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RESEARCH PAPER

Geographical and environmental range expansion through polyploidy in wild potatoes (*Solanum* section *Petota*)

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ABSTRACT

Aim To assess evidence for geographical and environmental range expansion through polyploidy in wild potatoes (*Solanum* sect. *Petota*). There are diploids, triploids, tetraploids, pentaploids and hexaploids in this group.

Location Wild potatoes occur from the south-western USA (Utah and Colorado), throughout the tropical highlands of Mexico, Central America and the Andes, to Argentina, Chile and Uruguay.

Methods We compiled 5447 reports of ploidy determination, covering 185 of the 187 species, of which 702 determinations are presented here for the first time. We assessed the frequency of cytotypes within species, and analysed the geographical and climatic distribution of ploidy levels.

Results Thirty-six per cent of the species are entirely or partly polyploid. Multiple cytotypes exist in 21 species, mostly as diploid and triploid, but many more may await discovery. We report the first chromosome count ($2n = 24$) for *Solanum hintonii*. Diploids occupy a larger area than polyploids, but diploid and tetraploid species have similar range sizes, and the two species with by far the largest range sizes are tetraploids. The fraction of the plants that are polyploids is much higher from Mexico to Ecuador than farther south. Compared with diploids, triploids tend to occur in warmer and drier areas, whereas higher-level polyploids tend to occur in relatively cold areas. Diploids are absent from Costa Rica to southern Colombia, the wettest part of the group's range.

Main conclusions These results suggest that polyploidy played an important role in this group's environmental differentiation and range expansion.

Keywords

Chromosome number, climate, geographical range, polyploidy, potato, range size, richness, section *Petota*, Solanaceae, *Solanum*.

INTRODUCTION

Polyploidy is an important mechanism in plant speciation (Grant, 1981) that has been associated with geographical and environmental range expansions (Soltis *et al.*, 2003; Brochmann *et al.*, 2004). Although recently formed polyploids are often less fertile than diploids, they may survive because of transgressive physiological characters such as higher tolerances to stress and disease, allowing them to occupy new ecological niches and expand their geographical ranges (Cain, 1944; Stebbins, 1947, 1971; Jackson, 1976; de Wet, 1980; Grant, 1981; Levin, 1983, 2002; Fowler & Levin, 1984; Bayer & Stebbins, 1987; Felber, 1991; Schrantz & Osborn, 2004), or they may occupy ecological niches intermediate to those of their progenitors (Ehrendorfer, 1980). It has also been shown that the production of unreduced gametes, through which polyploids are frequently formed, is stimulated by environmental factors such as temperature, water and nutrient stress (Belling, 1925; Kostoff, 1933; Sax, 1937; Grant, 1952; McHale, 1983; Ramsey & Schemske, 1998) that are likely to occur at the limit of a species' range. Polyploids are more common at higher latitudes than in the tropics, but this cannot be directly attributed to increased hardiness because herbaceous perennials, in which polyploidy is more frequent than in annuals or trees, dominate floras at high latitudes (Gustafsson, 1948). In fact, an important reason for the abundance of polyploids in arctic regions appears to be that they are more successful than diploids

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in colonizing after deglaciation (Stebbins, 1985; Brochmann *et al.*, 2004).

To avoid the presence of too many confounding factors, the role of polyploidy and its relation to range expansion is best studied by comparisons within groups of related species, rather than by comparisons of entire floras (Stebbins, 1971). Here we analyse evidence for range expansion through polyploidy in wild potatoes (*Solanum* sect. *Petota* Dumort.). Section *Petota* is a large and widespread group consisting of 187 species (Spooner & Salas, 2006). The group occurs from Utah and Colorado in the USA, throughout the tropical highlands of Mexico, Central America and the Andes, to Argentina, Chile and Uruguay, with the highest species richness in central Mexico and the central Andes (Hijmans & Spooner, 2001). Species of sect. *Petota* have a base chromosome number of $x = 12$. There are diploids ($2n = 2x = 24$), triploids ($2n = 36$), tetraploids ($2n = 48$), pentaploids ($2n = 60$) and hexaploids ($2n = 72$). Although polyploidy is common in sect. *Petota*, it is not known in the closely related sect. *Lycopersicum* (Mill.) Wettst. (tomatoes), sect. *Juglandifolium* (Rydb.) Child, and sect. *Etuberosum* Juz. (Contreras-M. & Spooner, 1999; Hunziker, 2001). The modes of origin of polyploidy in sect. *Petota* remain largely unresolved. According to Matsubayashi (1991) there are autopolyploids (4*x* in ser. *Tuberosa*) as well as allopolyploids (3*x* in *Solanum vallis-mexici Juz.*, 4*x*, 6*x* in ser. *Conicibaccata*, *Demissa* and *Longipedicellata*). Polyploid cytotypes of otherwise diploid species are likely to be of autopolyploid origin.

We provide a comprehensive compilation of ploidy reports in sect. *Petota* through a literature survey, and we present new reports for germplasm samples from the US Potato Genebank. We analyse the incidence of ploidy levels across and within plants, and map the individual records by ploidy level. We use grid maps and latitudinal bands to analyse the number of ploidy levels present in an area (ploidy richness), and the fraction of the species that are polyploid. We use range size and distribution of ploidy levels across climatic conditions to evaluate evidence for range expansion and habitat differentiation through polyploidy.

MATERIALS AND METHODS

Data collection

We compiled a total of 5447 reports of ploidy determination covering 185 of the 187 species. Reports were obtained by searching the standard cytological indices (listed in Appendix S1 in Supplementary Material). We checked every report in the original sources, and obtained additional records from the literature cited in those sources. Reports of ploidy levels were obtained by summarizing data from counts of mitotic metaphase chromosomes in root tip cells or counts of meiotic metaphase chromosomes in pollen mother cells, but not from other methods such as flow cytometry analysis or stomatal guard cell assessments. Our compilation includes data from 259 meiotic ploidy determinations. Such determinations from pollen mother cells are potentially suspect because of the occasional occurrence of mitotic ($2n$) pollen. We included these data in our analysis because the vast majority (198) identified diploid or triploid species, for which there are no grounds for doubting the determination, and none of the other meiotic counts revealed uncommon ploidy levels.

