



Frost tolerance in wild potato species: Assessing the predictivity of taxonomic, geographic, and ecological factors

Robert J. Hijmans^{1,*}, Mirjam Jacobs¹, John B. Bamberg² & David M. Spooner³

¹International Potato Center, Apartado 1558, Lima, Peru; ²USDA, Agricultural Research Service, Vegetable Crops Research Unit, Inter-Regional Potato Introduction Station, 4312 Hwy. 42, Sturgeon Bay, WI 54235-9620, U.S.A.;

³USDA, Agricultural Research Service, Department of Horticulture, University of Wisconsin, 1575 Linden Drive, Madison, WI 53706-1590, U.S.A.; (*author for correspondence, e-mail: r.hijmans@cgiar.org)

Received 7 February 2002; accepted 17 September 2002

Key words: genetic resources, GIS, *Solanum*, traits, wild crop relatives

Summary

The use of genetic resources could be more effective and efficient if we were able to predict the presence or absence of useful traits in different populations or accessions. We analyzed the extent to which taxonomic, geographic and ecological factors can predict the presence of frost tolerance in wild potatoes. We used screening data for 1646 samples from 87 species that had been collected in 12 countries in the Americas. There was a strong association of frost tolerance with species and to a lesser extent with taxonomic series. There was significant geographic clustering of areas with wild potatoes with similar levels of frost tolerance. Areas with a high level of frost tolerance are the central and southern Peruvian Andes, the lowlands of Argentina and adjacent areas, and a small area in the central Chilean Andes. There is a greater chance of finding wild potatoes with high levels of frost tolerance in areas with a yearly mean minimum temperature below 3 °C than there is in warmer areas. However, temperature is only a weak predictor of frost tolerance. Temperature data alone did not predict observed frost tolerance in eastern Argentina/Uruguay and falsely predicted it in the southwestern United States. Because many wild potato species occur over small areas, taxonomic, ecological, and geographical factors are difficult to disentangle.

Introduction

Wild crop relatives may have traits that can be useful for crop improvement. Particularly important traits are tolerances to biotic (insects, pathogens) and abiotic (e.g., cold, drought) stresses. Identifying wild populations or genotypes that possess such useful traits typically involves screening accessions from genebanks. There are usually many more populations in the wild than can be sampled, and screening all samples in genebanks is limited by available funding. It would, therefore, be valuable to be able to predict which populations would most likely possess specific traits of interest.

Taxonomic, ecological, and geographic factors could be used for prediction based on prior evidence of association, or on a priori assumptions. Taxonomic classification of organisms is based on mor-

phological similarity and/or evolutionary relatedness. Ideally, groups of closely related taxa would also have certain useful traits in common that were not used to construct the taxonomic classification. Plant breeders have implicitly used taxonomy in this predictive sense, by linking traits to particular species (Ross, 1986; Hawkes, 1990).

Certain ecological factors may also serve for predicting traits because the presence of these traits might reflect adaptation of wild plants to ecological conditions prevailing in their area of occurrence. For example, tolerance to drought might be likely in populations growing in dry areas (Rick, 1973; Nevo et al., 1982). Geographic factors could play a role in prediction because certain traits may have arisen in an area and spread among taxa and ecologies in that area, but not reached areas farther away. Such geographic effects may be due to chance, but also to coevolution.

For example, resistance to a certain disease may be present in areas where the pathogen is endemic, but absent in areas that, although similar from an ecological and/or taxonomic perspective, do not have the pathogen.

There are 199 wild potato species (196 in *Solanum* sect. *Petota*, and 3 in *Solanum* sect. *Etuberosum*; Spooner & Hijmans, 2001). They all occur in the Americas, from Colorado (United States) to Chile and Uruguay. Species richness is high around 20°N (Mexico), but much higher in the southern hemisphere, particularly in the Andean highlands between 8° and 20°S (Hijmans & Spooner, 2001). The wild potato species in sect. *Petota* have been grouped in 21 taxonomic series (Hawkes, 1990; Ochoa, 1999; Hijmans et al., 2002).

Researchers of wild potato have often associated traits with certain species (e.g., Ross, 1986; Hawkes, 1990; Ochoa 1999). Geographical and ecological factors have also been associated with traits. For example, associations have been found between the altitude of provenance and the frost tolerance in accessions of *Solanum acaule* (see Table 1 for full species names, including authors) (Li et al., 1980); between altitude and resistance to potato leaf hopper (Flanders et al., 1992); and between altitude and glycoalkaloid content (Ronning et al., 2000).

Van Soest et al. (1983) found that there was a concentration of wild potato species with cyst-nematode resistance near Potosí, Bolivia. Van Soest et al. (1984) concluded that wild potatoes with resistance to *Phytophthora infestans* (Mont.) De Bary occur near the tropics of Capricorn and Cancer. Flanders et al. (1992) found that species from hot and arid areas had resistance to Colorado potato beetle, potato flea beetle, and potato leafhopper. Species from cool or moist areas tended to be resistant to potato aphid. Flanders et al. (1997) found statistically significant differences between geographic areas for the presence of insect resistance in wild potatoes.

However, in most of these studies, factors that might explain geographic clustering of the level of a trait have been studied in isolation, and the validity of the associations found was not critically tested. For example, Van Soest et al. (1983) point out that in Bolivia, there are many wild potato species with cyst-nematode resistance near the city of Potosí. However, as this is also the area in Bolivia with highest species richness (Hijmans & Spooner, 2001), this would be expected when assuming a random distribution of this trait across species (wherever there are many species,

there would be a relatively high number of species with a certain trait). In this case, evidence is insufficient as it is based on absolute, and not on relative numbers of species or accessions with a certain level of resistance. Another complicating factor is the rather limited size of the area of distribution of wild potato species, which makes it difficult, if not impossible, to rigorously separate the distribution of a trait over species, geographic, and ecological space (Flanders et al., 1997).

Frost damage is an important constraint in potato production at high latitudes and in high areas at low latitudes. Compared to *Solanum tuberosum* L., the common cultivated potato, some wild potato species have high levels of frost tolerance (Li, 1977; Estrada, 1982; Barrientos et al., 1994; Vega & Bamberg, 1995). The objective of the present study was to investigate the extent to which taxonomic, ecological and geographic factors can be used to predict frost tolerance in wild potato species.

Materials and methods

Frost tolerance data for wild potatoes reported by Vega & Bamberg (1995) were used in this study. They screened 2635 accessions from 101 species in one field experiment in 1992 in Sturgeon Bay, Wisconsin, USA. The plants were scored twice for frost damage, first after two light frosts of about -2°C and later after a more severe frost of -5°C . Frost damage was assessed visually, using a scale with six classes that could be consistently distinguished by visual inspection from 0 (no damage) to 6 (all leaves and stems killed). The damage was averaged over the two readings, and the data was linearly transformed to percentages (a reading of 0 equals 0%, and a reading of 6 equals 100% survival). In this paper we refer to this percentage score as frost tolerance. We used these data because they represented the largest single trait screening dataset for wild potato that we could find, and because of the reasonable a priori expectation that the presence of frost tolerance could be predicted from temperature data.

