Wild and Cultivated Potato (*Solanum* sect. *Petota*) Escaped and Persistent Outside of its Natural Range

Reinhard Simon, Conghua H. Xie, Andrea Clausen, Shelley H. Jansky, Dennis Halterman, Tony Conner, Sandra Knapp, Jennifer Brundage, David Symon, and David Spooner*

Wild potato contains about 100 species that are native to the Americas from the southwestern United States to central Chile and adjacent Argentina, Uruguay, Paraguay, and southern Brazil. We report the occurrence of naturalized populations of the wild potato *Solanum chacoense* in seven sites in southern Australia, eastern China, England, New Zealand, the eastern United States, central Peru, and east-central Argentina. Modeling similar climatic niches on the basis of the distribution of *S. chacoense* from South America shows that observations of naturalized *S. chacoense* overlap with predicted areas. A literature review reveals that although *S. chacoense* possesses traits typical of an invasive species, all populations presently appear to be contained near their site of introduction.

Nomenclature: *Solanum chacoense* Bitter; wild tuber-bearing potatoes, *Solanum* L. section *Petota* Dumort; cultivated potato, *Solanum tuberosum* L.

Key words: Invasive species, Maxent, predictive habitat modeling.

Wild potato (*Solanum* L. section *Petota* Dumort.) contains about 100 species (Spooner et al. 2009). It is native to the Americas from the southwestern United States (Arizona, Colorado, New Mexico, Texas, Utah) to central Chile and adjacent Argentina, Uruguay, Paraguay, and southern Brazil (Spooner and Salas 2006). A wild tuber-bearing relative of cultivated potato (*Solanum tuberosum* L.), *Solanum chacoense* Bitter, is one of the most widespread and morphologically diverse species in section *Petota*

(Miller and Spooner 1996). It is a weed in cultivated fields within its natural range from southern Peru (Ochoa 1999; as *Solanum yungasense* Hawkes) and in adjacent Bolivia (Hawkes and Hjerting 1989; Ochoa 1990), south to Argentina, southern Brazil, Paraguay, and Uruguay (Hawkes and Hjerting 1969). It grows from sea level up to 3,700 m in a variety of disturbed habitats (Hawkes and Hjerting 1969, 1989; Ochoa 1990, 1999). In Argentina, it is reported to be an agricultural weed in a variety of crops (Valverde 2002). Although *S. chacoense* is not listed as an invasive species (Invasive Species Specialist Group 2008), it is listed as a weed (Randall 2002). Although *S. chacoense* is not an immediate relative of *S. tuberosum* (Spooner et al. 2005), it is a closely related wild species (Spooner and Castillo 1997) and is fully sexually compatible with it (Hermundstad and Peloquin 1985).

Solanum tuberosum, is native to the Andes Mountains from Venezuela south to northern Argentina and in the lowlands of south-central Chile. It was first exported outside of its native range into the Canary Islands in 1567 (Ames and Spooner 2008) and today ranks as the world's fourth most important food crop (FAO 2009). Despite its widespread cultivation worldwide in a variety of habitats, neither cultivated nor wild potatoes are known to escape into the wild. On the Chonos Archipelago in southern Chile during the voyage of *H.M.S. Beagle*, Charles Darwin (1839) noted the broad adaptability of the *S. tuberosum*, which he saw in abundance on beaches and shores: ''… it is

Interpretive Summary

Wild potato (*Solanum* section *Petota*) contains about 100 species that are native to the Americas from the southwestern United States to central Chile and adjacent Argentina, Uruguay, Paraguay, and southern Brazil, and landrace populations of the cultivated potato (*Solanum tuberosum*) are native to the Americas in the Andes Mountains from western Venezuela south to northern Argentina, with disjunct populations in the lowlands of south-central Chile. Wild and cultivated potato rarely escape into the wild, but we here document the occurrence of an invasive wild potato species, *Solanum chacoense*, that has freely escaped from cultivation in seven sites in southern Australia, eastern China, England, New Zealand, the eastern United States, central Peru, and east-central Argentina. Maxent software was able to predict the occurrences of these populations and show many other areas where *S. chacoense* might be found in the future. We speculate on many aspects of *S. chacoense* allowing its escape, and one of them might be that it produces tubers in long-day conditions, unlike many wild potato species. Currently, all populations presently appear to be contained near their site of introduction.

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 these southern islands.'' We have been able to find only two such reports for *S. tuberosum*—in Africa (Brücher 1966; Correll 1962) and Hawaii (Medeiros et al. 1998) (Table 1)—although ''volunteer'' *S. tuberosum* sometimes pose management problems within cultivated fields (Lawson 1983; Lutman 1977).