We omitted some reports gleaned from the cytological indices, such as those appearing in abstracts of oral presentations or involving colchicine-induced polyploids and experimental interspecific hybrids (e.g. Lamm, 1943; Hermsen & Ramanna, 1969). The indices sometimes list records that do not appear to be original (e.g. Hrubý, 1957; Ugent, 1967) and we made every attempt to compile only original data. We also used 702 ploidy determinations, including the first determination for *S. hintonii*, for germplasm samples from the US Potato Genebank that were determined subsequent to those published in Bamberg *et al.* (1996). These new reports were obtained from mitotic analyses of root tips by the acetocarmine squash technique (Smith, 1974) from plants grown in pots in greenhouses. Individual records for these new reports are available in Appendix S2 in Supplementary Material, and a summary of the ploidy determination reports is provided as Appendix S3 in Supplementary Material.

For each ploidy report, we recorded, when available, collector and collector number, collection date, genebank number, the species name as reported, the currently valid name, the gametophytic or sporophytic chromosome number, the bibliographic reference and the locality description, altitude, latitude and longitude. When latitude and longitude were not provided, we georeferenced the localities, whenever possible, using maps and digital gazetteers. Geographical coordinates were checked by overlay techniques as described in Hijmans *et al.* (1999), by inspecting distribution maps for each species, and by looking for climatic outliers using DIVA-GIS (Hijmans *et al.*, 2004). After these procedures, geographical coordinates were available for 80% of the records.

Data analysis

We assessed the frequency of cytotypes within species to infer the number of additional ploidy levels that may still await discovery. To do so we calculated the probability of detection of a rare cytotype and applied the binomial distribution to estimate the number of samples that needed to be screened to reach a 95% level of confidence for detecting a rare cytotype. Distribution maps were made for each ploidy level. We used additional distribution records from Hijmans *et al.* (2002) and Spooner *et al.* (2004) to show the complete known distribution of sect. *Petota*, and to predict the presence of ploidy levels in areas from which no ploidy reports were available. Such predicted ploidy levels were identified with a different colour. Yet another colour was used to map occurrences of species with multiple known cytotypes if these included the cytotype being mapped. We made an exception for *Solanum acaule*, which throughout this paper is treated as an entirely tetraploid species despite a single hexaploid record (Kardolus, 1998), because the species determination of this record is questionable (Appendix S3) as it occurs far outside the known range of this species.

To analyse the spatial distribution of ploidy levels, maps of species and ploidy richness and of the polyploid fraction were made on a grid with a 100-km spatial resolution using DIVA-GIS.

These variables were also plotted by bands of 1° latitude. Species richness was derived from all distribution records. For ploidy richness, we used both observed and predicted ploidy of the species with a single known cytotype. Additional records for species with multiple cytotypes were used only when all of the multiple levels were otherwise absent in a cell. For example, if there were no reports of either diploids or triploids in a cell, nor any record for an exclusively diploid or triploid species, an occurrence record for a species with diploid and triploid populations would be used to add one level to the ploidy richness in that cell. The polyploid fraction was calculated as the number of polyploid observations to all observations. Diploid species for which rare triploid cytotypes were known were included as diploid species in this analysis, but other species with multiple cytotypes in addition to diploid were excluded from this calculation.

The extent of the distribution of different cytotypes and species was calculated using the relative circular area (RCA) statistic with a radius of 25 km (RCA_{25}). Circular area (CA) is calculated by assigning a circle with a fixed radius, of 25 km in this case, to each observation, and then calculating the total area covered by all the circles; that is, areas in which circles overlap are only included once (Hijmans & Spooner, 2001; Hijmans *et al.*, 2002). The RCA is then calculated by dividing the total area by the area of one circle.

To assess differences in intraspecific distributions of cytotypes, we mapped cytotypes of four species for which we had more than 10 observations for each of multiple cytotypes: *Solanum leptophyes*, *Solanum microdontum*, *Solanum medians* and *Solanum oplocense*. We also mapped *Solanum chacoense* and *Solanum calvescens* together because Brücher (1975) suggested that *S. calvescens* represents triploid populations of *S. chacoense*.

Estimated total annual precipitation and mean annual temperature data were extracted from the *c.* 1-km spatial resolution WorldClim data base (Hijmans *et al.*, 2005) for the collecting locations of the plants for which we had ploidy determinations. We compared the distribution of ploidy levels across climate for the whole group, and by bands of 5° latitude, using logistic regression in the R environment (lrm command; Design package).

RESULTS

Ploidy levels

The first published ploidy determinations of wild potato species were for *Solanum demissum* and *Solanum ×edinense* (Salaman, 1926). We here provide the first report for *S. hintonii* ($2n = 2x = 24$). Only the ploidy of *Solanum donachui* and *Solanum woodsonii* remain unreported (Appendix S3). For 123 species we found only reports of diploids, while 43 species were exclusively polyploid. Thirty species contain tetraploid populations, 20 contain triploids, 14 contain hexaploids and only two contain pentaploid populations (Appendix S3). Reports of multiple cytotypes occurred in 21 species (11%). Twelve of these had diploids and triploids exclusively, and five species had diploids and tetraploids exclusively. Two species had three cytotypes: *Solanum verrucosum* with diploids (predominately), triploids and tetraploids; and *S. oplocense* with diploids, tetraploids and hexaploids (Appendix S3). For six of the 20 species with triploid reports, we found no reports of other ploidy levels. Of these species for which only triploidy has been reported, *Solanum ×indunii* had 25 ploidy determinations and *Solanum ×neoweberbaueri* had 11 determinations, but the ploidy of the other four species was assessed only once.

