Recreation of the Edinburgh potato *Solanum × edinense* Berthault – a historically and economically important potato hybrid

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Abstract

Solanum × *edinense* Berthault is a spontaneously occurring hybrid between *S. demissum* Lindl. and the cultivated potato, *S. tuberosum* L., found near potato fields in Mexico. Although not described until 1911, this hybrid was in cultivation at the Royal Botanic Garden Edinburgh (RBGE) shortly after the Irish Potato Famine of 1845–1849 and proved to be highly resistant to late blight, *Phytophthora infestans*. In the mid-19th century late blight caused widespread failure of the potato crop across Europe and played a central role in the Irish Potato Famine. Using the parent species in controlled crosses we have recreated the hybrid that was named by Berthault in recognition of RBGE as the source of his plant material. We have also researched the early history of this hybrid potato in Edinburgh and demonstrated disease resistance through field exposure during the outbreak of late blight in Edinburgh in 2019. This work underlines the important role of this hybrid in the breeding of disease-resistant potato cultivars.

Introduction

Solanum × *edinense* Berthault (Solanaceae Juss.) was named to commemorate the Royal Botanic Garden Edinburgh (RBGE) by Pierre Berthault (Berthault, 1911). This hybrid potato is only found naturally occurring in parts of Mexico, so the choice of name is somewhat unexpected and reflects the fact that Berthault had sourced his plant material indirectly from RBGE, knowing nothing else of its origin at the time (Berthault, 1911). However, this potato is of more than purely scientific interest, as it represents the first introduction of disease resistance into the cultivated potato from a wild relative (Ross, 1979). The search for disease resistance (R) genes in wild *Solanum* species is ongoing and is potentially of great economic importance (e.g. Chen *et al*., 2018).

Resistance to late blight, *Phytophthora infestans*, is a notable feature of the hybrid *Solanum* × *edinense* and because of this it has been extensively used in potato breeding programmes (Ross, 1979; Akino *et al*., 2014). However, although *S.* × *edinense* demonstrated good disease resistance at RBGE in the latter part of the 19th century (Sutton, 1896), the continual evolution of the

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pathogen means that this resistance has been overcome in some cases (Salaman, 1985; Akino *et al.*, 2014).

Late blight resistance in *Solanum* × *edinense* is inherited from *S. demissum* Lindl., a Mexican wild potato. Despite resistance being repeatedly broken down, the diversity of R genes present in *S. demissum* means that it is still a useful source of resistance to late blight, and the recreation of *S.* × *edinense* has been the first step on a pathway to disease-resistant cultivars of commercial value (Akino *et al.*, 2014). Interestingly, the considerable variation in late blight resistance in *S. demissum* is highlighted in the first published account of this species, in which John Lindley notes that the material he was cultivating exhibited symptoms of late blight (Lindley, 1848).

An early case of breeding and selection for late blight resistance derived from *Solanum demissum* that ultimately failed is provided by Salaman (1985). From 1906 the potato breeder Redcliffe N. Salaman used *Solanum* × *edinense*, mistakenly identified as *S. maglia* Schltdl., for breeding experiments with cultivated potatoes and noticed disease resistance in some of the progeny. These plants were selectively bred from, and Salaman (1985) writes 'By 1926 I was in possession of over a score of seedling varieties endowed with reasonably good economic characters which, no matter what their maturity, appeared to be immune to blight.' Unfortunately, this optimism was short-lived, and in 1932 and 1936 these previously resistant varieties proved to be susceptible to disease, suggesting that evolution of the pathogen had taken place (Salaman, 1985).

A factor that complicates the study of wild material of this hybrid is that there are few reliable distinguishing characters that separate *Solanum* × *edinense* from *S. demissum*, and some of the most useful require microscopic examination. The authors of the most recent relevant *Solanum* monograph (Spooner *et al.*, 2004) have noted that 'frankly it is impossible for us to determine with confidence all herbarium specimens as one or the other taxon'. In addition, cultivation appears to increase the vegetative similarity between these two taxa (Ugent, 1967).

We have recreated *Solanum* × *edinense* from its parent species, *S. demissum* and the cultivated potato *S. tuberosum* L., to study its distinguishing characters and to interpret, via living plant displays, the role of wild potato species in potato improvement for visitors to RBGE. In the process we researched the history of *S.* × *edinense* contained in the RBGE archive.