Richardson and Pysek (2006) define an invasive species as a subset of naturalized plants that produce reproductive offspring, often in large numbers, at considerable distances from parent plants and, thus, have the potential to spread over a large area. An understanding of the dynamics of plant invasions requires insight into traits of the plant (elements of species invasiveness) and features of the environment (components of community invasibility), but neither aspect can be fully evaluated without reference to the other. Invasions are context specific, and invasiveness only materializes when certain environmental requirements are met. Richardson and Pysek (2006) define naturalized plants as alien plants that form self-replacing populations for at least 10 yr without direct intervention by people (or despite human intervention) by recruitment from seeds or ramets capable of independent growth. We here report the occurrence of such self-replicating populations of *S. chacoense* and *S. tuberosum* at locations outside their native geographic ranges and assess the potential of *S. chacoense* as an invasive species.

Materials and Methods

Locality Records. To assess areas of potential invasion, we predicted climatically similar niches worldwide to those of *S.* *chacoense* in its native range; the estimate of native range was taken from a monographic study of wild potatoes of southern South America by David Spooner, Andrea Clausen, and collaborators (unpublished data under review). This data set includes locality records of *S. chacoense* and all other names that Spooner and Clausen consider synonymous with *S. chacoense* (including *Solanum arnezii* Cárdenas, *Solanum calvescens* Bitter, and *S. yungasense*). All records with sufficient locality information were provided with georeferences using DIVA-GIS (Hijmans et al. 2001), resulting in a data set of 880 accessions. Out of these, the program Maxent (Phillips et al. 2008; see below) eliminated duplicate records and used 376 accessions for analysis. A second data set was constructed of locality records from seven disjunct naturalized populations of *S. chacoense* in southern Australia, China, England, New Zealand, the eastern United States, central Peru, and east-central Argentina (Table 1; Supplementary Figures 1–7).

For comparative purposes, similar records were compiled for naturalized populations of *S. tuberosum* in Hawaii and in southern and east-central Africa; this data set contained 34 accessions compiled from Brücher (1966) and Medeiros et al. (1998).

Environmental Modeling. To assess the environmental suitability of regions in which escaped populations of *S. chacoense* occur we used Maxent version 3.3.1 (Phillips et al. 2008), a predictive modeling program based on estimating the probability distribution of maximum entropy (Phillips et al. 2006, 2008; see Wang et al. [2007] for an application). Maxent can use presence-only data. We used bioclimatic variables as an important subset of environment attributes following recommendations in the software tutorial. A global grid of 19 bioclimatic variables at 10-min resolution from the world climate database (Hijmans et al. 2005), available with DIVA-GIS, was used: annual mean temperature, mean monthly temperature range, isothermality (quantification of ''hot'' vs. ''cold'' regions), temperature seasonality (coefficient of variance [CV] $\times$ 100), maximum temperature of warmest month, minimum temperature of coldest month, temperature annual range, mean temperature of wettest quarter, mean temperature of driest quarter, mean temperature of warmest quarter, mean temperature of coldest quarter, annual precipitation, precipitation of wettest month, precipitation of driest month, precipitation seasonality (CV), precipitation of wettest quarter, precipitation of driest quarter, precipitation of warmest quarter, and precipitation of coldest quarter.

No preprocessing to select or reduce the number of covariates (e.g., to select only the most distinct variables) was performed because, overall, an approach with all variables has been shown to work best (Drake et al. 2006). The analysis was performed with the use of standard Maxent settings, except the options ''create variable response curves''

Table 1. Localities of persistent naturalized populations of *Solanum chacoense* and *Solanum tuberosum*.

Solanum chacoense

1. **AUSTRALIA. Victoria**: Victoria Plant Research Institute, Melbourne. January 8, 1985, *Jane Urquhart s.n.* (herbaria AD, MEL). (Supplementary Figure 4).
2. **USA. Maryland. Prince George's Co.**: Beltsville, U.S. Department of Agriculture Beltsville Agricultural Research Center (BARC), 39°01′N, 76°52′W, 30 m elevation, plants up to 1.3 m tall, growing among grasses in buffer strip around and sometimes invading fields of soybeans and corn, mostly in sunny areas but sometimes in shade of mature trees, *invading* several agricultural fields over an extent of about 1 mile, forming tubers, flowering vigorously and forming mature fruits (Supplementary Figure 7).
3. **CHINA. Hubei Province**: Southern Potato Research Centre of China, Tianchishan (108.00°E, 30.17°N). Photos by David Spooner, April 2007 (Supplementary Figure 2).
4. **NEW ZEALAND. Canterbury**: Lincoln. Grounds of Canterbury Agriculture and Science Centre, 172°28′43.61″E, 43°38′23.82″S, 9 m elevation, well established on a soil/compost heap and spread apparently clonally up to 50 to 70 m from this rubbish heap, first collected January 18, 1982 (herbarium voucher specimens CHR 400584, CHR 518333, CHR 571412). In addition, spread at three other locations in the near vicinity, 0.7 to 1.0 km away to the west (CHR 571411), north (CHR 571424, CHR 571427), and SE (CHR 571425, CHR 571426). Plants emerge in mid–late spring [late September–early October], flowering December–March, followed by fruiting through to April–May; plants die back as frosts start to occur from mid-April (Supplementary Figure 3).
5. **UK. England. Birmingham**: Winterbourne, environs of Birmingham University Botanic Garden, 52°27′N, 1°55′W, 30 m elevation, known as an invasive plant for at least 10 yr, currently growing about the botanic Gardens and nearby in an adjacent field.
6. **PERU. Lima**: Type specimen of *Solanum limense* Correll, Wrightia 2: 188. 1961.—TYPE: PERU. Lima: garden of the college of Salecianos, January 1948, *J. Soukup 3555* (herbarium F). (Supplementary Figure 1).
7. **ARGENTINA. Buenos Aires Province**: INTA Estacion Experimental de Balcarce, 37°49′59.00″S, 58°15′33.00″W