Solanum acaule was the species with the most ploidy reports (604). Conversely, 24 species were assessed for ploidy only once and 104 species fewer than 10 times. The median number of ploidy reports for species with multiple cytotypes was 28, whereas the median number for species with a single cytotype was eight. For nine species, the frequency of detecting the less common cytotype(s) was ≥ 0.2. In all other species with multiple cytotypes, there was one common level and one (in one case two) rare level(s). For five of the 22 species with multiple levels, the frequency of detection of the rare cytotype was < 0.04. Defining rare cytotypes as those with at least a 4% probability of detection, and applying the binomial distribution, at least 74 genotypes need to be examined to have a 95% probability of detecting a rare cytotype within a species. When 10 genotypes are examined, the probability of detection is only 34%. We found multiple cytotypes for eight of the 20 species for which we had more than 73 reports. This suggests that there could be as many as $0.4 \times 187 = 75$ species with 4% or more plants with an uncommon cytotype, of which to date only 28% have been discovered.

Geographical distribution

The diploid species combined occupy the greatest geographical range within sect. *Petota*, followed by the tetraploids (Figs 1 & 2). The odd-level polyploids (3*x*, 5*x*) have much smaller ranges than the even-level polyploids (4*x*, 6*x*). Diploids occur at the extreme northern (south-western USA) and southern (Argentina, Chile, Uruguay) latitudes of the distribution of wild potatoes. Diploids are relatively rare in northern Mexico, where tetraploids are dominant.

Diploids are conspicuously absent between 2° and 11° N, that is, from southern Colombia to Costa Rica (Fig. 1). All wild potatoes in this area are tetraploids except for two hexaploid species in southern Colombia: *Solanum moscopanum* and *Solanum sucubunense*. Tetraploids are also common just south of this area, in Ecuador. Further south, in Peru, there are only two tetraploid species: the rare *Solanum nubicola* and the very common *S. acaule*, which has a range that extends to northern Argentina. Southern Bolivia and northern Argentina have an additional seven tetraploid species.

Triploid *S. calvescens* is the only species that occurs at the extreme eastern end of the distribution of sect. *Petota* in Brazil. Triploids also occur in the south-eastern end of the distribution (Argentina and Uruguay) as triploid cytotypes of typically diploid *S. commersonii*, but none of the triploid reports had sufficient locality data to be reliably mapped. Triploid records are particularly frequent on the coast and the western slopes of the Andes in Peru. They also occur on the eastern slopes of the Andes in Bolivia and Argentina, but are rare in the higher parts of the Andes.