The Edinburgh connection

Berthault (1911) obtained his plant material from the seed merchant Sutton & Sons, who had in turn received material from RBGE. Examination of the RBGE archive has identified two occasions when tubers of this potato, mistakenly referred to as *S. etuberosum* Lindl., were sent to Sutton & Sons – in 1887 and again in 1897. Although Berthault knew nothing of the supposed wild origins of this potato, he considered it to be a hybrid resulting from a cross between the cultivated potato and an unknown wild species (Berthault, 1911).

The wild distribution of *Solanum* × *edinense* is summarised by Ugent (1967) as being in and along the edges of cultivated fields, roadsides, ditches and the margins of forests in the Central Volcanic Cordillera of Mexico at altitudes from 2,000 to 3,500 m. Evidence of intermediate morphology between *S. demissum* and *S. tuberosum* was

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taken by Ugent (1967) as proof that *S.* × *edinense* was derived from these two species. The same view was taken by Spooner *et al.* (2004). A detailed study of the hybrid in its native range has demonstrated that it is repeatedly formed where *S. demissum* grows alongside cultivated potatoes (Ugent, 1967). Although the hybrid is not generally valued by farmers in Mexico, due to an astringent taste, the presence of highly fertile individuals could provide a genetic bridge allowing genes from the wild to diversify the cultivated potato, leading to potential benefits (Ugent, 1967).

Early details of *Solanum* × *edinense*, wrongly referred to as *S. etuberosum*, appear in a paper written by Arthur W. Sutton, senior partner at Sutton & Sons (Sutton, 1896). He confirms the source of his plants as RBGE and Robert Lindsay, Curator at RBGE, as the source of accompanying information sent in 1887. According to Sutton (1896) Lindsay had stated that 'the original plants had been left in the same beds for at least thirty years. They produced long, running shoots having very few and small tubers'. Lindsay also writes, 'When left in the ground all the winter the tubers appeared to be quite unaffected by frost, and no disease had been observed'. The absence of disease is significant as the cultivation of this potato at RBGE potentially began around 1860, shortly after the emergence of late blight in the 1840s. At that time late blight caused widespread devastation of the potato crop and contributed to famine in Ireland (Seekamp & Feiritear, 2008; Reader, 2009).

Materials and methods

Sourcing plant material

Minimising the risk of introducing virus-infected potato seed tubers and true potato seed required all plant material to be sourced from suppliers that routinely check for virus infection. Potato viruses are a major cause of losses for potato farmers and given the importance of the potato industry to Scotland's economy we only sourced from two suppliers who operate the strictest controls: Science and Advice for Scottish Agriculture (SASA) and the Commonwealth Potato Collection (CPC) at the James Hutton Institute (JHI). Plant material was supplied under a Material Transfer Agreement with EU Plant Passports.

To recreate *Solanum* × *edinense* we sourced material of the parent species *S. demissum* and *S. tuberosum*. Fertility was an important consideration in the selection of *S. tuberosum* cultivars as many cultivated potatoes are partially or completely sterile. Ploidy was another factor we had to consider. Although most commercial potato cultivars are tetraploid ($2n = 4x$) with 48 chromosomes, there are some diploids ($2n = 2x$) with 24 chromosomes. Work that has identified sexually compatible groups within *Solanum* suggests that the hexaploid ($2n = 6x$) *S. demissum* with 72 chromosomes is compatible with tetraploid cultivars of *S. tuberosum*, but not with cultivars that are diploid (Whitson, 2019). Consequently, the hybrid *S.* × *edinense* is pentaploid ($2n = 5x$) and has 60 chromosomes.

Pollination protocol

Controlled crossing was carried out using the two parent species as both males and females. This was done to take account of the fact that hybridisation success is sometimes unidirectional. Previous experience indicates that this hybrid is normally only formed when *Solanum demissum* is used as the female parent.

Tubers of nine European tetraploid cultivars of *Solanum tuberosum* were planted in April and early May 2018. The material grown was: 'BF 15'; 'Dunbar Rover'; 'Erntestolz';

'Lumper'; 'Morene'; 'Paterson's Victoria'; 'Red Craigs Royal'; 'Salad Blue'; and 'Vanessa'. A further 11 Andean diploid cultivars of unknown name were planted in June. Late planting was necessary due to the adaptation of these cultivars to short days, leading to improved tuber formation during late summer. The Andean diploids were included to further assess their reproductive incompatibility with *S. demissum*. Material of *S. demissum* was grown from true potato seed, sown under glass in March. Hand pollination began once the flowers started appearing in early July.