Solanum tuberosum

1. **REPUBLIC OF SOUTH AFRICA. Makhaleng**: Maseru, mountains of Basutoland, *van der Plank s.n.* (herbarium LD), (Supplementary Figure 6).
2. **HAWAII. Maui**: Kaupo Gap within Haleakala Crater, 9,000 feet, sparingly naturalized and flowering and fruiting in foggy rainy grassy glade, August 29, 1927, *Otto Degener 7379* (herbaria AA, NY). (Supplementary Figure 5). Medeiros et al. (1998) published previously unpublished field notes of Charles N. Forbes (1883–1920), who mentioned *S. tuberosum* first present at this location.

and "jackknifing to measure variable importance" were enabled. The software can be used to test whether a set of locations or "test" locations is within the probability range derived from a training set of locations. The *S. chacoense* database of 337 accessions for Latin America was used as a training set; the *S. chacoense* escape database of seven accessions was used as a test set to evaluate the probability of the observed accessions outside the native range. Maps were constructed with the maps (Brownrigg et al. 2007) and maptools packages (Lewin-Koh et al. 2008) in the R statistical programming language (R Development Core Team 2008). The Maxent results were also used to assess the quality of the prediction and to apply a jackknife approach to determine the relative importance of the predictor variables.

The program results range between 0 (low probability of occurrence) and 1 (high probability of occurrence) for each location or pixel. A statistically significant cut-off value was used to maximize inclusion of *S. chacoense* escape (or test) locations while minimizing false positives; this value is called "maximum test sensitivity plus specificity." The relatively low cut-off value leads to a high proportion of false positives, as qualitatively confirmed in an intermediate

visualization (results not shown). In particular, the Maxent algorithm might predict more false positives than necessary for locations in which the variable values are lower or higher than the range of values for each bioclimatic variable over all training sites. Therefore, a postprocessing step was included to reduce the number of false positive locations. Following a basic protocol in Ficetola et al. (2007), the predicted sites were filtered as follows: for all 19 variables, the minimum and maximum values for each variable were summarized on the basis of training site locations. All other locations, or pixels, whose bioclimatic variable values were below the respective minimum or above the maximum values for training sites were excluded from the final predicted distribution of *S. chacoense*. Thus, the predicted distribution should better fit the natural distribution range.

Results

The predictive quality of the Maxent value was excellent based on the receiver operating characteristic (ROC) curve, which plots sensitivity vs. specificity or true positive vs. false positive rates, respectively. The value of the area under
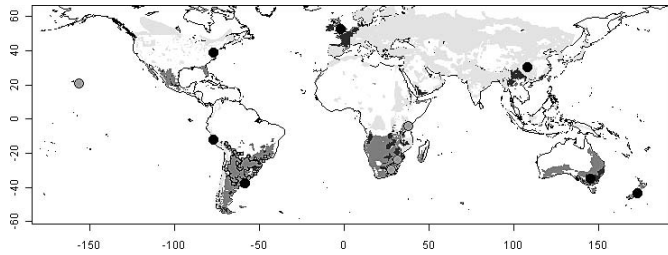
Figure 1. Distribution of *Solanum chacoense* escapes. Large black dots show the locations of *S. chacoense* escapes. Large gray dots show the locations of *Solanum tuberosum* escapes. The light gray shaded area shows the distribution of *S. tuberosum*. The areas enclosed in black borders in intermediate gray represent the native distribution of wild *S. chacoense* accessions. Areas shaded in intermediate gray without borders are the predicted distribution of *S. chacoense*. Dark gray areas represent overlapping areas between the predicted distribution of *S. chacoense* and areas of *S. tuberosum*. Small gray dots of irregular shapes in the Americas enclosed in black borders are isolated areas of native *S. chacoense* distribution.

the curve (AUC) for the training data was 0.994 (of maximum possible 1.0) and for the testing data was 0.873 (of maximum possible 0.976). The overall model predictive performance is also indicated by 13.7 times likelihood of presence of an accession vs. a random background location.