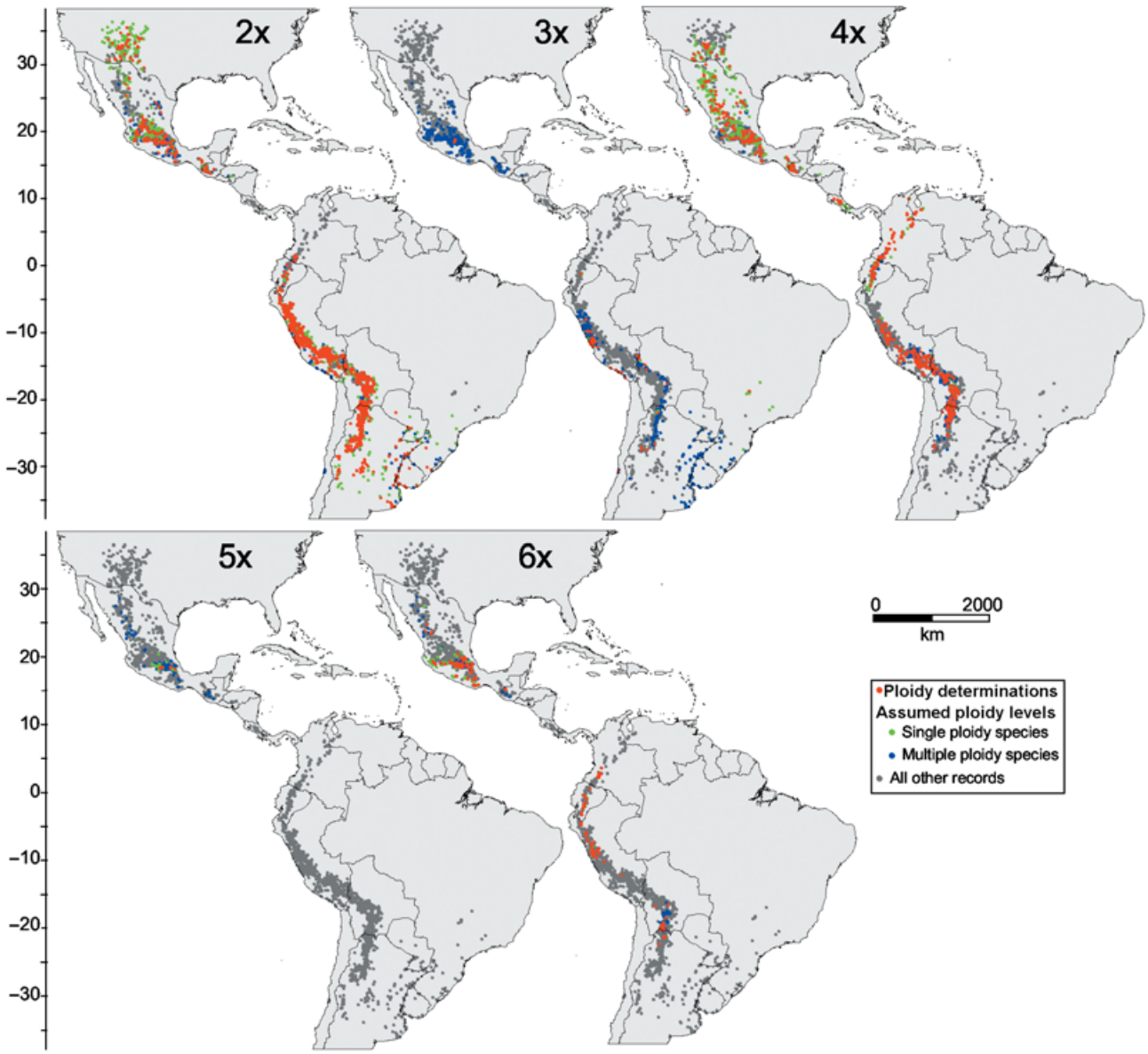

Figure 1 Geographical distribution of ploidy levels in wild potato species. We show, for each ploidy level (2*x*, 3*x*, 4*x*, 5*x* and 6*x*): (1) the localities where plants with that ploidy level were found; (2) localities for which we have no observations of that level but where it may be assumed to be present given the species that occur there, distinguishing species with a single known cytotype and those with multiple known cytotypes; and (3) all other known wild potato collecting localities. Maps have a Lambert azimuthal equal-area projection.

The RCA_{25} for all species combined is 628, whereas for diploids it is 489, suggesting that 28% of the group's range is exclusively occupied by polyploids. The larger range size of all the diploids combined, in comparison with the polyploids (Fig. 2), is partly a reflection of the fact that there are many more diploid species. The mean RCA_{25} for all species is 13.1. For diploid species (including those with rare triploids) it is 10.7 and for tetraploids it is 24.0. These differences are large but not statistically significant (Mann–Whitney test) because they are strongly influenced by two tetraploid species with exceptionally large ranges. Without these two species, the mean range size of the tetraploids would be 8.3, below that of diploids. The two most widespread species are tetraploids: *Solanum stoloniferum* in Mexico (RCA_{25} = 223) and *S. acaule* in South America (RCA_{25} = 156), followed at some distance by the diploids *S. chacoense* (RCA_{25} = 109), *Solanum jamesii* (RCA_{25} = 106) and *S. bukasovii* (RCA_{25} = 82).

Ploidy richness and polyploid fraction

Ploidy richness is particularly high in central Mexico, where all five levels known in wild potatoes co-occur in a single 100-km resolution grid cell (Fig. 3). Ploidy richness is also high in Guatemala, parts of Ecuador and small areas in Peru and other parts of Mexico. Ploidy richness is somewhat related to species richness (Fig. 4), yet there is a much larger area of high ploidy richness

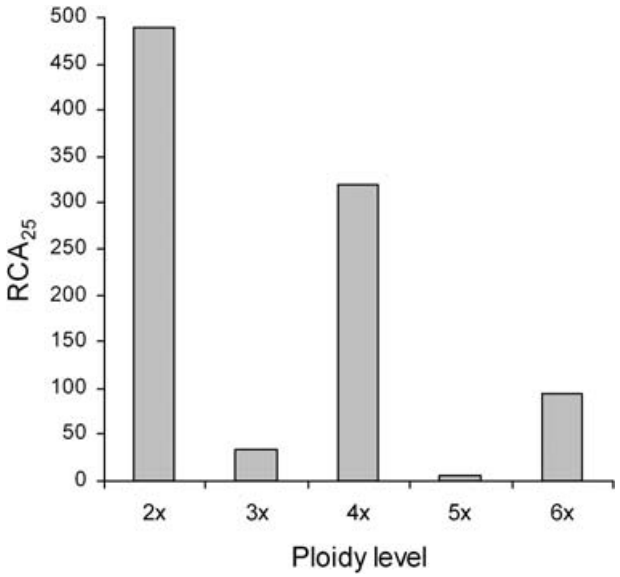

Figure 2 Total range size (RCA_{25}, the unit is the area of a circle with a radius of 25 km = 1963 km^2) for wild potatoes by ploidy level. This statistic is calculated by assigning a circle with a radius of 25 km to each observation, and then calculating the total area covered by the circles, which is divided by the area of one circle.

(more than two levels of ploidy) in the central Mexican area with high species richness of wild potatoes than in the Peruvian areas of high species richness, despite the higher number of species in Peru (Fig. 3). The area with highest species richness in Peru (around Cusco) has only diploids. Tetraploid *S. acaule* occurs nearby, but only at higher elevations. In the secondary Peruvian area of high species richness (the Ancash Department in north-central Peru), there is higher ploidy richness, because of the presence of diploids, three species with triploid cytotypes (*S. medians*, *Solanum multiinteruptum* and *Solanum sogarandinum*), a tetraploid (*S. acaule*) and a hexaploid (*Solanum albicans*) species.

The distribution by latitude of the polyploid fraction (number of polyploids over all observations) has a conspicuously different pattern to ploidy richness and species richness (Fig. 4). Species richness has two peaks, one in central Mexico and one in the Andes. The polyploid fraction oscillates around 0.5 from the United States to Guatemala and is 1 between Costa Rica and northern Ecuador. There is a sharp transition near the border of Peru and Ecuador, south of which the polyploid fraction is low, oscillating around 0.2 until, south of 30° S, it becomes zero.

Climate

Estimated mean temperature at collection localities for wild potatoes ranged between −1 and 26 °C, and annual precipitation ranged between 0 and 4359 mm. The record with 0 mm precipitation was on the Peruvian coastal desert where rainfall is extremely low. Triploid wild potatoes are more abundant than diploids in the extreme dry and warm areas of the group's distribution (Fig. 5). This result is strongly influenced by the abundance of triploids in (low-elevation) western Peru, and despite the sometimes triploid species *Solanum yungasense*, which occurs at low elevations in warm and wet areas of the eastern foothills of the Andes of Peru and Bolivia. In contrast, tetra-, penta- and hexaploids tend to occur in areas that are colder and wetter than the areas where diploids occur (Fig. 5). The 10th–90th percentile climate envelope for annual precipitation and mean temperature of the whole group is 20% larger than for the diploids alone (Fig. 6), mainly due to a notable expansion of polyploids into wetter areas.