Pollen extraction was conducted indoors, but the preparation of emasculated flowers and the application of pollen took place outdoors, making measures to limit the likelihood of uncontrolled open pollination essential (see below).

Pollen donor flowers were selected when newly opened to reduce the likelihood of contamination with pollen from other flowers. Flowers used as pollen donors were removed and pollen was buzzed out of them onto a glass slide using a specially designed tool to mimic buzz pollination vibrations produced by bumblebees (King & Buchmann, 1996). Collected pollen was used immediately.

Flowers chosen to act as females in controlled crosses were selected to be on the cusp of opening, as judged by the appearance of the initial split in the corolla. Both species used in the crosses are known to be self-compatible (Spooner *et al*., 2004), although we are not aware of self-pollination occurring prior to flower opening in either species. The flowers were manually opened by applying gentle pressure to the bud and the anthers were carefully removed with fine forceps, leaving the stigma and the ovary exposed. Other flowers in the inflorescence were removed to reduce the possibility of pollen contamination and to direct maximum resources to the controlled cross. Emasculated flowers prepared in this way were pollinated immediately to minimise the risk of pollen contamination.

Donor pollen was loaded onto a fine paintbrush and brushed lightly onto the exposed stigma of the prepared flower. Pollinated flowers were covered with a fine-mesh teabag, secured with thread, to exclude insect pollinators. Teabags were numbered and a separate label was also attached. Details of the controlled crosses were recorded using the standard practice of noting the female parent first.

Fruit development was checked weekly. We found on average that berries tended to appear 3–4 weeks after fertilisation. Unsuccessful crosses would generally abort prior to this.

Seed extraction and storage

Berries were left to fully ripen on the female plants for 10–12 weeks. The berries were then harvested and stored at room temperature to allow for post-harvest ripening. Once the berries had become soft enough to easily remove the contents, the seeds were extracted into water and washed repeatedly until all surrounding pulp had been removed. This was done to reduce the likelihood of mould growth and to remove any potential chemical inhibitors of germination present in the pulp. Once extracted the seeds were dried on newspaper and then stored in paper envelopes in the refrigerator at 5° C until sowing in spring 2019.

Results

Crossing success

Forty-four controlled crosses were carried out. Of this total, thirty-five had *Solanum tuberosum* as female parents and nine had *S. demissum* as female parents. Fruit formation was influenced by the choice of maternal species. Fruit was formed in one out of thirty-five crosses when using *S. tuberosum* as the female parent: a 3 per cent success rate. In contrast, fruit was formed in seven out of nine crosses when using *S. demissum*: a 78 per cent success rate.

Germination and growing on to flowering

Seeds were sown in March 2019 in an unheated polytunnel to maintain temperatures above freezing. Small pots were used with a standard growing medium. As additional protection, pots were covered with fleece when frost was forecast. Plants were potted on under cover as required and planted outdoors in the open ground around mid-May. The time from germination to planting outside was approximately one month.

Fruit was produced from eight crosses and seed was sown from five of these: 6, 8, 16, 26 and 42. Details of the parent plants in each cross are provided in the Appendix. No germination was observed in cross 16 and it is worth noting here that this could be explained by the male parent in this cross being a diploid cultivar of *Solanum tuberosum*.

Of the four crosses that germinated, two (26 and 42) displayed vegetative morphology that was inconsistent with a hybrid origin. This was later confirmed by detailed examination of floral morphology. Cross 26 had a *Solanum demissum* female parent and produced offspring consistent with pure *S. demissum*. Cross 42 had a diploid *S. tuberosum* female parent and produced offspring consistent with pure *S. tuberosum*. In both cases pollen contamination, possibly via self-pollination, could explain these results.

Two crosses (6 and 8) gave rise to morphologically intermediate offspring interpreted as hybrids and consistent with detailed descriptions of *Solanum* × *edinense* (Spooner *et al*., 2004). In both cases *S. demissum* was pollinated using pollen collected from the tetraploid *S. tuberosum* cultivar 'Lumper', a historically interesting potato as it was being widely grown in Ireland when late blight first emerged in the 1840s. Measurement of anther length was used to compare the parent species and the putative hybrids to provide further confirmation of their hybrid origin, as this character is useful in distinguishing closely related *Solanum* taxa (Särkinen *et al*., 2018). Five plants from cross 6 and one plant from cross 8 grew to maturity and flowered.