The *S. chacoense* escape sites were just above the cut-off value of 0.002 which has P = 0.00003338. Six of the *chacoense* escape locations used for testing had probability values between 0.0023 and 0.0511; the remaining one had a value of 0.5641. In comparison, the *S. chacoense* training locations ranged from 0.0081 to 0.8756. The major predicted areas for the presence of *S. chacoense* outside the native range are Mexico (except coastal areas), southern California, Florida, Ireland, England, France, northern Germany, northern Atlantic coast of Spain, southern Africa, Madagascar, eastern and southern Australia, New Zealand, and central China. A less likely distribution is predicted for a few other spots across Africa and southern Arabia (Figure 1).

The five most important variables contributing the most to the Maxent model describing the bioclimatic niche of *S. chacoense* were temperature seasonality, 31.4%; isothermality, 20%; mean temperature of driest quarter, 17.4%; precipitation of warmest quarter, 7.9%; and mean temperature of wettest quarter, 6.4%. Thus, 25% of the variables contribute 83.1% of the final model. No sites from the test sites have months in which the minimum temperatures remain on average below 0 C, except the site in the United States with a global database of monthly average minimum temperature data from the WorldClim (2008) database. This does not exclude the possibility of days with frost.

For comparative purposes, we also report observations of naturalized *S. tuberosum* outside of agricultural production areas in Africa and Hawaii (Figure 1). Particularly interesting is a case reported by Brücher (1966), wherein populations near Lesotho, Africa, initially led Correll (1962) to speculate that these were potential native wild species populations. Brücher (1966) was able to show, however, that these were persistent cultivated populations from early European settlers.

Discussion

Persistent naturalized populations of *S. chacoense* have become established in widespread localities in North and Central America, Europe, Asia, Australia, and New Zealand, with *S. tuberosum* in Africa and Hawaii. The results show that the *S. chacoense* escapes are within their bioclimatic niche. The U.S., Australian, Argentinean, Chinese, and New Zealand populations of *S. chacoense* grow about plant breeding stations and most certainly were introduced as part of breeding and evaluation programs. The other site in England is at a botanical garden known to cultivate scores of different wild potato species. The New Zealand population might have been introduced as early as the early 1960s when this species was studied there (Pandey 1962). None of the new populations has average climate conditions with months of frost that would eliminate tubers, except the U.S. site. According to Boydston et al. (2006) potato tuber mortality is usually initiated when minimum soil temperature reaches −2.0 C at tuber depth for brief periods of time. The U.S. escape site has 3 mo below that temperature. However, these minimum temperatures might not adequately describe the microclimatic conditions. Alternatively, *S. chacoense* could have tubers more resistant to cold than other species. Thus, *S. chacoense* might just have general adaptability to new environments, as already speculated for *S. tuberosum* by Darwin (1839). On the other hand, the biology of *S. chacoense* fulfills the criteria for an invasive species, and below, we summarize traits that might allow it to become invasive and establish new populations.

Ability to Reproduce Asexually. *Solanum chacoense* typically produces an extensive mass of long stolons (Leue and Peloquin 1980). This would allow a single plant to spread underground as long as tubers survive until they overcome dormancy and complete another growing season. Consequently, even if a founder plant is destroyed, its offspring several meters away could survive. Asexual reproduction presents an additional challenge that *S. chacoense* might have been able to overcome. Wild *Solanum* species typically do not tuberize under the long summer days of temperate regions of the world (Rudorf 1958). Therefore, a plant that has escaped a controlled environ-

ment might not be able to produce tubers before being killed by frost as the nights lengthen in fall. However, we have observed that, unlike other wild *Solanum* species, some genotypes of *S. chacoense* produce tubers under long-day conditions.

Broad Adaptability. *Solanum chacoense* is considered to be the most adaptable and aggressive South American wild *Solanum* species (Hawkes 1990; Hawkes and Hjerting 1969). It occupies a broad range of geographic regions and altitudes, ranging from 0 to 3,200 m. *Solanum chacoense* is very vigorous (Leue and Peloquin 1980) and is reported to have heat and drought tolerance (Hawkes 1990; Veilleux et al. 1997), allowing it to survive in a broader environmental range than many other wild *Solanum* species. Genes for adaptation to low-input environments are likely to be present in *S. chacoense* (Buso et al. 1999a), contributing to its success in natural environments.

