, and inferential. Molecular examinations of the plastid *trn*V-UAC/*ndh*C intergenic spacer region, however, provide the first direct evidence to bear upon the long-held controversy of the extra-Andean origin of this major food plant and completely change our understanding of the history of the potato outside of South America.

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