Across latitudinal bands, polyploids (excluding triploids) consistently occur in colder areas than diploids (Fig. 7), both in the

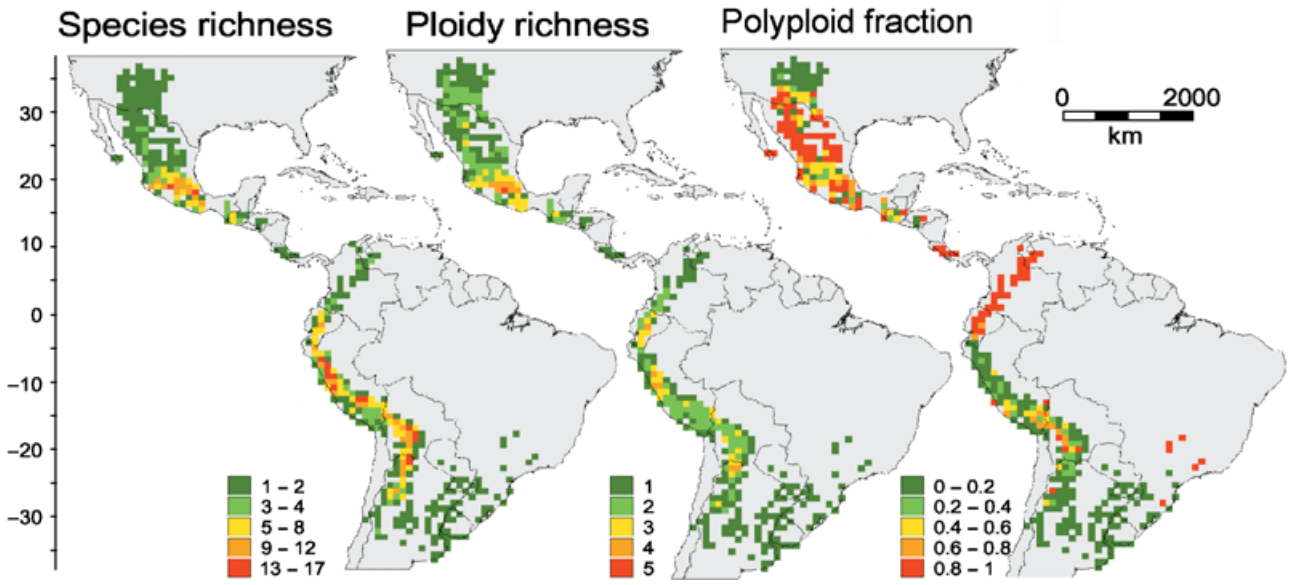

Figure 3 Species richness, ploidy richness and the polyploid fraction of wild potatoes in grid cells with a 100-km spatial resolution. Species and ploidy richness equal the number of these units per cell and the polyploid fraction is the number of polyploid observations over all observations. Maps have a Lambert azimuthal equal-area projection.

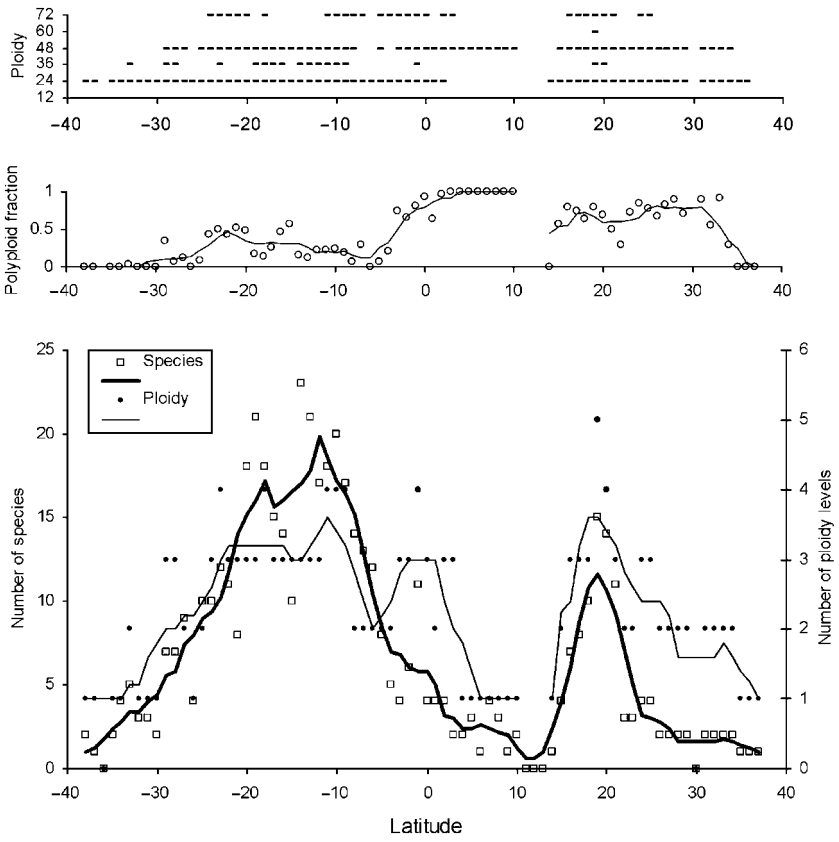

Figure 4 Presence/absence of ploidy levels (upper panel), polyploid fraction (the number of polyploid observations over all observations, middle panel) and ploidy and species richness (lower panel) by latitude (1° bands) for wild potato species. Middle and lower panels show lines of the 5° moving average.