High Frequency of 2*n* Gametes. The combination of the triploid block in potato and 2*n* gamete production via meiotic mutations allows the production of spontaneous tetraploids in potato. This phenomenon has been demonstrated in *S. chacoense* (Marks 1966). *Solanum chacoense* produces relatively high frequencies of both 2*n* pollen and 2*n* egg cells (Den Nijs and Peloquin 1977; Leue and Peloquin 1980; Quinn et al. 1974). Consequently, a diploid *S. chacoense* plant that produces 2*n* egg cells could be fertilized by a diploid plant that produces 2*n* pollen. Self-pollination is even possible. The resulting tetraploids are expected to be highly heterozygous because allelic diversity is contributed by both parents. In addition, they are expected to be highly competitive because of increased vigor (Hutten et al. 1995; Mendiburu and Peloquin 1977; Werner and Peloquin 1991) and disease resistance (Oswald and Nuismer 2007). Tetraploid clones containing *S. chacoense* germplasm have been reported to have higher tuber yields than elite cultivars (Buso et al. 1999b). To date, however, only diploid and triploid (but no tetraploid) natural populations of *S. chacoense* have been reported (Hijmans et al. 2007).

Prolific Sexual Reproduction and Potential Long-Distance Seed Dispersal. *Solanum chacoense* typically produces vigorous plants that flower profusely and over an extended period of time (Leue and Peloquin 1980). The flowers are highly male and female fertile (Leue and Peloquin 1980). In addition, although most wild *Solanum* species, including *S. chacoense*, are self-incompatible (Hawkes 1990), *S. chacoense* is the only wild *Solanum* species in which a self incompatibility inhibitor has been documented (Hosaka and Hanneman 1998). The loss of self-incompatibility is conditioned by a single dominant gene found in some *S. chacoense* genotypes. Consequently, if a single plant carrying the self-incompatibility inhibitor

gene escapes, it would be capable of perpetuating itself by self-pollination.

Ugent (1981) reviewed the potential of grazing animals to distribute wild *Solanum* species and concluded that a variety of animals could play a bigger role than previously thought in long-distance dispersal. Additionally, Ugent (1981) reasoned that articulated fruiting pedicels (as possessed by *S. chacoense*) facilitate the distribution by birds, wind, and rain.

Insect Resistance. *Solanum chacoense* produces a unique array of glycoalkaloids. In addition to producing the glycoalkaloids commonly found in wild *Solanum* species, chaconine and solanine, *S. chacoense* produces rare glycoalkaloids such as leptines, demissine, and tomatine (Lawson et al. 1993; Sinden et al. 1986). Production of high levels of these glycoalkaloids reduces feeding, survival, and reproductive ability of herbivorous insect pests such as the Colorado potato beetle (Hawkes 1990; Rangarajan et al. 2000; Sinden et al. 1986; Yencho et al. 2000), which are capable of rapidly defoliating potato plants.

Disease Resistance. *Solanum chacoense* appears to be particularly rich in disease resistance genes. Resistance to soft rot, caused by bacterial species in the genus *Pectobacterium* (formerly *Erwinia*), has been reported in *S. chacoense*. This resistance would prevent tubers from rotting in the soil while they are dormant (Bains et al. 1999; Hawkes 1990; Rousselle-Bourgeois and Priou 1995). *Solanum chacoense* also contains major genes for resistance to *Verticillium* species, which causes early dying, (Concibido et al. 1994; Lynch et al. 1997) and *Ralstonia solanacearum* (Smith) Yabuuchi, the causal agent of bacterial wilt (Hawkes 1990). Resistance to virus diseases would prevent a decline in plant vigor that would reduce a plant's competitive ability in a natural environment over time. High levels of resistance to major virus diseases such as potato virus Y and potato leafroll virus have been found in *S. chacoense* (Brown and Thomas 1994; Hawkes 1990; Valkonen 1997). *Solanum chacoense* is also reported to be resistant to root knot nematode, *Meloidogyne incognita* (Kofoid and White) Chitwood, as well as common scab caused by *Streptomyces scabies* (Lambert and Loria) (Hawkes 1990).

In a few cases, single genes confer resistance to multiple pathogens (Bisgrove et al. 1994; Rossi et al. 1998). However, in the majority of plant–microbe interactions, the mechanisms for resistance to different pathogens within a single species are likely to be as diverse as the pathogens themselves. In both plants and animals, defense responses and resistance are induced on host recognition of pathogen molecules, termed effectors (Jones and Dangl 2006). Pathogens, on the other hand, have evolved mechanisms to suppress host defenses or elude detection through mutation of effector encoding genes to cause disease. It is

widely accepted that infectious disease limits reproductive fitness. Therefore, natural selection favors hosts that contain heritable resistance traits. The proliferation of resistant hosts then adds to the selective pressure on the pathogen to evolve to overcome resistance and cause disease.