The accessions were originally collected in 12 countries in the Americas, covering most of the distribution area of wild potatoes. We only used data from accessions for which we had geographic coordinates. The correctness of the coordinates was checked following procedures described by Hijmans et al. (1999). In the case of errors, coordinates were changed where

Table 1. Number of observations and mean frost tolerance for 87 wild potato species from 17 series

| Series | Species | obs ¹ | Frost tolerance ² | |
|---|---|------------------------------------|------------------------------|----|
| <i>Acaulia</i> Juz. | <i>S. acaule</i> Bitter | 320 | 100 | |
| | <i>S. albicans</i> (Ochoa) Ochoa | 7 | 100 | |
| <i>Bulbocastana</i> (Rydb.) Hawkes | <i>S. bulbocastanum</i> Dunal | 22 | 10 | |
| | <i>S. clarum</i> Correll | 3 | 17 | |
| <i>Circaeifolia</i> Hawkes | <i>S. circaeifolium</i> Bitter | 2 | 21 | |
| <i>Commersoniania</i> Bukasov | <i>S. commersonii</i> Dunal | 27 | 99 | |
| <i>Conicibaccata</i> Bitter | <i>S. agrimonifolium</i> Rydb. | 2 | 17 | |
| | <i>S. chomatophilum</i> Bitter | 1 | 83 | |
| | <i>S. colombianum</i> Bitter | 4 | 27 | |
| | <i>S. moscopanum</i> Hawkes | 1 | 33 | |
| | <i>S. subpanduratum</i> Ochoa | 2 | 17 | |
| | <i>S. tundalomense</i> Ochoa | 2 | 42 | |
| | <i>S. × blanco-galdosii</i> Ochoa | 2 | 33 | |
| <i>Cuneolata</i> Hawkes | <i>S. infundibuliforme</i> Phil. | 78 | 42 | |
| | <i>S. brachycarpum</i> Correll | 25 | 16 | |
| <i>Demissa</i> Bukasov | <i>S. demissum</i> Lindl. | 83 | 92 | |
| | <i>S. hougasii</i> Correll | 5 | 13 | |
| | <i>S. schenckii</i> Bitter | 3 | 28 | |
| | <i>S. etuberosum</i> Lindl. | 22 | 82 | |
| <i>Etuberosa</i> Juz. | <i>S. fernandezianum</i> Phil. | 1 | 33 | |
| | <i>S. palustre</i> Poepp. | 63 | 58 | |
| | <i>S. lignicaule</i> Vargas | 1 | 8 | |
| <i>Lignicaulia</i> Hawkes | <i>S. fendleri</i> A. Gray | 33 | 21 | |
| <i>Longipedicellata</i> Bukasov | <i>S. hjertingii</i> Hawkes | 4 | 42 | |
| | <i>S. papita</i> Rydb. | 14 | 19 | |
| | <i>S. stoloniferum</i> Schldl. and Bouchet | 80 | 18 | |
| | <i>S. wightianum</i> Rydb. | 31 | 17 | |
| | <i>Megistacroloba</i> Cárdenas and Hawkes | <i>S. boliviense</i> Dunal | 7 | 56 |
| | | <i>S. dolichocremastrum</i> Bitter | 2 | 29 |
| | | <i>S. megistacrolonum</i> Bitter | 94 | 83 |
| <i>S. raphanifolium</i> Cárdenas and Hawkes | | 16 | 56 | |
| <i>S. sanctae-rosae</i> Hawkes | | 4 | 86 | |
| <i>S. sogarandinum</i> Ochoa | | 1 | 67 | |
| <i>Morelliformia</i> Hawkes | <i>S. morelliforme</i> Bitter and G. Muench | 4 | 0 | |
| <i>Pinnatisecta</i> (Rydb.) Hawkes | <i>S. brachistotrichium</i> (Bitter) Rydb. | 13 | 23 | |
| | <i>S. cardiophyllum</i> Lindl. | 14 | 22 | |
| | <i>S. jamesii</i> Torr. | 7 | 20 | |
| | <i>S. nayaritense</i> (Bitter) Rydb. | 1 | 17 | |
| | <i>S. pinnatisectum</i> Dunal | 12 | 20 | |
| | <i>S. tarnii</i> Hawkes and Hjert. | 1 | 50 | |
| | <i>S. trifidum</i> Correll | 2 | 17 | |
| <i>Piurana</i> Hawkes | <i>S. acroglossum</i> Juz. | 3 | 0 | |
| | <i>S. albornozii</i> Correll | 2 | 8 | |
| | <i>S. hypacrarthrum</i> Bitter | 1 | 8 | |
| | <i>S. paucissectum</i> Ochoa | 2 | 92 | |
| <i>Polyadenia</i> Bukasov | <i>S. lesteri</i> Hawkes and Hjert. | 2 | 8 | |
| | <i>S. polyadenium</i> Greenm. | 10 | 20 | |

Table 1. Continued

| Series | Species | obs ¹ | Frost tolerance ² |
|------------------------------------|--|------------------|------------------------------|
| <i>Tuberosa</i> (Rydb.) Hawkes | <i>S. acroscopicum</i> Ochoa | 1 | 50 |
| | <i>S. alandiae</i> Cárdenas | 6 | 17 |
| | <i>S. ambosinum</i> Ochoa | 1 | 33 |
| | <i>S. andreanum</i> Baker | 3 | 14 |
| | <i>S. avilesii</i> Hawkes and Hjert. | 1 | 17 |
| | <i>S. berthaultii</i> Hawkes | 37 | 19 |
| | <i>S. brevicaule</i> Bitter | 11 | 38 |
| | <i>S. bukasovii</i> Juz. | 33 | 71 |
| | <i>S. cajamarquense</i> Ochoa | 1 | 25 |
| | <i>S. candolleanum</i> P. Berthault | 2 | 63 |
| | <i>S. × doddsii</i> Correll | 1 | 17 |
| | <i>S. gandarillasii</i> Cárdenas | 2 | 17 |
| | <i>S. hoopesii</i> Hawkes and K. A. Okada | 1 | 42 |
| | <i>S. huancabambense</i> Ochoa | 2 | 38 |
| | <i>S. immite</i> Dunal | 1 | 25 |
| | <i>S. incamayoense</i> K. A. Okada and A. M. Clausen | 5 | 53 |
| | <i>S. kurtzianum</i> Bitter and Wittm. | 44 | 33 |
| | <i>S. leptophyes</i> Bitter | 137 | 49 |
| | <i>S. marinasense</i> Vargas | 6 | 18 |
| | <i>S. medians</i> Bitter | 3 | 17 |
| | <i>S. microdontum</i> Bitter | 14 | 17 |
| | <i>S. multiinterruptum</i> Bitter | 8 | 24 |
| | <i>S. neocardenasii</i> Hawkes and Hjert. | 1 | 17 |
| | <i>S. neorosii</i> Hawkes and Hjert. | 1 | 33 |
| | <i>S. okadae</i> Hawkes and Hjert. | 12 | 17 |
| | <i>S. oplocense</i> Hawkes | 38 | 27 |
| | <i>S. orophilum</i> Correll | 2 | 21 |
| | <i>S. pampasense</i> Hawkes | 2 | 46 |
| | <i>S. scabrifolium</i> Ochoa | 1 | 17 |
| | <i>S. sparsipilum</i> (Bitter) Juz. and Bukasov | 39 | 29 |
| | <i>S. spagazzinii</i> Bitter | 40 | 38 |
| | <i>S. × sucrensense</i> Hawkes | 20 | 31 |
| | <i>S. tarapatanum</i> Ochoa | 1 | 42 |
| | <i>S. venturii</i> Hawkes and Hjert. | 1 | 17 |
| <i>S. vernei</i> Bitter and Wittm. | 23 | 57 | |
| <i>S. verrucosum</i> Schltdl. | 19 | 24 | |
| <i>S. vidaurrei</i> Cárdenas | 12 | 56 | |
| <i>Yungasensia</i> Correll | <i>S. arnezii</i> Cárdenas | 2 | 8 |
| | <i>S. chacoense</i> Bitter | 28 | 31 |
| | <i>S. tarijense</i> Hawkes | 48 | 17 |
| | Total | 1646 | |