Hybrid identification

Floral characters have been found to be more stable than vegetative characters in a comparative study that included both cultivated and wild collected material of *Solanum* × *edinense* (Ugent, 1967). Based on this and subsequent taxonomic work on the genus *Solanum*, anther length was chosen as a reliable character for the identification of hybrids (Ugent, 1967; Särkinen *et al*., 2018).

A total of six plants of *Solanum* × *edinense* and six of *S. demissum* were measured for anther length, with measurements replicated for each plant using five flowers. For one of the *S.* × *edinense* plants only three flowers were measured, due to the comparatively small size of the plant with few fully developed flowers. It is also notable that two flowers of two individuals of *S. demissum* were missing a stamen, resulting in flowers with four anthers. Additionally, 60 anthers of *S. tuberosum* 'Lumper' were measured as a reference point. However, these data were not included in the analysis as our focus was on distinguishing the morphologically closely similar taxa *S.* × *edinense* and *S. demissum*.

For the analysis, a total of 288 anthers were measured. As the data consisted of a single variable, simple statistics were generated for the data. Means for each flower and individual plants were produced, together with their standard deviations ×2 (×2 SD). By using ×2 SD instead of ×1 SD, 95 per cent of the variation displayed by individual plants was observed. Once the measurements for individuals were grouped by taxon, a mean and ×2 SD for the groups was calculated. Results for means and ×2 SD statistics for individuals can be seen in Table 1 and for taxa in Table 2. Bar charts of these data are provided for individuals in Fig. 1 and for taxa in Fig. 2.

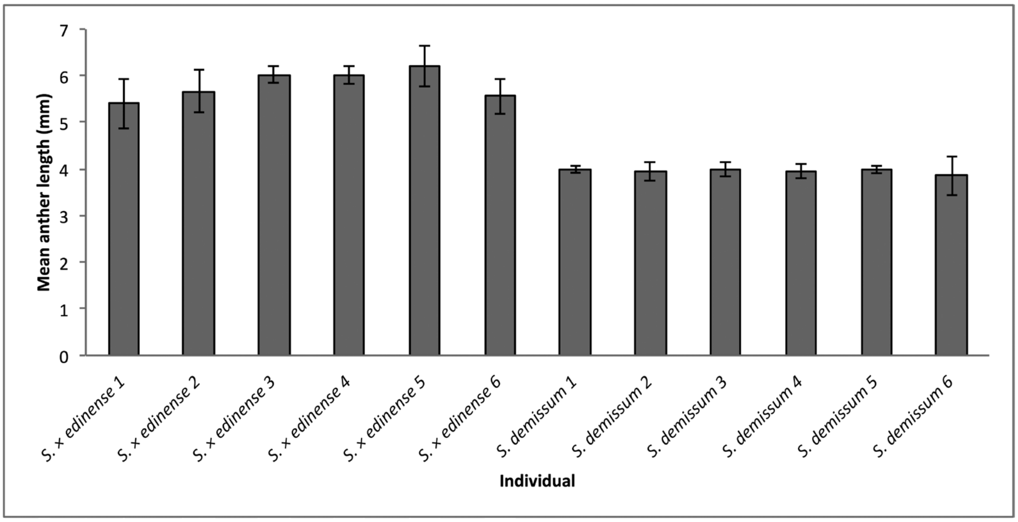

Fig. 1 Bar chart of the average anther length (mm) of six plants of *Solanum* × *edinense* and six plants of *S. demissum*, with error bars showing ×2 SD.