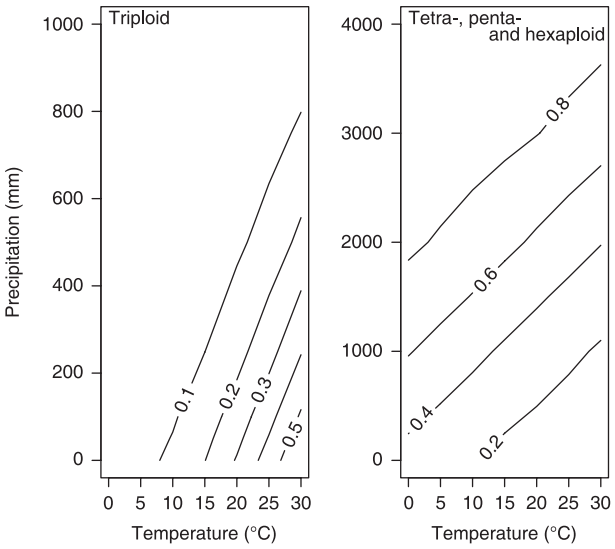

Figure 5 Contour plots of the probability of encountering a triploid vs. a diploid (left panel) and of encountering tetra-, penta- or hexaploid vs. a diploid (right panel) wild potato across the group's range, as a function of annual precipitation and mean temperature. Probabilities were estimated using logistic regression, and in both cases the intercept and predictors were highly significant (Wald statistic, $P < 0.001$).

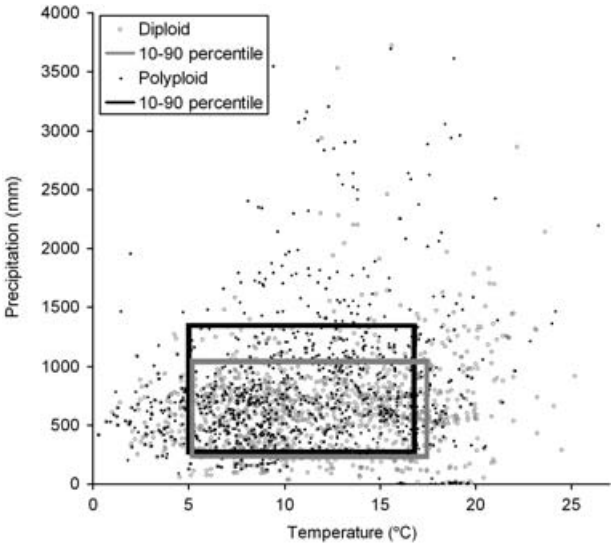

Figure 6 Average annual temperature and precipitation for diploids and polyploids, indicating their 10th–90th percentile 'climate envelope'.

Southern and Northern Hemispheres, with the only exception being the area around 25° N. These differences are statistically significant in 10 out of 13 bands of 5° latitude where both diploids and polyploids occur. The relationship between precipitation and ploidy level is less consistent, with polyploids mostly occurring in wetter areas near the equator and in drier areas at higher latitudes, and this relationship is significant in only five of the 13 bands. However, the zone from southern Colombia to Costa Rica, where only tetraploids and a few hexaploids occur, stands out for being much wetter than the other areas where wild potatoes occur.