¹ obs = number of accessions tested.² Frost tolerance = percent non-damaged tissue after two frosts at -2°C and one at -5°C in Sturgeon Bay, Wisconsin, USA in 1992.

possible but accessions were deleted where it was not possible to assign precise coordinates. This left a total of 1646 accessions from 87 species (Table 1). The species with most observations was *Solanum acaule* ($n = 320$). On average there were 19 observations per species, but the median was only 4 observations per species. The species belonged to 17 series with an mean of 5.1 and a median of 3.0 species per series.

The difference between mean and median was largely due to the representation of the ser. *Tuberosa*, for which data for 36 species were available. The second and third largest series, in terms of species for which data were available, were *Pinnatisecta* (seven species), *Conicibaccata* and *Megistacroloba* (six species).

Species and series

The species names used by Vega and Bamberg (1995) are all still current according to the review by Spooner and Hijmans (2001), except for *S. polytrichon* that was renamed *S. wightianum* (Hijmans et al., 2002). Series membership follows Hawkes (1990) except for subsequent changes for Peruvian species by Ochoa (1999). For the analysis in this paper we treat sect. *Etuberosa* as a series in sect. *Petota*.

Mean frost tolerance was calculated over species and series. χ^2 tests were used to test the hypothesis that the occurrence of frost tolerance and species or series are associated. The mean frost tolerance of a series was compared with that of its constituent species using linear regression.

Geography

A map of square 100×100 km grid cells was made of the mean and maximum observed frost tolerance per grid cell, using the DIVA-GIS software (Hijmans et al., 2002). Calculations were made with each individual observation weighted equally, irrespective of species or series. We used a Lambert equal-area azimuthal projection, with 80° W as the central meridian and the equator as the reference latitude.

To investigate spatial autocorrelation, Moran's I statistic was calculated for the grid using IDRISI v32 software (Clark Labs, Worcester, MA, USA). We used the king's case (i.e., considering the eight adjacent cells of each cell). Positive spatial autocorrelation means that locations close to each other are more similar than locations farther apart, and negative autocorrelation means the opposite. Moran's I is basically positive for positive autocorrelation and negative

for negative autocorrelation, except that the expected value for no autocorrelation is slightly negative (Bonham-Carter, 1994).

The degree to which taxonomic and geographic factors are confounded was investigated in two ways. We plotted the mean observed frost tolerance in a grid cell versus the relative amount of observations from the nine most frost-tolerant wild potato species in that cell. We also plotted the drop in mean frost tolerance in a grid cell when these most tolerant species are not considered.

Temperature

The ecological variable that a priori would be expected to be associated most with frost tolerance is frost incidence. Because of a lack of frost incidence (or daily minimum temperature) data we used mean monthly temperature data instead. Monthly minimum and maximum temperature data were assigned to all accessions, using data on interpolated climate grids by Jones (1991) for Latin America and New et al. (1999) for the USA. For each accession, the mean minimum and maximum temperature during the year, and during the estimated growing season, were calculated.

The dominant growing season for all locations where wild potatoes have been observed was estimated using the wild potato distribution database described by Hijmans & Spooner (2001). For a grid of 50 by 50 km cells, and a circular neighborhood with a 100 km diameter, the mode (most frequent observation) of the month of collecting was determined, using DIVA-GIS. A modal filter was then used to remove spatial outliers, using IDRISI. Some manual editing was carried out, for example for the coast of Peru, where a small strip (with 'lomas' vegetation) has a different growing season than that in the nearby Andes (Spooner et al., 1999). Because most wild potatoes are collected as seed, the growing season was assumed to be the month of collection and the three previous months.

Temperatures were plotted against frost tolerance. The GLM procedure (Type III sum of squares) in SAS was used to determine whether there were effects of temperature, species and series on frost tolerance, and whether there were temperature effects on frost tolerance within species and within series. A map was made predicting the presence of frost-tolerant wild potatoes on the basis of temperature using the climate data described above.

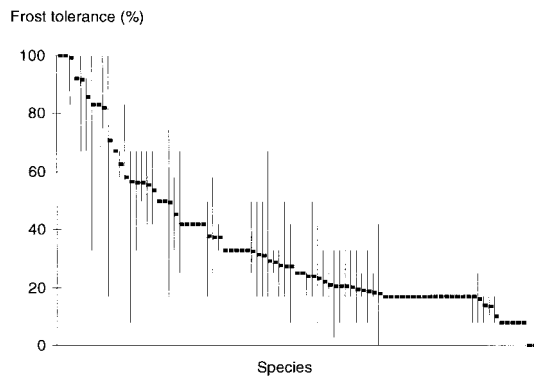


Figure 1. Mean frost tolerance (percentage non-damaged tissue) by wild potato species (lines indicate maximum and minimum values). Data for 87 species and 1646 accessions (mean of 19, and median of 4 accessions per species).

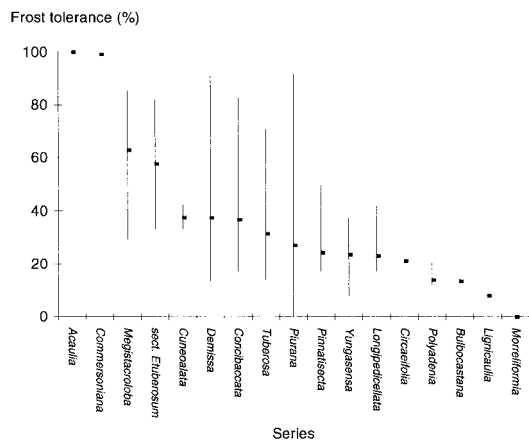


Figure 2. Mean frost tolerance (percentage non-damaged tissue) by wild potato series (lines indicate maximum and minimum values). Data for 17 series containing 5 species on average (in our sample).