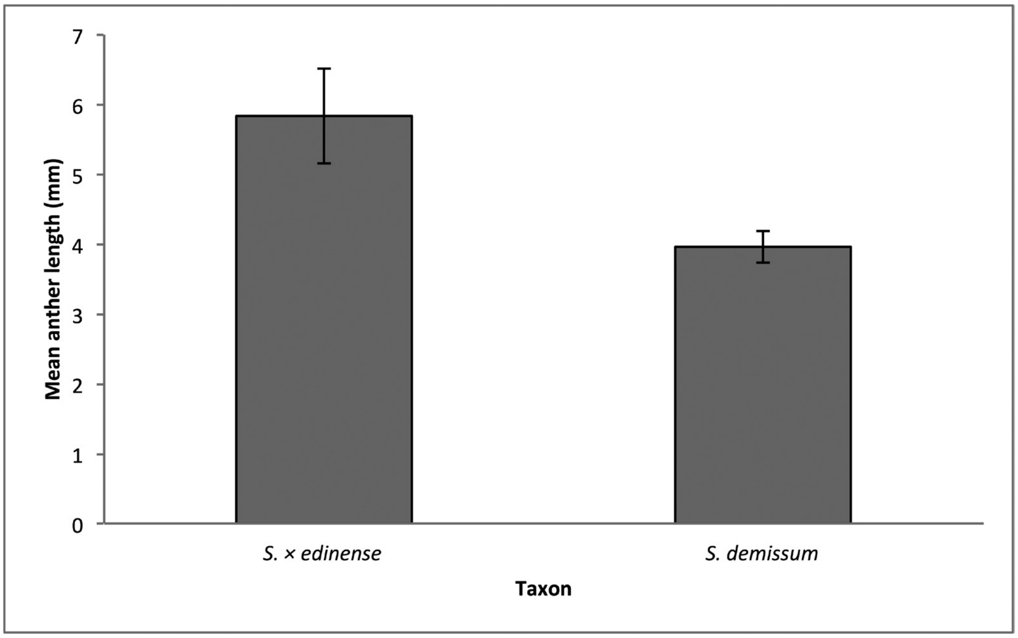

Fig. 2 Bar chart of the average anther length (mm) of *Solanum* × *edinense* and *S. demissum*, with error bars showing ×2 SD.

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Table 1 Average anther length (mm) and ×2 SD of six plants of *Solanum* × *edinense* and six plants of *S.* × *demissum*.

	Individual mean	**SD**	**×2 SD**
S. × *edinense* 1	5.40	0.26	0.53
S. × *edinense* 2	5.67	0.23	0.46
S. × *edinense* 3	6.02	0.09	0.17
S. × *edinense* 4	6.01	0.09	0.18
S. × *edinense* 5	6.19	0.22	0.44
S. × *edinense* 6	5.55	0.18	0.37
S. demissum 1	4.00	0.04	0.08
S. demissum 2	3.94	0.10	0.19
S. demissum 3	3.99	0.07	0.15
S. demissum 4	3.96	0.08	0.16
S. demissum 5	3.98	0.04	0.08
S. demissum 6	3.86	0.21	0.42

Table 2 Average anther length (mm) and ×2 SD of *Solanum* × *edinense* and *S. demissum*.

	Taxon mean	**SD**	**×2 SD**
S. × *edinense*	5.83	0.34	0.69
S. demissum	3.96	0.12	0.23

The main result of this statistical treatment of anther length is that this character is useful for distinguishing between *Solanum* × *edinense* and *S. demissum*. Our data show that these taxa can be identified by non-overlapping ranges in anther length. Our taxon mean values are broadly consistent with previous measurements (Spooner *et al.*, 2004). However, *S.* × *edinense* is at the lower end of the range with 5.83 mm and *S. demissum* is at the upper end of the range with 3.96 mm. *S.* × *edinense* anther measurements occupy the morphological gap between the parent species (Ugent, 1967). The reference measurements of anther length taken from *S. tuberosum* 'Lumper' showed a mean of 7.46 mm (*N* = 60).

Discussion

Distinguishing hybrids from the Mexican parent

After 20 years of cultivating *Solanum* × *edinense* in the nursery of Sutton & Sons, Arthur W. Sutton published further observations that provide a useful comparison with our hybrids (Sutton, 1908). During this period Sutton notes the absence of disease and that tubers remained small, roughly the size of a walnut. Notable observations made by Sutton include the pollen being of normal form, calyces being covered with spreading hairs and fruits having widely spaced white spots on the surface. In each of these characters all six of our hybrid plants agree with Sutton (1908).

Spooner *et al.* (2004) does not mention the disposition of hairs on the calyx in either taxon, but we observed that in *S.* × *edinense* the calyx hairs are spreading and in *S. demissum* they are more or less flat against the surface of the calyx. Line drawings showing the possibly useful calyx hair character differences in *S.* × *edinense* and *S. demissum* are provided in Fig. 3, but it should be noted that further material of all three taxa needs to be studied in order to establish how useful this character is.

Type material of the hybrid held in the RBGE Herbarium (E) was examined and the calyx hair disposition was found to be neither obviously spreading nor flattened against the calyx surface. The material examined was: *Solanum salamanii* Hawkes isotype, Mexico, Paraje Mungia, Nevado de Toluca, 3,550 m, 12 Jul 1938, Balls 5010 (this name is a synonym of *S.* × *edinense*).