In summary, why might *S. chacoense* be able to escape into the wild so effectively compared with other *Solanum* species? Escape of a host plant into an environment in which pathogens are not adapted to overcome resistance of the host would lead to an immediate increase in the plant's fitness and ability to reproduce. However, this increase in fitness is expected to be short-lived because the pathogens eventually will elude detection and overcome resistance through natural selection. However, it is possible that *S. chacoense* has accumulated resistance genes that have evolved to recognize pathogen effectors that are essential for pathogenicity. It is expected that such resistance genes would be more durable because the pathogen cannot survive without the corresponding effector. This would extend the reproductive fitness of the host species over others that are more susceptible to rapid pathogen evolution. Bae et al. (2008) have found that Verticillium wilt resistance in *S. chacoense*–derived potato hybrids is linked to a homolog of the tomato (*Solanum lycopersicum* L.) *Ve* gene. In tomato, the *Ve* gene encodes a receptor-like protein that has been used successfully to control this fungus for more than 60 yr, suggesting that evolution of the pathogen to overcome *Ve* recognition carries a high fitness penalty on the pathogen (Kawchuk et al. 2001).

Given the broad spectrum of resistance present in *S. chacoense*, another possibility is that it contains an unusually strong basal defense response. Basal defense responses are not pathogen specific and are induced on recognition of microbe-derived compounds (Jones and Dangl 2006). Usually, these defenses are suppressed by the invading pathogen to colonize the host and cause disease. However, a strong and prolonged basal defense response that is not easily suppressed would potentially allow the plant to maintain a higher fitness level, even when exposed to a wide variety of pathogens. The basal defense response of *S. chacoense* has not been characterized, and it would be interesting to determine whether basal defense responses are responsible for its wide spectrum resistance capabilities.

Finally, the broad adaptability of *S. chacoense* provides it with the ability to adapt easily to environments that are less hospitable to pathogens, thereby allowing for escape from pathogen pressure. Although this might expose plants to a new set of pathogens, a combination of broad adaptability and increased resistance would result in a population that is capable of acclimatizing to and naturalizing in a wide range of environments. There are still only a few observations of *S. chacoense* escapes, and none appears to be aggressive where they occur, but the species should be monitored.

Literature Cited

Ames, M. and D. M. Spooner. 2008. DNA from herbarium specimens settles a controversy about origins of the European potato. Am. J. Bot. 95:252–257.

Bae, J., D. Halterman, and S. H. Jansky. 2008. Development of a molecular marker associated with *Verticillium* wilt resistance in diploid interspecific potato hybrids. Mol. Breed. 22:61–69.

Bains, P. S., V. S. Bisht, D. R. Lynch, L. M. Kawchuk, and J. P. Helgeson. 1999. Identification of stem soft rot (*Erwinia carotovora* subspecies a*troseptica*) resistance in potato. Am. J. Potato Res. 76:137–141.

Bisgrove, S. R., M. T. Simonich, N. M. Smith, A. Sattler, and R. W. Innes. 1994. A disease resistance gene in Arabidopsis with specificity for two different pathogen avirulence genes. Plant Cell 6:927–933.

Boydston, R. A., M. D. Seymour, C. R. Brown, and A. K. Alva. 2006. Freezing behavior of potato (*Solanum tuberosum*) tubers in soil. Am. J. Potato Res. 83:305–315.

Brown, C. R. and P. E. Thomas. 1994. Resistance to potato leafroll virus derived from *Solanum chacoense*: characterization and inheritance. Euphytica 74:51–57.

Brownrigg, R., T. P. Minka, R. A. Becker, and A. R. Wilks. 2007. Maps library for R: http://cran.r-project.org/web/packages/maps/index.html. Accessed: October 27, 2009.

Brücher, H. 1966. "Wildkartoffeln" in Afrika? Sonderh. Z. Pflanzen. 56:147–163.

Buso, J. A., L. S. Boiteux, and S. J. Peloquin. 1999a. Comparison of haploid Tuberosum–*Solanum chacoense* versus *Solanum phureja*–haploid Tuberosum hybrids as staminate parents of 4*x*–2*x* progenies evaluated under distinct crop management systems. Euphytica 109:191–199.

Buso, J. A., L. S. Boiteux, and S. J. Peloquin. 1999b. Evaluation under long-day conditions of 4*x*–2*x* progenies from crosses between potato cultivars and haploid Tuberosum–*Solanum chacoense* hybrids. Ann. Appl. Biol. 135:35–40.

Concibido, V. C., G. A. Secor, and S. H. Jansky. 1994. Evaluation of resistance to *Verticillium* wilt in diploid, wild potato interspecific hybrids. Euphytica 76:145–152.

Correll, D. S. 1962. The potato and its wild relatives. Contr. Texas Res. Found. Bot. Stud. 4:1–606.

Darwin, C. 1839. Journal of the researches into the geology and natural history of various countries visited by *H.M.S. Beagle*, under the command of Captain Fitzroy, R.N. from 1832 to 1836. London: Henry Colburn.

Den Nijs, T. P. M. and S. J. Peloquin. 1977. 2*n* gametes in potato species and their function in sexual polyploidization. Euphytica 26:585–600.