Results

Species and series

There is a significant ($\chi^2 = 1508$; $df = 86$; $p < 0.001$) association between species and frost tolerance (Figure 1). Few species have high frost tolerance, whereas many species have a relatively low frost tolerance. Out of the 87 species, only 5 species have a frost tolerance score of more than 90%, and 9 species have a score of 82% or higher. Highest frost tolerance was for *Solanum acaule* (100%; $n = 320$ observations) and *S. albicans* (100%; $n = 7$), and for *S. commersonii* (99%; $n = 27$).

There also is a significant association between series and frost tolerance ($\chi^2 = 357$; $df = 17$; $p < 0.001$). Species from ser. *Acaulia* and *Commersoniana* had the highest frost tolerance, followed at some distance by ser. *Megistacroloba*, and sect. *Etuberosa* (Figure 2). For most series there are important differences in frost tolerance among the constituent species (Figure 3), as illustrated by the low coefficient of determination (r^2) of 0.51 between the mean (over species) frost tolerance by series versus that of the series' constituent species. Variation is particularly high in ser. *Concibacata*, *Demissa*, *Piurana*, and *Tuberosa*, and in sect. *Etuberosa*, which are all series with an intermediate to low mean frost tolerance (Figure 2).

Geography

Our sample contains wild potatoes from most of the areas where wild potatoes occur (Hijmans and Spooner, 2001). Important exceptions are areas in Central America, Colombia, and Ecuador (Figure 4). Areas where high mean levels of frost tolerance were observed constitute a zone from central to south Peru and a small part of adjacent northern Bolivia; and a zone stretching south and east from Paraguay into adjacent Argentina, Brazil and Uruguay, and a small area in central Chile (Figure 4). Northern Argentina has a zone with an intermediate level of frost tolerance. There are many grid cells with a high maximum observed frost tolerance ($> 99\%$; Figure 5) that did not have a very high mean frost tolerance ($< 75\%$; Figure 4). These cells are in central Mexico, north-central Peru, Bolivia, and north Argentina.

Spatial autocorrelation between grid cells is positive and highly significant. Moran's $I = 0.521$ for mean frost tolerance, and $I = 0.498$ for maximum frost tolerance (number of cells = 185, $p < 0.001$ in both cases). This indicates the presence of geographic clustering of areas with wild potatoes that have similar levels of frost tolerance.

Geography and Species

The relative abundance of one or more of the nine most tolerant species (above 80%; Figure 1) in a grid cell is a reasonably good predictor of overall frost tolerance in that grid cell (Figure 6). When discarding these nine most frost tolerant species, there are cells in which the mean frost tolerance decreases sharply. This decrease is conspicuous in areas with medium to high levels of frost tolerance. This was to be expected because there cannot be much decrease in areas where tolerance is

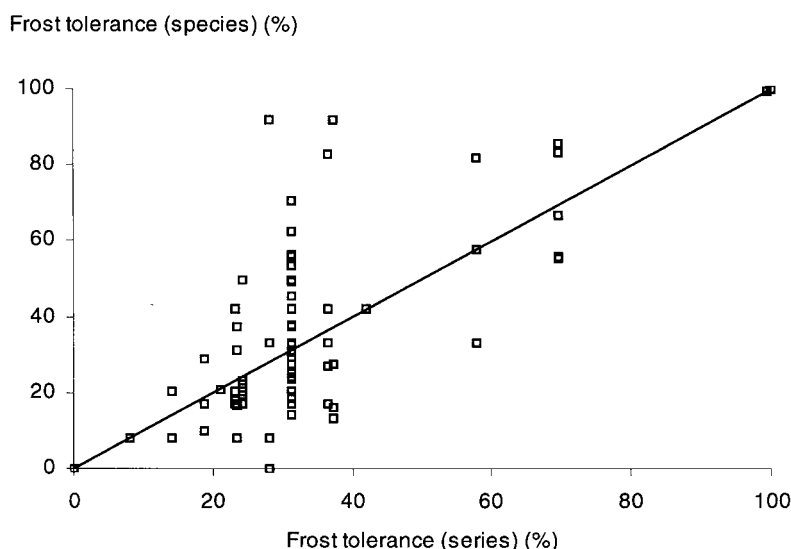


Figure 3. Mean frost tolerance (percentage non-damaged tissue) of wild potato series (averaged over species) versus the frost tolerance of the species in those series. $r^2 = 0.513$. Data for 18 series containing 4.8 species on average (in our sample). Regression line: $y = x$ (by definition).

already low. Nevertheless, some of the cells with very high levels of frost tolerance maintain high levels even without the most tolerant species (Figure 7). These cells are all located in southern Peru.

Solanum acaule, the most frost tolerant species in our sample, is also one of the most common and widespread wild potato species (Hijmans & Spooner, 2001). The high maximum tolerance scores observed across Peru, Bolivia, and north Argentina (Figure 5) largely coincide with the distribution of this species. The distribution of mean frost tolerance (Figure 4) is less associated with the presence of *S. acaule*.

Temperature

Temperature data of the areas where the accessions were collected predicts frost tolerance well at low levels of tolerance. If only the scores between 0 and 42% are considered, there is a strong association between mean annual minimum temperature and frost tolerance ($r^2 = 0.87$; Figure 8). In this range, wild potatoes collected from warmer places are less likely to have frost tolerance than those collected from colder places. However, at higher levels of tolerance (between 42 and 100%), there is a weak ($r^2 = 0.31$) and even positive association (more frost tolerance in wild potatoes from warmer areas). Thus there is only a weak overall association between frost tolerance and temperature. The results do not change whether minimum or maximum temperature is used, or whether

temperature is averaged over the whole year or only over the apparent growing season.

Within series or species, the predictivity of temperature data was low. For the series, the coefficient of determination between frost tolerance and mean annual minimum temperature was below 0.14 and not significant ($p > 0.05$) except for ser. *Conicibaccata* ($r^2 = 0.88$), *Piurana* ($r^2 = 0.54$; but with a positive relationship between temperature and frost tolerance!), *Demissa* ($r^2 = 0.38$), and *Tuberosa* ($r^2 = 0.18$). For individual species, there was a significant association ($p < 0.05$) of minimum temperature with frost tolerance for only two species: *S. colombianum* ($r^2 = 0.95$) and *S. verrucosum* ($r^2 = 0.45$).