From our own observations we would highlight: the obvious difference in pigmentation on the upper and lower surfaces of the corolla in *Solanum demissum* as opposed to the greater pigment uniformity in *S.* × *edinense*; the calyx hairs lying more or less flat in *S. demissum* as opposed to spreading in *S.* × *edinense*; and the smaller anthers in *S. demissum* compared to *S.* × *edinense*, with non-overlapping anther length ranges in these taxa. It should be noted that the corolla colour must be observed in living material.

The hybrids produced a few small tubers ranging in size between 0.5 and 2 cm. The tuber skin was pale yellow with patches of faint purple around the eyes. In *Solanum demissum* the size and appearance of tubers was markedly different, with tubers being no larger than 0.5 cm and white. Tubers were also less frequently produced than in the hybrids.

To assist the comparison between *Solanum* × *edinense* and *S. demissum* see Fig. 4, which illustrates a flowering shoot of *S. demissum*.

Response to late blight

Given the continued importance of *Solanum* × *edinense* as a source of disease resistance, the occurrence of widespread late blight during August 2019 provided an opportunity for us to observe resistance in the field. All plants of *S. tuberosum* growing in our trials in the Demonstration Garden at RBGE, representing 20 cultivars of diploid and tetraploid potatoes, displayed symptoms diagnosed as late blight on 20 August. In response to this, the above-ground parts (‘shaws’) were removed to reduce the risk of infection spreading to other plants and entering the tubers. At the same time, all cultivars of *S. tuberosum* being grown nearby also succumbed to late blight. Throughout the remainder of the growing season *S. demissum* remained free of disease. One of the six *S.* × *edinense* plants developed a few possible late blight lesions on leaves near the soil surface. However, the fact that the disease did not appear to progress suggests a greater degree of late blight resistance than was observed in all examples of *S. tuberosum*.

This view was supported by experimental culturing of pathogens from leaf lesions collected from ten cultivars of *Solanum tuberosum* and one of the *S.* × *edinense* hybrids carried out by the RBGE plant health laboratory (Katherine Hayden, pers. comm.). Six of the ten pathogen samples taken from *S. tuberosum* developed morphology during culture that was consistent with them being the late blight pathogen *Phytophthora infestans*. Of the other four, two were not grown on, one failed to grow and one was infected with an oomycete that did