Drake, J. M., C. Randin, and A. Guisan. 2006. Modelling ecological niches with support vector machines. J. Appl. Ecol. 43:424–432.

[FAO] Food and Agriculture Organization of the United Nations. 2009. http://faostat.fao.org. Accessed: October 27, 2009.

Ficetola, G. F., W. Thuiller, and C. Miaud. 2007. Prediction and validation of the potential global distribution of a problematic alien invasive species — the American bullfrog. Divers. Distrib. 13: 476–485.

Hawkes, J. G. 1990. The potato: evolution, biodiversity, and genetic resources. Washington, DC: Smithsonian Institution Press.

Hawkes, J. G. and J. P. Hjerting. 1969. The potatoes of Argentina, Brazil, Paraguay and Uruguay: a biosystematic study. Oxford: Oxford University Press.

Hawkes, J. G. and J. P. Hjerting. 1989. The potatoes of Bolivia: their breeding value and evolutionary relationships. Oxford: Oxford University Press.

Hermundstad, S. H. and S. J. Peloquin. 1985. Germplasm enhancement with potato haploids. J. Hered. 76:463–467.

Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. Int. J. Climatol. 25:1965–1978.

Hijmans, R., T. Gavrilenko, S. Stephenson, J. Bamberg, A. Salas, and D. M. Spooner. 2007. Geographic and environmental range expansion through polyploidy in wild potatoes (*Solanum* section *Petota*). Glob. Ecol. Biogeogr. 16:485–495.

Hijmans, R., L. Guarino, M. Cruz, and E. Rojas. 2001. Computer tools for spatial analysis of plant genetic resources: 1 DIVA-GIS. Pl. Gen. Res. Newsl. 127:15–19.

Hosaka, K. and R. E. Hanneman, Jr. 1998. Genetics of self-compatibility in a self-incompatible wild diploid potato species *Solanum chacoense*. 1. Detection of an S locus inhibitor (*Sli*) gene. Euphytica 99:191–197.

Hutten, R. C. B., M. G. M. Schippers, J. G. T. Hermsen, and E. Jacobsen. 1995. Comparative performance of diploid and tetraploid progenies from 2x–2x crosses in potato. Euphytica 81:187–192.

Invasive Species Specialist Group. 2008. Database. http://www.issg.org/. Accessed: Oct 27, 2009.

Jones, J. D. G. and J. L. Dangl. 2006. The plant immune system. Nature 444:323–329.

Kawchuk, L. M., J. Hachey, and D. R. Lynch, et al. 2001. Tomato *Ve* disease resistance genes encode cell surface-like receptors. Proc. Natl. Acad. Sci. USA 98:6511–6515.

Lawson, D. R., R. E. Veilleux, and A. R. Miller. 1993. Biochemistry and genetics of *Solanum chacoense* steroidal alkaloids: natural resistance factors to the Colorado potato beetle. Curr. Top. Bot. Res. 1: 335–352.

Lawson, H. M. 1983. True potato seed as arable weeds. Potato Res. 26: 237–246.

Leue, E. F. and S. J. Peloquin. 1980. Selection for 2*n* gametes and tuberization in *Solanum chacoense*. Am. Potato J. 57:189–195.

Lewin-Koh, N. J., E. J. Pebesma, and E. Archer, et al. 2008. Maptools library for R. http://cran.r-project.org/web/packages/maptools/index.html. Accessed: October 27, 2009.

Lutman, P. J. W. 1977. Investigations into some aspects of the biology of potatoes as weeds. Weed Res. 17:123–132.

Lynch, D. R., L. M. Kawchuk, J. Hachey, P. S. Bains, and R. J. Howard. 1997. Identification of a gene conferring high levels of resistance to Verticillium wilt in *Solanum chacoense*. Plant Dis. 81: 1011–1014.

Marks, G. E. 1966. The origin and significance of intraspecific polyploidy: experimental evidence from *Solanum chacoense*. Evolution 20:552–557.

Medeiros, A. C., L. L. Loope, and C. G. Chimera. 1998. Flowering plants and gymnosperms of Haleakala National Park. Honolulu, Hawaii: University Of Hawaii at Manoa, Department of Botany Technical Report 120, Pacific Cooperative Studies Unit.

Mendiburu, A. O. and S. J. Peloquin. 1977. Bilateral sexual polyploidization in potatoes. Euphytica 26:573–583.

Miller, J. T. and D. M. Spooner. 1996. Introgression of *Solanum chacoense* (*Solanum* sect. *Petota*): upland populations reexamined. Syst. Bot. 21:461–475.

Ochoa, C. M. 1990. Actual release date 13 June, 1991. The potatoes of South America: Bolivia. New York: Cambridge University Press, Cambridge.

Ochoa, C. M. 1999. Las papas de sudamerica: Peru (Parte I). Lima, Peru: International Potato Center.