Temperature, species and geography

In a single factor statistical analysis, mean annual minimum temperature is significantly associated with frost tolerance ($df = 1$; $F = 279$; $p < 0.001$; $r^2 = 0.15$). However, species ($df = 86$; $F = 304$; $p < 0.001$; $r^2 = 0.94$) and series ($df = 17$; $F = 345$; $p < 0.001$; $r^2 = 0.78$) effects are much stronger. In combined models of species or series and minimum temperature, the minimum temperature effect is not significant. Very similar results were obtained when all the observations with 100% frost tolerance scores were deleted, in order to have a more normal distribution of the data.

The map of areas with a mean minimum temperature below 3 °C within the area where wild potatoes

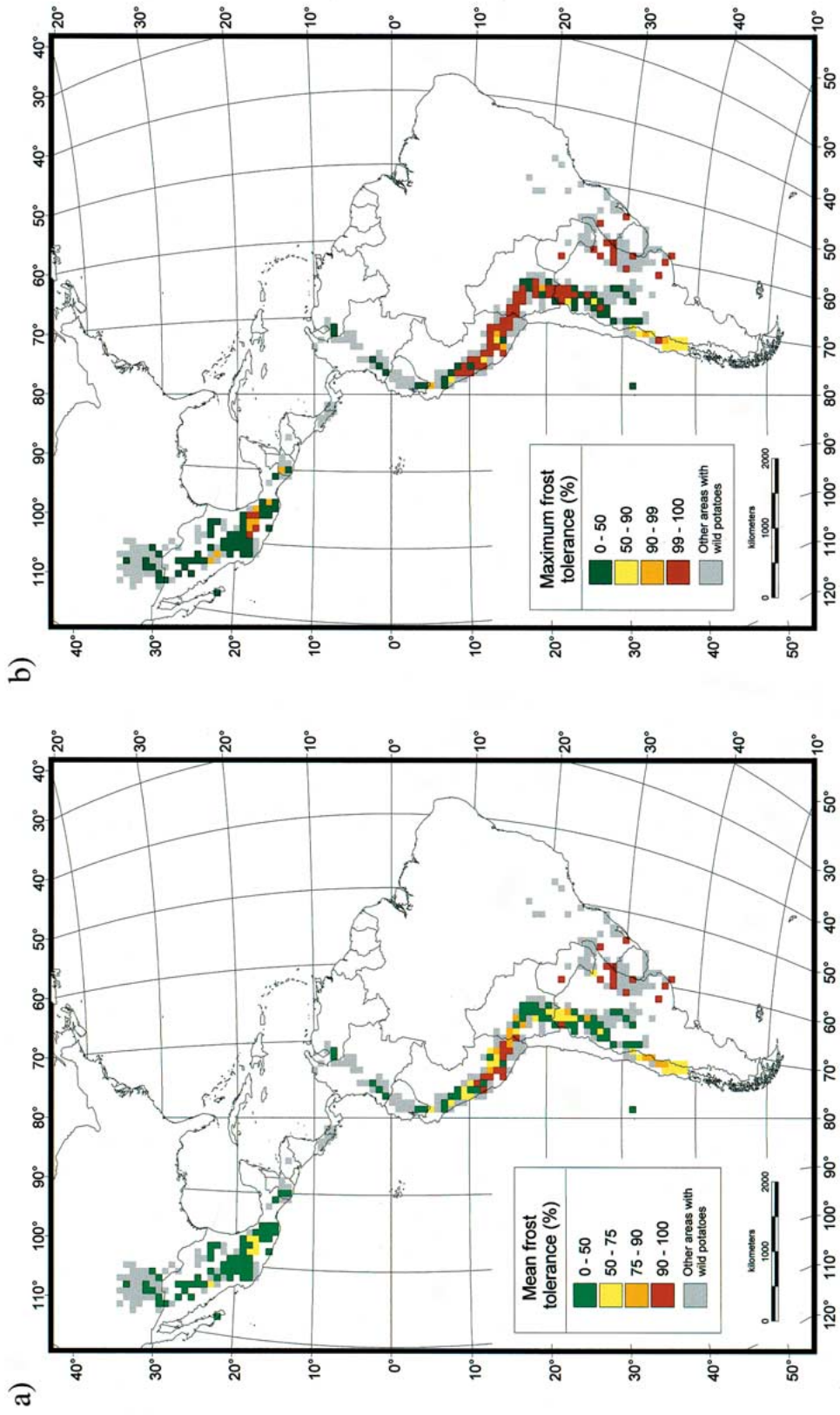


Figure 4. Spatial distribution of the mean (A) and maximum (B) observed frost tolerance (percentage non-damaged tissue) in wild potatoes in 100 by 100 km grid cells. Each observation (n = 1646) referred to the locality where a wild potato species was collected.

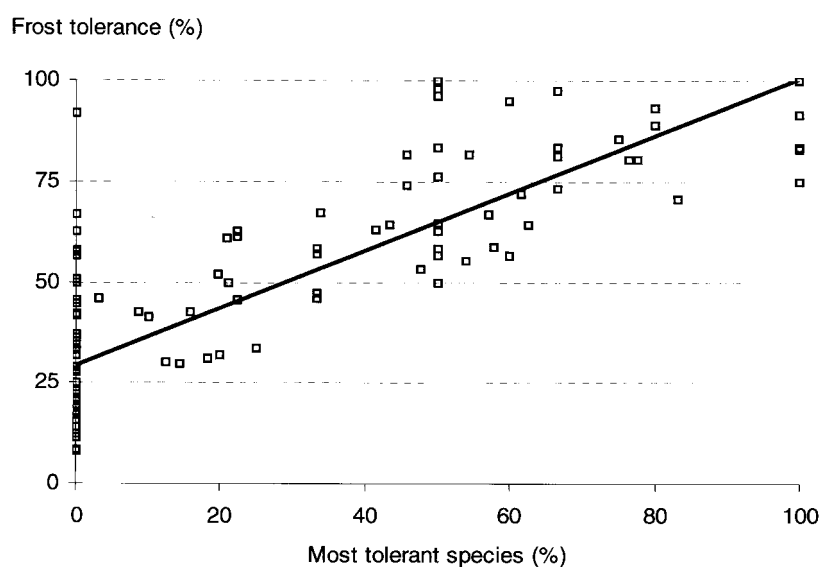


Figure 5. Percentage of observations per grid cell for the nine most frost tolerant wild potato species (out of a total 87 species in the sample) versus the mean frost tolerance (percentage non-damaged tissue) for all observations. Each dot on the graph represents one 100 by 100 km grid cell. Regression line: $y = 0.71x + 29.4$; $r^2 = 0.767$.