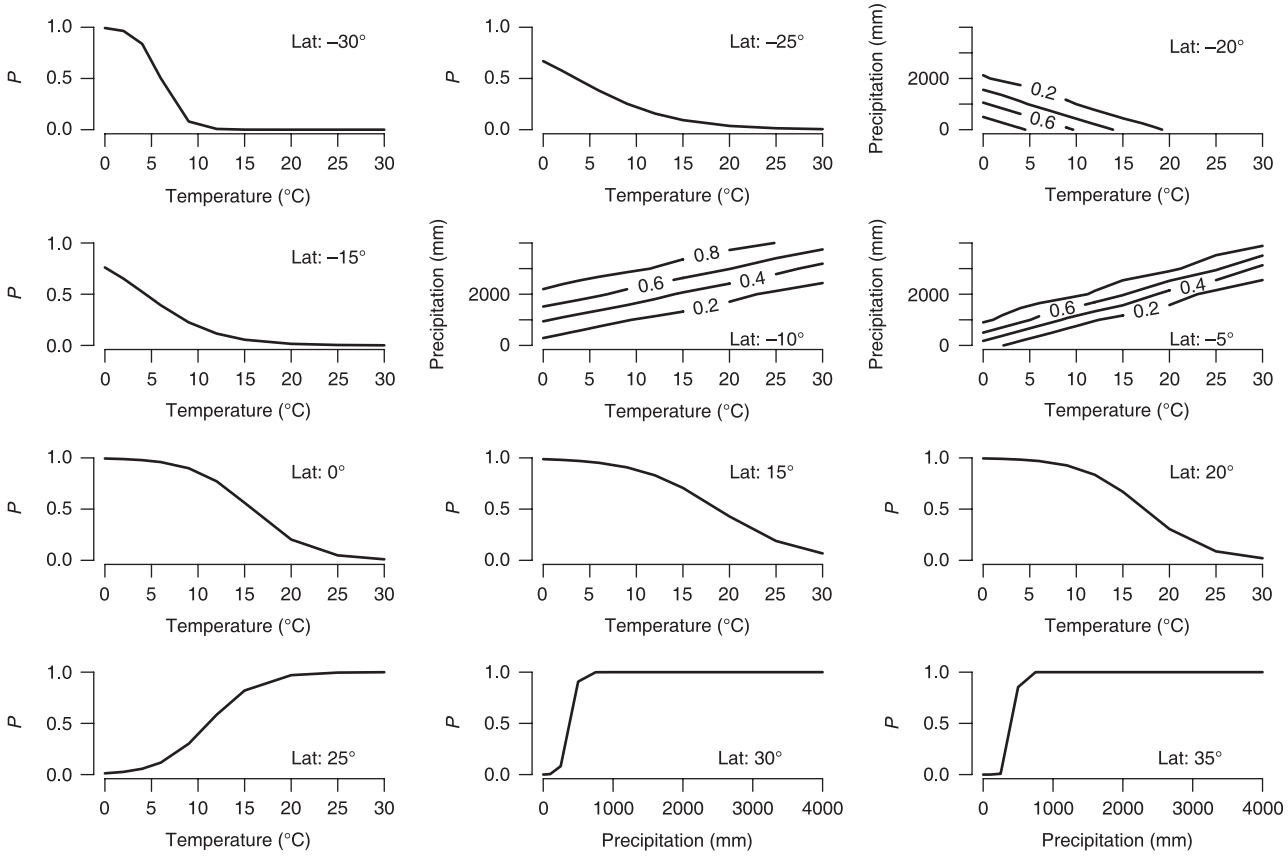

Figure 7 The probability of encountering tetra-, penta- or hexaploid vs. a diploid wild potato for bands of 5° latitude across the group's range (the latitude on the graphs are the midpoints), as a function of annual precipitation, mean temperature or both. Probabilities were estimated using logistic regression. Only significant predictors (Wald statistic, $P < 0.05$) were used in the graphs, and areas where only polyploids occur were omitted.

Intraspecific comparisons

Diploid populations of *S. leptophyes* (Fig. 8a) and *S. microdontum* (Fig. 8b) are much more widely distributed than their polyploid populations, whereas the distribution of diploid and triploid populations of *S. medians* (Fig. 8c) are similar. *Solanum microdontum* and *S. medians* appear to have a relatively large number of triploid populations at the margins of the range of the diploids. The polyploid populations of *S. oplocense* (Fig. 8d) have a much larger geographical distribution than the diploid populations. The only case of clear disjunct distributions between different cytotypes within a species is for *S. calvescens/S. chacoense*, assuming, as proposed by Brücher (1975), that these are conspecific (Fig. 8e; Appendix S3, footnote f).

DISCUSSION

Ploidy levels

We have shown how a quantitative analysis of individual reports of ploidy determination can provide new insights into the distribution of ploidy in a large and widespread group of plants, and can be used to estimate the number of cytotypes that await discovery. Given the low fertility, or even sterility, of triploids, and because many ploidy assessments in potato are from germplasm collected as seed, we suspect that triploids are particularly under-reported in the group. Triploids have been shown to be much more common than previously thought when extensive intrapopulation surveys are conducted (Husband, 2004). In contrast, six species are known only as triploids, and these species are likely to have diploid populations as well. The dynamics of triploids in wild potato populations deserves further research. We are not aware of any studies of wild potatoes that have extensively determined the distribution of cytotypes within populations (such as Baack, 2004), compared the fitness of different cytotypes within populations or between different habitats, or assessed the relative importance of reproduction by seed and tubers. *Solanum medians* would make an excellent species to study because it is relatively abundant and occurs in the relatively accessible coastal desert and lower slopes of the western Andes of Peru. Ochoa (1990) classified the cytotypes as morphologically distinct, with the triploids as var. *medians* and the diploids as var. *autumnale* Correll, but our observations of germplasm samples of these plants suggest that they are not worthy of taxonomic recognition (unpublished data).

Only two of the 187 wild potato species remain to be assessed for ploidy. *Solanum donachui* occurs in a remote area of the