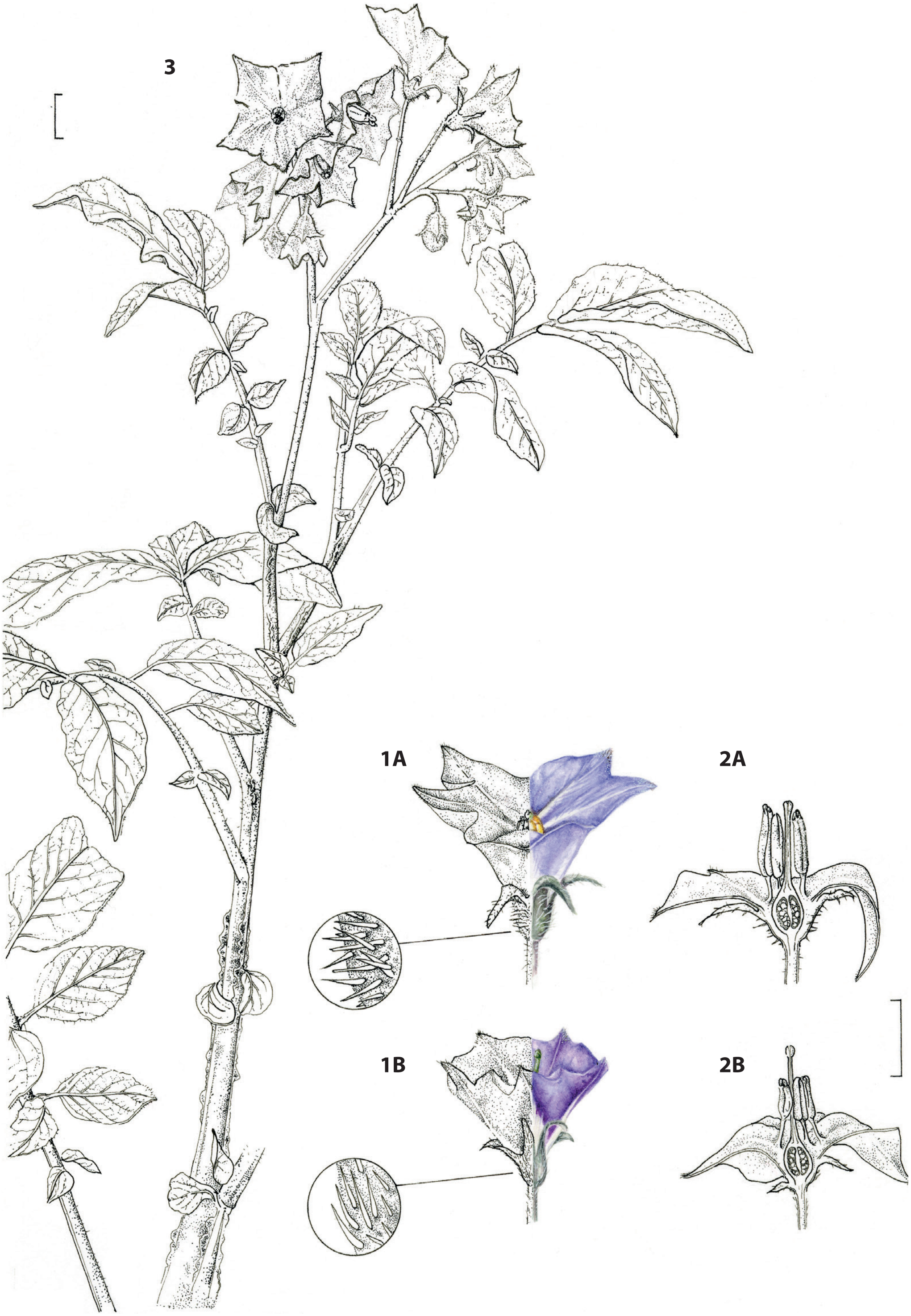

Fig. 3 *Solanum* × *edinense* and *S. demissum* distinguishing floral characters. 1: corolla pigmentation and calyx hairs – A *S.* × *edinense*, B *S. demissum*; 2: anther length – A *S.* × *edinense*, B *S. demissum*; 3: *S.* × *edinense* flowering shoot. All scale bars represent 10 mm. Drawings by Alison Cutts.

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Fig. 4 *Solanum demissum* flowering shoot. Scale bar represents 10 mm. Painting by Lizzie Sanders.

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not display morphology consistent with *P. infestans*. The single hybrid with possible late blight was also found to be infected with an oomycete that did not display morphology consistent with *P. infestans*, although it should be noted that this cannot be interpreted as evidence that late blight was not present on the hybrids.

Other disease issues

During the latter stages of the growing cycle unusual leaf morphology was observed in five out of the six hybrids. To rule out the presence of viruses, leaf material of all six hybrids was tested at SASA. The three protocols used were: (1) DAS ELISA as described in SOP PH009 Version 7 (testing for APLV, APMV, AVBO, BRSV, PBRSV, PLRV, PMTV, PotLV, PVA, PVM, PVP/PRDV, PVS, PVT, PVV, PVX, PVY, PYBV, PYV and TSWV); (2) Conventional RT-PCR as described in SOP PH011 Version 9 (testing for *Potyvirus* group, including PVA, PVV, PVY); and (3) Real-time PCR as described in SOP PH011 Version 9 (testing for PLRVAll). All results were negative for the presence of viruses.

The symptoms observed were chlorosis, necrosis and curling of the leaves; these could also be explained by an autoimmune-like response known as hybrid necrosis in which epistatic interactions between genes result in deleterious phenotypes. Hybrid necrosis has been previously documented in interspecific crosses in *Solanum* (Bomblies & Weigel, 2007). The exact cause of the unusual leaf morphology observed remains unknown.

As a precautionary measure to prevent the introduction of viruses via, for example, aphid vectors, the entire plot was isolated under fleece. Following the conclusion of the trial, all plant material was safely disposed of in sealed bags to landfill, or by burning on site.

To establish whether the unidentified disease seen in five out of the six hybrids had altered the floral morphology, we compared data on anther length. The symptom-free hybrid (plant 5) had the longest mean anther length, but the six individuals all shared a degree of overlap in the variability of this measure. In our opinion, a possible reduction in anther length in plants with unusual leaf morphology does not alter the key finding that the hybrid was successfully recreated. All drawings reproduced in Fig. 3 show hybrid material that was free of disease symptoms.

It should be reiterated that all potato breeding needs be carried out in close cooperation with the relevant statutory authorities to minimise the risks presented to the potato industry.