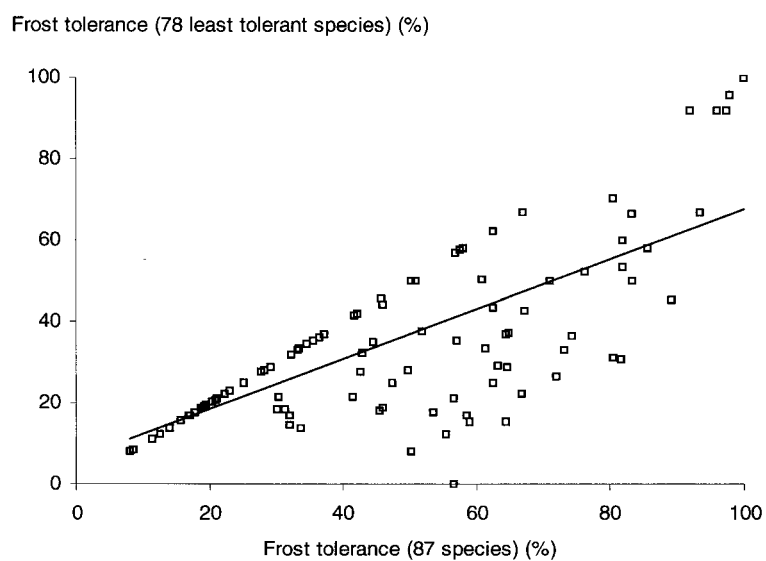


Figure 6. Mean frost tolerance (percentage non-damaged tissue) per grid cell with and without the nine most tolerant wild potato species (out of 87 species in the sample). The number of observations decreased from 1646 to 1086. Each dot on the graph represents one 100 by 100 km grid cell. Regression line: $y = 0.61x + 6.45$; $r^2 = 0.589$.

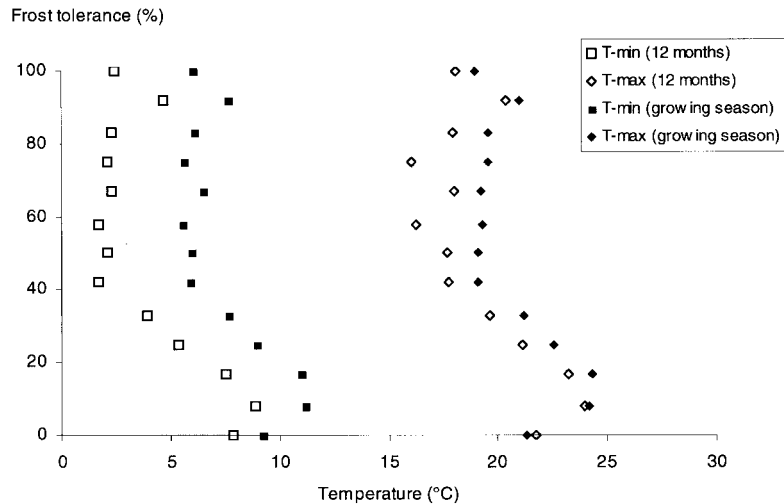


Figure 7. Mean frost tolerance versus temperature of the locations where the wild potato accessions in our sample were collected, for the monthly minimum temperature (T-min), maximum temperature (T-max) averaged over the year (12 months), or over the most likely growing season of four months (growing season).

occur is not a very good predictor of the level of frost tolerance in wild potatoes from these areas (Figure 8). The map correctly identifies the Central Andes and parts of Chile, but it misses the lowland area of Argentina and Uruguay (where *S. commersonii* occurs) and wrongly predicts the southwestern USA as an area with frost tolerant wild potatoes. The species present in the United States are *S. jamesii* (7 accessions; 20% frost tolerance score) and *S. fendleri* (33 accessions; 21% frost tolerance score).

Discussion

This study illustrates the need for simultaneously analyzing different factors to predict the presence of an agronomic trait in wild species. We showed that taxonomic categories, particularly species, are strongly related to frost tolerance in wild potatoes. Ecology and geography were also associated with frost tolerance, but probably not to the extent that they would be very useful to guide further screening or collecting. If further screening of wild potatoes is warranted, priority could be given to those species not yet tested, particularly those from series with high frost tolerance, and that occur in southern Peru, and to species with a high level of frost tolerance for which only a few accessions were tested (e.g., *S. paucisetum*). It would also be important to test the most tolerant accessions (particu-

larly those with 100% frost tolerance scores) to more severe frosts.

Species were associated with different levels of frost tolerance. This is of value for prediction within, but not beyond the species examined. The latter was important in our study for which data for fewer than half the existing wild species were available. Taxonomic series might be used for prediction of frost tolerance in species that have not yet been tested. However, there was much variation within those series with a relatively high number of observations. Other series may be too small to be of much use in prediction. For example, we examined data for two species (*S. acaule* and *S. albicans*) of ser. *Acaulia*, the most frost tolerant series. There are only two additional species in this group *S. × indunii* and *S. × viirsoii*, both of which are rare and assumed to be of hybrid origin, with *S. acaule* as one of the parents. The other series associated with very high frost tolerance, ser. *Commersoniana*, only has two species: *S. commersonii*, for which we had data, and *S. calvescens*, for which we did not.

The species and series conclusions also depend on the accuracy, consistency, and relevance of the taxonomic system used. Ongoing research is continuing to refine wild potato taxonomy, and in the future there will likely be a reduction in the number of species and changes in series memberships (Van den Berg et al., 1998; Spooner & Hijmans, 2001). The commonly