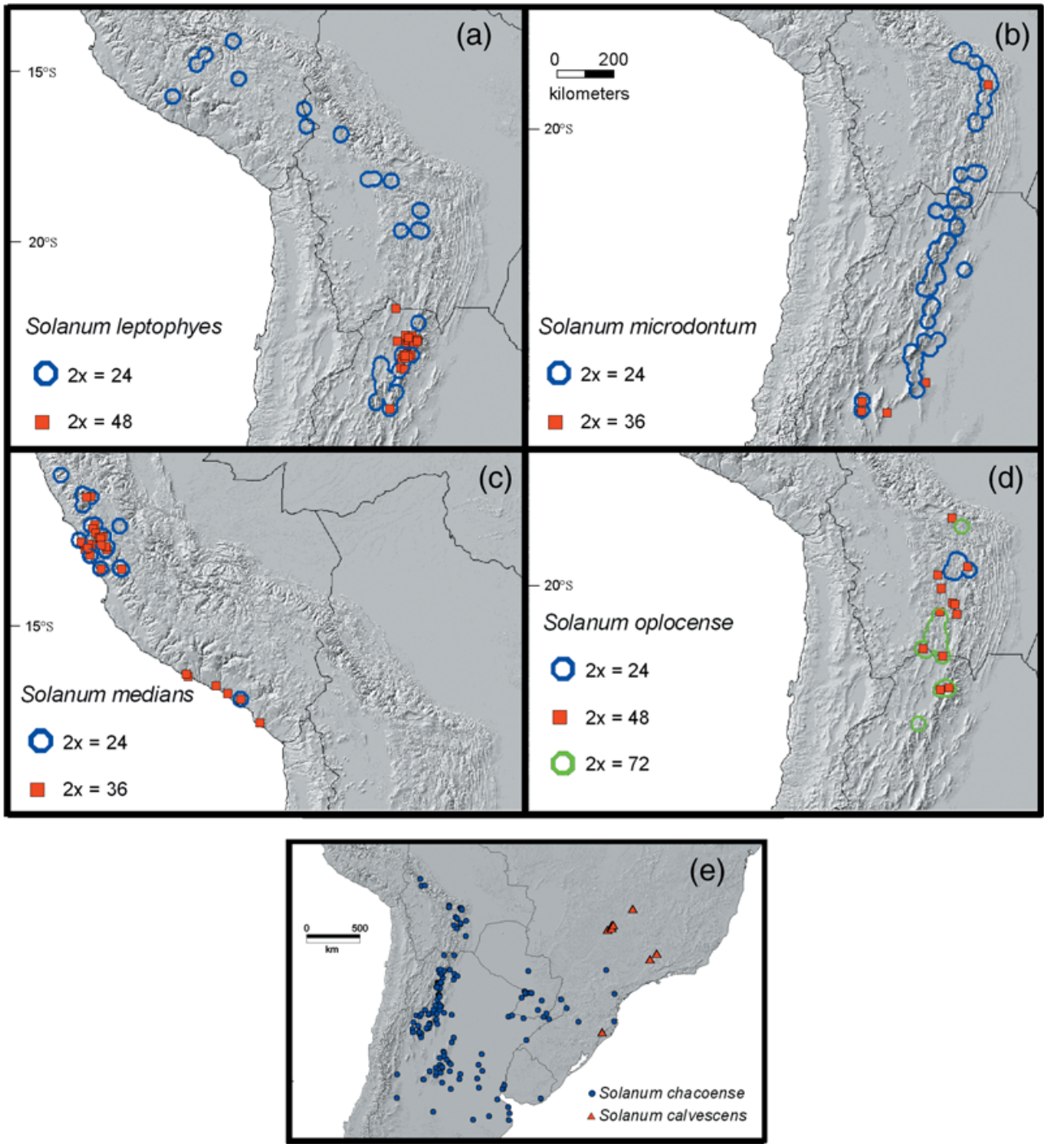

Figure 8 Distribution maps for cytotypes for four wild potato species (a–d) and for *S. calvescens* and the possibly conspecific (Brücher, 1975) *S. chacoense* (e). Maps have a Lambert azimuthal equal-area projection.

Sierra Nevada de Santa Marta in northern Colombia and has not yet been collected as germplasm. Germplasm of *S. woodsonii* (from Panama) has been collected (Spooner *et al.*, 2004) but ploidy has not yet been determined. All other species in southern Central America (Costa Rica and Panama) and northern South America (Venezuela and Colombia) are tetraploids, and we therefore expect that *S. donachui* and *S. woodsonii* are tetraploids also.

Geographical ranges and climatic distribution

While our results support the importance of polyploidy in range extensions they also underline the complexity of this phenomenon. Although we did not find support for the expectation of overall larger range sizes for polyploid species, the two most widespread species, by far, are tetraploids: *S. stoloniferum* in North and Central America and *S. acaule* in South America.

We examined the geographical distribution of five cases where there was intraspecific polymorphism for ploidy. In the four cases of a diploid/triploid combination, the triploid populations of *S. leptophyes* and *S. microdontum* always occurred in the extremes of these species distributions, except for *S. medians*, where triploids occurred throughout the range. In the case of *S. calvescens* (triploid *S. chacoense sensu* Brücher, 1975), the diploid and triploid populations are disjunct, lending some support to the idea of increased polyploidy formation at the extremes of the range of a species, resulting in range expansion. However, the cytotypes of other diploid/triploid species are sympatric, presumably because triploids have very low seed production and therefore limited dispersal ability. Therefore, rather than area expansion, *S. calvescens* may represent relict populations in an area where the diploid cytotype has become very rare or has gone extinct. Moreover, we only found one ploidy determination for *S. calvescens* and more ploidy determinations for this species are warranted. *Solanum oplocense* was the only case for which we have sufficient data to map intraspecific variation in even-numbered ploidy levels, and this species showed strong range expansion of polyploids.

The northern and southern extremes of the distribution of sect. *Petota* are occupied by diploids. But within the group's range, polyploids do frequently occur at ecological extremes. We found that triploid wild potatoes tend to occur in relatively warm and often dry areas, whereas species with higher ploidy level tend to occur in areas that are relatively cold. Polyploids also occurred in areas that are wetter than the areas where diploids occur. The evidence for the occurrence of polyploids at the edge of the ecological distribution of wild potatoes was particularly strong in our analysis by latitudinal bands. In this analysis, polyploids consistently occurred in colder areas than diploids (with one exception).

Only polyploids occurred in very wet areas from Colombia to Costa Rica. The absence of diploids and the low species richness there may be the result of a range extension of polyploids into the region from southern Colombia to Costa Rica, into atypical ecological niches for sect. *Petota*. Potatoes are herbaceous perennials adapted to climates with dry periods, during which they survive as dormant tubers, a trait of reduced advantage in areas that are warm and wet all year round. This notion is supported by the occurrence in the wettest areas in Central America (southern Mexico, Guatemala and Honduras) of the only two epiphytic (that is, occupying a relatively dry habitat) or near-epiphytic species of sect. *Petota*: *Solanum clarum* and *Solanum morelliforme* (Spooner *et al.*, 2004). This impressive range expansion by polyploids into an atypical environment for sect. *Petota* suggests that expansion of polyploids into new habitats does not necessarily have to occur in cold or recently disturbed areas.

Range expansion associated with polyploidy may have played an important role in the evolutionary history of the group. Based on ploidy, genome types and morphological data, Hawkes (1990) postulated that (diploid) wild potatoes originated in Mexico and expanded to South America, from where a newly evolved group returned to North America. This hypothesis was supported by chloroplast DNA evidence (Spooner *et al.*, 1991), but needs corroboration with more data, particularly nuclear markers. Distributional and ploidy data suggest a South American origin, however. The sister groups of potatoes (tomatoes and sect. *Etuberosum*) are all confined to South America. A South American origin also fits better with the large fraction of polyploids in the group's range in areas north of Peru, which can be interpreted as a signature of invasion into new habitats. In contrast, there is a striking dominance of diploids in the Cusco area, where species richness is highest. Diploids may have been well established and diversified there for a long time, creating fewer opportunities for invasion of new habitats by polyploids. Fjeldså *et al.* (1999) proposed that the high level of endemism of Andean birds in that area was caused by long-term climatic stability. The dominance of diploids in sect. *Petota* in this area lends some support to this theory. In contrast, the most widespread polyploid in Peru, *S. acaule*, occurs at high elevations, that is, in cold areas into which it may have expanded during interglacial periods.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 Cytological indices consulted

Appendix S2 Data base of ploidy reports of wild potatoes

Appendix S3 Summary of reports of ploidy determination in wild species of *Solanum* sect. *Petota*

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