Oswald, B. P. and S. L. Nuismer. 2007. Neopolyploidy and pathogen resistance. Proc. R. Soc. Biol. Sci. Ser. B 274:2393–2397.

Pandey, K. K. 1962. Interspecific incompatability in *Solanum* species. Am. J. Bot. 49:874–882.

Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. Ecol. Model. 190:231–259.

Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2008. Maxent software, version 3.2.1. http://www.cs.princeton.edu/~schapire/maxent/. Accessed October 27, 2009.

Quinn, A. A., D. W. S. Mok, and S. J. Peloquin. 1974. Distribution and significance of diplandroids among the diploid Solanums. Am. Potato J. 51:16–21.

R Development Core Team. 2008. R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing.

Randall, R. 2002. A Global Compendium of Weeds. R.G. and F.J. Richardson: Victoria, Australia: R.G. and F.J. Richardson.

Rangarajan, A., A. R. Miller, and R. E. Veilleux. 2000. Leptine glycoalkaloids reduce feeding by Colorado potato beetle in diploid *Solanum* sp. hybrids. J. Am. Soc. Hortic. Sci. 125:689–693.

Richardson, D. M. and P. Pysek. 2006. Plant invasions: merging the concepts of species invasiveness and community invisibility. Prog. Phys. Geogr. 30:409–431.

Rossi, M., F. L. Goggin, S. B. Milligan, I. Kaloshian, D. E. Ullman, and V. M. Williamson. 1998. The nematode resistance gene *Mi* of tomato confers resistance against the potato aphid. Proc. Natl. Acad. Sci. USA 95:9750–9754.

Rousselle-Bourgeois, F. and S. Priou. 1995. Screening tuber-bearing *Solanum* spp. for resistance to soft rot caused by *Erwinia carotovora* ssp. *atroseptica* (van Hall) dye. Potato Res. 38:111–118.

Rudorf, W. 1958. The significance of wild potato species for potato breeding. Eur. Potato J. 1:10–20.

Sinden, S. L., L. L. Sanford, and K. L. Deahl. 1986. Segregation of leptine glycoalkaloids in *Solanum chacoense* Bitter. J. Agric. Food Chem. 34:372–377.

Spooner, D. M., M. Ames, D. Fajardo, and F. Rodríguez. 2009. Species boundaries and interrelationships of *Solanum* sect. *Petota* (wild and cultivated potatoes) are drastically altered as a result of PBI-funded research *in* Abstract, Botany and Mycology 2009 Annual Meeting. http://2009.botanyconference.org/engine/search/index.php.

Spooner, D. M. and R. Castillo. 1997. Reexamination of series relationships of South American wild potatoes (Solanaceae: *Solanum* sect. *Petota*): evidence from chloroplast DNA restriction site variation. Am. J. Bot. 84:671–685.

Spooner, D. M., K. McLean, G. Ramsay, R. Waugh, and G. J. Bryan. 2005. A single domestication for potato based on multilocus AFLP genotyping. Proc. Natl. Acad. Sci. USA. 102:14,694–14,699.

Spooner, D. M. and A. Salas. 2006. Structure, biosystematics, and genetic resources. Pages 1–39 *in* J. Gopal and S. M. Khurana, eds. Handbook of Potato Production, Improvement, and Post-Harvest Management. Binghampton, NY: Haworth's Press.

Ugent, D. 1981. Biogeography and origin of *S. acaule* Bitter. Phytologia 48:85–92.

Valkonen, J. P. T. 1997. Novel resistances to four potyviruses in tuber-bearing potato species, and temperature-sensitive expression of

hypersensitive resistance to potato virus Y. Ann. Appl. Biol. 130: 91–104.

Valverde, B. E. 2002. Weed management in Latin America. Pesticide Outlook 13:79–81.

Veilleux, R. E., M. M. Paz, and D. Levy. 1997. Potato germplasm for warm climates: genetic enhancement of tolerance to heat stress. Euphytica 98:83–92.

Wang, Y., B. Xie, F. Wan, Q. Xiao, and L. Dai. 2007. The potential geographic distribution of *Radopholus similis* in China. Agric. Sci. China 6:1444–1449.

Werner, J. E. and S. J. Peloquin. 1991. Yield and tuber characteristics of $4x$ progeny from $2x \times 2x$ crosses. Potato Res. 34:261–267.

WorldClim. 2008. WorldClim—A Global Database. http://www.worldclim.org/.

Yencho, G. C. K., P. Stanley, G. G. Kennedy, and L. L. Sanford. 2000. Segregation of leptine glycoalkaloids and resistance to Colorado potato beetle (*Leptinotarsa decemlineata* (Say)) in F_2 *Solanum tuberosum* ($4x$) $\times$ *S. chacoense* ($4x$) potato progenies. Am. J. Potato Res 77:167–178.