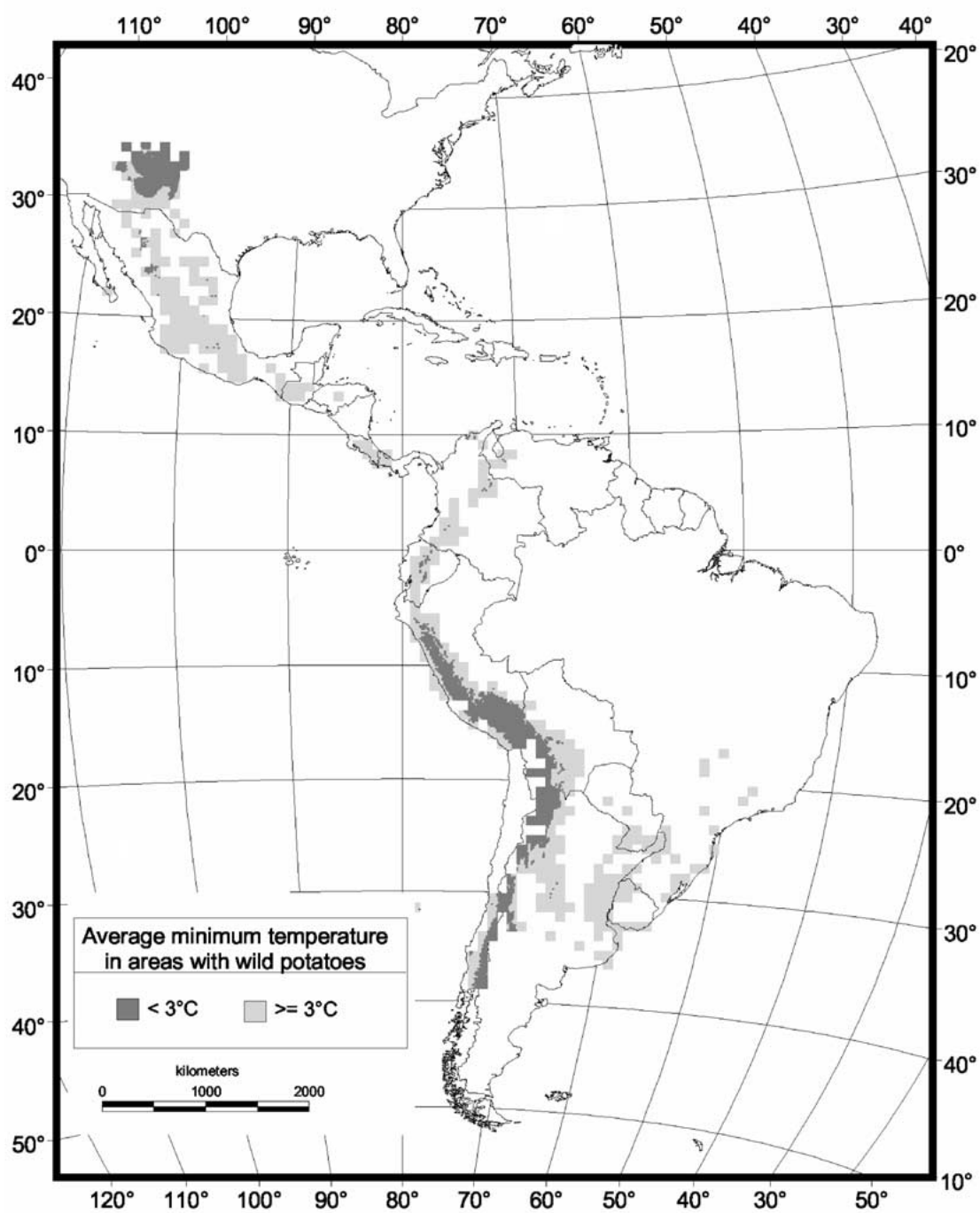


Figure 8. Mean annual minimum temperature in areas where wild potatoes have been observed.

used series classification by Hawkes (1990) has received little support in any molecular marker data set used to date (Spooner & Hijmans, 2001). For example, chloroplast DNA restriction site data supported only four clades within sect. *Petota*, and not the 19 series (of 21) that were examined (Spooner & Sytsma, 1992; Spooner & Castillo, 1997). Other nuclear molecular markers such as nuclear restriction fragment length polymorphisms (Bonierbale et al., 1990) and amplified fragment length polymorphism data (Debener et al., 1990; Kardolus, 1998) also fail to support many traditional series. The predictivity of series classifications may be greatly improved with new data. For example, there is compelling support for including *S. demissum* in ser. *Acaulia*, rather than in ser. *Demissa* (Spooner & Hijmans, 2001; Spooner et al., 1995). It is noteworthy that *S. demissum* had a high frost tolerance (92%), comparable to the members of ser. *Acaulia*, but unlike the other members of ser. *Demissa*.

Our findings corroborate the weak association of genetic variation with eco-geographic factors (Chapman, 1984; Peeters et al., 1990; Del Rio et al., 2001). However, our findings are discordant with the results of Li et al. (1980), who found a strong and simple positive linear relation between frost tolerance and altitude of provenance for 15 accessions of *S. acaule*. Perhaps this relation is specific to *S. acaule*, but we could not test this because we did not have differentiation within *S. acaule* (for which all accessions had a 100% frost tolerance score).

We had many observations originating from a large geographic area. The frost tolerance screening data used here constitutes the largest single evaluation of the US Department of Agriculture potato genebank database. Yet data quality problems in the coordinates or in the interpolated climate data may have hampered our ability to find relationships between temperature and frost tolerance to some extent, particularly because most of the wild potatoes that were evaluated occur in highly dissected mountain ranges, with steep climate gradients. Detailed studies with a few species from a small area and with more precise temperature data would be useful to validate our results. We used mean minimum temperature data instead of perhaps more informative data such as monthly extreme temperatures. This may have weakened the relationships found. Yet a likely more important factor is the low resolution of the interpolated weather data. This may be particularly problematic in the Andes where there are large changes in altitude (and hence temperature) over relatively small distances. In all areas there may

be micro-climatic differences that play a role which cannot be captured with our data. Nevertheless, we used the best data available, and these data did not have a strong predictive value.

In previous studies, altitude has sometimes been used as a proxy for ecological factors (Flanders et al., 1992). However, altitude is only a good proxy for temperature in small areas. It is less useful for studies of large areas such as considered in the present study. Also, variation is sometimes compared using countries or groups of countries (Peeters et al., 1990). These areas are often rather different in size and shape and may not allow for appropriate comparison. Grid cells, as used in this study, are more appropriate for these comparisons.

Other trait/crop combinations could be studied to re-evaluate the emphasis that is typically given to eco-geographic stratification in genetic resources collection (e.g., Brown & Marshall, 1995; Von Bothmer & Seberg, 1995). It is noteworthy that wild potato collectors in particular have given much more emphasis to taxonomic considerations (Spooner et al., 1999). Yet this taxonomic bias is compensated by the fact that many wild potato taxa occur in small areas. Consequently taxonomy and geography (and hence also ecology) of wild potatoes are somewhat confounded. With some species being differentiated on the basis of the area they occur in (Spooner & Van den Berg, 1992), sampling by species is to some extent also sampling by geographic area.

Acknowledgements

We thank Meredith Bonierbale, Louise Fresco, Karen Garret, Luigi Guarino, Martin Kropff, and John Stares for review.

References

- Barrientos, M., E. Mol, G. Perruzo, A. Contreras & M. Alberdi, 1994. Responses to cold of Chilean wild *Solanum* species. *Environ Exp Bot* 34: 47–54.
- Bonham-Carter, G., 1994. Geographic Information Systems for Geoscientists. Modelling with GIS. Computer Methods in the Geosciences 13. Pergamon/Elsevier, London, UK.
- Bonierbale, M., W. Ganal & S.D. Tanksley, 1990. Applications of restriction fragment length polymorphisms and genetic mapping in potato breeding and molecular genetics. In: M.E. Vayda & W.D. Park (Eds.), *The Molecular and Cellular Biology of the Potato*, pp. 13–24. CAB International, Wallingford, U.K.
- Brown, A.H.D. & D.R. Marshall, 1995. A basic sampling strategy: theory and practice. In: L. Guarino, V. Ramanatha Rao & R. Reid