Unresolved questions

Some important aspects of the history of *Solanum* × *edinense* in Edinburgh remain unknown. Exactly when this hybrid potato arrived at RBGE is still to be established. The information passed from Lindsay to Sutton suggests a date around 1860 (Sutton, 1896). The actual date and the source of the material may never be known, but further searching of the archive would be worthwhile. What can reasonably be assumed is that the presence of this potato at RBGE in the years after the emergence of late blight would have drawn attention by virtue of its disease resistance.

Agricultural botany was an interest of Sir Isaac Bayley Balfour, Regius Keeper at RBGE from 1888 to 1922. It is possible that his influence contributed to the continued cultivation of unusual and potentially promising wild potatoes during this period. Balfour is recorded in the RBGE archive as being the source of the second shipment of tubers of *Solanum* × *edinense* to Sutton in 1897.

Another important question, currently a matter of speculation, is whether plant material was ultimately sourced from the wild in Mexico or arose in cultivation at a location where both parent species were being grown. Such a location could have been a garden in Europe or could equally have been at RBGE. Consequently, records of *Solanum demissum* arriving at RBGE would also be of potential significance in unravelling the origin of *S.* × *edinense* at RBGE. Glendinning (1983) states that *S.* × *edinense* 'initially arose in the Edinburgh Botanic Garden', suggesting an origin in cultivation at RBGE. However, the absence of any further detailed information or supporting references means this statement must be treated with caution. The detail in the descriptions of various wild *Solanum* species sent to the UK from Mexico prior to 1848 to John Lindley is rather inconsistent (Lindley, 1848). Included in the shipment was *S. demissum*, which was described as a new species by Lindley (1848). However, it is also possible that the shipment could have contained *S.* × *edinense*.

It is interesting that our only successful crosses involved *Solanum tuberosum* 'Lumper'. This is an old cultivar of uncertain origin that probably came to prominence in Ireland in the 18th century. Due to its age this cultivar has no genetic input from *S. demissum*. This is potentially significant as cultivars with *S. demissum* in their ancestry display cytoplasmic male sterility, a condition that is passed down the female line from the initial F1 hybrid to all subsequent generations (Sanetomo & Gebhardt, 2015). This fact may account for the failure of our crosses that used modern varieties as the male parent since *S. demissum* is common in the ancestry of cultivars released since the 1950s.

Conclusion

The history and origin of *Solanum* × *edinense* remains somewhat enigmatic. The successful recreation of this hybrid potato has allowed more to be learnt about how it differs from the parent species that give rise to it, particularly the closely similar *S. demissum*. We have also demonstrated that this hybrid continues to be a useful source of resistance to late blight.

Solanum × *edinense* was the first instance of useful genes entering the cultivated potato from a wild relative (Ross, 1979), giving this hybrid an important place in the history of potato improvement. The role of crop wild relatives in the creation of new and improved cultivars is a message that needs to be widely appreciated in the drive for greater food security. Genome analysis is highlighting the narrow genetic base of the cultivated potato and the potential of genome-guided improvement, including novel traits found in wild potatoes (Jansky & Peloquin, 2006; Hirsch *et al*., 2013). The benefits arising from the inclusion of wild relatives in crop breeding are clearly illustrated by the example of *S.* × *edinense*, highlighting the need to conserve the widest possible gene pool in all crop plants. The role of gene banks such as the CPC in conserving crop diversity is vital, as is species conservation in the wild.

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In memory of Lizzie Sanders (1950–2020)

Lizzie Sanders' skill at illustrating plants shines through in her paintings of *Solanum* for this research project. Sadly, she did not see its publication, so it is with fond memories that we dedicate this paper to Lizzie.

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Appendix

Parentage of eight controlled crosses that resulted in seed.

Cross	Female parent	Male parent	Germination
6	*S. demissum*+	*S. tuberosum* 'Lumper'*++	Yes
7	*S. demissum*+	*S. tuberosum* 'Lumper'*++	Not sown
8	*S. demissum*+	*S. tuberosum* 'Lumper'*++	Yes
9	*S. demissum*+	*S. tuberosum* 'Lumper'*++	Not sown
16	*S. demissum*+	*S. tuberosum* 4875-72-5**+	No
17	*S. demissum*+	*S. tuberosum* 4875-72-5**+	Not sown
26	*S. demissum*+	*S. tuberosum* BF 15*++	Yes
42	*S. tuberosum* 4875-41-1**+	*S. demissum*+	Yes

Ploidy of *Solanum tuberosum* and source: *tetraploid; **diploid; +JHI; ++SASA.