- (Eds.), *Collecting Plant Genetic Diversity, Technical Guidelines*, pp. 75–91. CAB International, Wallingford, U.K.
- Chapman, C.D.G., 1984. On the size of a genebank and the genetic variation it contains. In: J.H.W. Holden & J.T. Williams (Eds.), *Crop Genetic Resources: Conservation and Evaluation*, pp. 102–119. George Allen and Unwin, London, U.K.
- Debener, T., F. Salamini & C. Gebhardt, 1990. Phylogeny of wild and cultivated *Solanum* species based on nuclear restriction fragment length polymorphisms (RFLPs). *Theor Appl Genet* 79: 360–368.
- Del Rio, A.H., J.B. Bamberg, Z. Huamán, A. Salas & S.E. Vega, 2001. Association of ecogeographical variables and RAPD marker variation in wild potato populations of the USA. *Crop Sci* 41: 870–878.
- Estrada, R.N., 1982. Breeding wild and primitive potato species to obtain frost-resistant cultivated varieties. In: P.H. Li & A. Sakai (Eds.), *Plant Cold Hardiness & Freezing Stress: Mechanisms and Crop Implications*, Volume 2, pp. 615–633. Academic Press, New York.
- Flanders, K.L., J.G. Hawkes, E.B. Radcliffe & F.I. Lauer, 1992. Insect resistance in potatoes: sources, evolutionary relationships, morphological and chemical defenses, and ecogeographical associations. *Euphytica* 61: 83–111.
- Flanders, K.L., E.B. Radcliffe & J.G. Hawkes, 1997. Geographic distribution of insect resistance in potatoes. *Euphytica* 93: 201–221.
- Hawkes, J.G., 1990. *The Potato: Evolution, Biodiversity and Genetic Resources*, Belhaven Press, London.
- Hijmans, R.J. & D.M. Spooner, 2001. Geographic distribution of wild potato species. *Amer J Bot* 88: 2101–2112.
- Hijmans, R.J., M. Schreuder, J. de la Cruz & L. Guarino, 1999. Using GIS to check co-ordinates of genebank accessions. *Genet Res Crop Evol* 46: 291–296.
- Hijmans, R.J., L. Guarino, C. Bussink & E. Rojas, 2002. DIVA-GIS, version 2. A geographic information system for the analysis of biodiversity data. Manual. International Potato Center, Lima, Peru.
- Hijmans, R.J., D.M. Spooner, A. Salas, L. Guarino & J. de la Cruz, 2002. *Atlas of Wild Potatoes. Systematic and Ecogeographic Studies of Crop Gene pools*. International Plant Genetic Resources Institute, Rome, Italy.
- Jones, P.G., 1991. The CIAT Climate Database Version 3.41. Machine readable dataset. CIAT, Cali.
- Kardolus, J.P., 1998. *A Biosystematic Study of Solanum acaule*. Thesis, Wageningen Agricultural University, The Netherlands.
- Li, P.H., 1977. Frost killing temperatures of 60 tuber-bearing *Solanum* species. *Amer Potato J* 54: 452–456.
- Li, P.H., J.P. Palta & J.G. Hawkes, 1980. A scientific note: inter-relationship between frost hardiness and elevation of genotype origin. *Amer Potato J* 57: 184–185.
- Nevo, E., E. Golenberg, A. Beiles, A.H.D. Brown & D. Zohary, 1982. Genetic diversity and environmental associations of wild wheat, *Triticum dicoccoides*, in Israel. *Theor Appl Genet* 62: 241–254.
- New M., M. Hulme & P. Jones, 1999. Representing twentieth-century space-time climate variability. Part I: Development of a 1961–1990 mean monthly terrestrial climatology. *J Climate* 12: 829–856.
- Ochoa, C.M., 1999. *Las papas de Sudamérica: Peru (Parte I)*. International Potato Center, Lima, Peru.
- Peeters, J.P., H.G. Wilkes & N.W. Galwey, 1990. The use of ecogeographical data in the exploitation of variation from genebanks. *Theor Appl Genet* 80: 110–112.
- Rick, C.M., 1973. Potential genetic resources in tomato species: clues from observations in native habitats. In: A.M. Srb (Ed.), *Genes, Enzymes, and Populations*, pp. 255–269. Plenum, New York, USA.
- Ronning, C.M., S.P. Kowalsky, L.L. Sanford & J.R. Stommel, 2000. Geographic variation of solanidane aglycone glycoalkaloids in the wild potato species *Solanum chacoense* Bitter. *Genet Res Crop Evol* 47: 359–369.
- Ross, H., 1986. *Potato Breeding: Problems and Perspectives*. Advances in Plant Breeding 13. Paul Parey Verlag, Berlin, Germany.
- Spooner, D.M. & R.T. Castillo, 1997. Reexamination of series relationships of South American wild potatoes (Solanaceae: *Solanum* sect. *Petota*): Evidence from chloroplast DNA restriction site variation. *Amer J Bot* 84: 671–685.
- Spooner, D.M. & R.J. Hijmans, 2001. Potato systematics and germplasm collecting 1989–2000. *Amer J Potato Res* 78: 237–268; 395.
- Spooner, D.M. & K.J. Sytsma, 1992. Reexamination of series relationships of Mexican and Central American wild potatoes (*Solanum* sect. *Petota*): Evidence from chloroplast DNA restriction site variation. *Syst Bot* 17: 432–448.
- Spooner, D.M. & R.G. Van den Berg, 1992. An analysis of recent taxonomic concepts in wild potatoes (*Solanum* sect. *Petota*). *Genet Res Crop Evol* 39: 23–37.
- Spooner, D.M., A. Salas, Z. Huamán & R.J. Hijmans, 1999. Potato germplasm collecting expedition in southern Peru (Departments of Apurímac, Arequipa, Cusco, Moquegua, Puno, Tacna) in 1998: Taxonomy and new genetic resources. *Amer J Potato Res* 76: 103–119.
- Spooner D.M., R.G. Van den Berg & J. Bamberg, 1995. Examination of species boundaries of *Solanum* series *Demissa* and potentially related species in series *Acaulia* and series *Tuberosa* (sect. *Petota*). *Syst Bot* 20: 295–314.
- Van den Berg, R.G., J.T. Miller, M.L. Ugarte, J.P. Kardolus, J. Villand, J. Nienhuis & D.M. Spooner, 1998. Collapse of morphological species in the wild potato *Solanum brevicaulle* complex (Solanaceae: sect. *Petota*). *Amer J Bot* 85: 92–109.
- Van Soest, L.J.M., H.J. Rumpfenhorst & C.A. Huijsman, 1983. Resistance to potato cyst-nematodes in tuber-bearing *Solanum* species and its geographical distribution. *Euphytica* 32: 65–74.
- Van Soest, L.J.M., B. Schober & M.F. Tazelaar, 1984. Resistance to *Phytophthora infestans* in tuber-bearing species of *Solanum* and its geographical distribution. *Potato Res* 27: 393–411.
- Vega, S.E. & J.B. Bamberg, 1995. Screening the U.S. potato collection for frost hardiness. *Amer Potato J* 72: 13–21.
- Von Bothmer, R. & O. Seberg, 1995. Strategies for the collecting of wild species. In: L. Guarino, V. Ramanatha Rao & R. Reid (Eds.), *Collecting Plant Genetic Diversity, Technical Guidelines*, pp. 93–111. CAB International, Wallingford, U.K.

