Antioxidant capacity and secondary metabolites in four species of Andean tuber crops: native potato (Solanum sp.), mashua (Tropaeolum tuberosum Ruiz & Pavón), Oca (Oxalis tuberosa Molina) and ulluco (Ullucus tuberosus Caldas)

David Campos,1 Giuliana Noratto,2 Rosana Chirinos,1 Carlos Arbizu,3 Willian Roca3 and Luis Cisneros-Zevallos2

1Instituto de Biotecnología, Universidad Nacional Agraria-La Molina, Lima 12, Peru
2Department of Horticultural Sciences, Texas A&M University, College Station, TX 77843-2133, USA
3International Potato Center, Lima 12, Peru

Abstract: Four species of edible tubers endemic to and domesticated in the Andes, native potato (Solanum sp.), mashua (Tropaeolum tuberosum Ruiz & Pavón), oca (Oxalis tuberosa Molina) and ulluco (Ullucus tuberosus Caldas), were studied for their antioxidant capacity and associated secondary metabolites. The antioxidant capacity was measured using ABTS− radicals and total phenolics, carotenoids, anthocyanin, betaxanthin and betacyanin content were also characterized. The antioxidant capacity found in the crops studied ranged from 483 to 9800 µg trolox equiv. g−1, phenolics ranged from 0.41 to 3.37 mg chlorogenic acid equiv. g−1, anthocyanins ranged from 0.08 to 2.05 mg cyanidin 3-glucoside g−1 and carotenoids ranged from 1 to 25 µg β-carotene g−1. The content of bioactive compounds was high and variable between crops and within the genotypes studied. In general, mashua tubers showed the highest antioxidant capacity and phenolic, anthocyanin and carotenoid content compared with other crops. Ulluco was the only crop that contained betalains in the acid form of betaxanthins (22–96 µg g−1) and betacyanins (64 µg g−1) with no presence of carotenoids or anthocyanins. This is the first publication regarding the antioxidant capacity of and associated secondary metabolites in Andean tubers. This information can be useful in the identification of Andean tubers species and genotypes with potential value as a novel dietary source of antioxidants for food, and also for medicinal use.

Keywords: antioxidants; Andean tuber crops; potato; mashua; oca; ulluco

INTRODUCTION
There is a continuous search for new plant compounds with antioxidant potential. Interest in natural antioxidants has increased considerably in recent years.1–4 Antioxidants, which can neutralize free radicals, may be of central importance in the prevention of cancer and cardio- and cerebrovascular diseases.5–9 Many natural antioxidants exhibit a wide range of biological effects, including antibacterial, antiviral, anti-inflammatory, antiallergic, antithrombotic and vasodilatory activity.10 The Andean region is well known for its great genetic diversity in different types of crops, which unfortunately have been poorly studied. Andean crops show variability in colors, forms, sizes, primary nutrient constituents and bioactive secondary metabolites.

People from the Andean region have utilized native potato (Solanum sp.), mashua (Tropaeolum tuberosum Ruiz & Pavón), oca (Oxalis tuberosa Molina) and ulluco (Ullucus tuberosus Caldas) tubers for their nutritional and medicinal properties since ancient times. It is thought that the health-related properties of Andean tuber crops claimed from folklore use could be in part attributed to the antioxidants present in these crops. However, little is known about the chemical nature and identity of the bioactive compounds present. Hence there is a need for scientific data on the antioxidant content of these Andean crops in order to increase our understanding of their role in the diet and in reducing chronic diseases. These initial steps may lead to an increased antioxidant intake by breeding Andean crops with higher antioxidant activity.

There have been a few attempts at quantifying the nutritional value of Andean tubers,11,12 but this study is the first attempt to measure accurately the
antioxidant capacity and related bioactive compounds of a wide germplasm of different Andean tubers.

The objective of this study was to provide new data regarding Andean tuber crops as a source of antioxidant compounds and compare them with other commercial crops. The information obtained should stimulate an increase in the evaluation and conservation of tuber diversity within the Andean region and in the identification of these crops as new sources of functional foods.

**MATERIALS AND METHODS**

**Plant material**

Fifteen native potato (*Solanum* sp.), 14 oca genotypes (*Oxalis tuberosa* Molina), 15 ulluco (*Ullucus tuberosus* Caldas) and 11 mashua (*Tropaeolum tuberosum* Ruiz & Pavón) genotypes were supplied by the International Potato Center (CIP) (Lima, Peru). The tubers were harvested during June 2002 from CIP’s experimental fields in Huancayo (3700–3800 m), Peru. Strawberry was harvested during June 2002 from CIP’s experimental fields in Huancayo (3700–3800 m), Peru. Strawberry was analyzed for total phenolics (TPH), anthocyanins (ACY), carotenoids (CTC), betaxanthins (TBX), betacyanins (TBC), hydrophilic antioxidant capacity (HAC) and lipophilic antioxidant capacity (LAC). Strawberries were analyzed for ACY and TPH and betacyanins (TBC), hydrophilic antioxidant capacity (HAC) and lipophilic antioxidant capacity (LAC).

**Chemicals**

All solvents and other chemicals were of analytical grade and obtained from Merck (Darmstadt, Germany), J.T. Baker (Phillipsburg, NJ, USA) and Mallinckrodt (Phillipsburg, NJ, USA). 2,2′-Azinobis(3-ethylbenzthiazoline-6-sulfonic acid (ABTS) and Folin–Ciocalteu reagent (Catalog #F9252) were purchased from Sigma Aldrich (St Louis, MO, USA).

**Total phenolic compounds (TPH)**

Total phenolics were determined using the Folin–Ciocalteu reagent following the procedure reported by Swain and Hillis. A 5-g sample was homogenized with 20 mL of 95% ethanol to a uniform consistency using an Ultra-Turrax homogenizer and left at 4°C for 24 h before filtration. An aliquot of extract (0.5 mL) was diluted with 8 mL of water. Simultaneously, a blank sample was prepared with 95% ethanol and treated in the same way as the samples. The Folin–Ciocalteu reagent was diluted with water (1:7) and 0.5 mL were added to the diluted extracts, vortex mixed and allowed to react for 3 min. At 3 min, 1 mL of 0.5 mol L−1 Na2CO3 was added and allowed to react for 10 min. The absorbance was measured at 725 nm until a constant reading was reached. Chlorogenic acid was used as standard for the calibration curve and TPH were expressed as mg of chlorogenic acid equiv. g−1 fresh weight. A Genesys-5 UV–visible spectrophotometer (Milton Roy, New York, USA) was used for absorbance readings.

**Total anthocyanins (ACY)**

The method reported by Fuleki and Francis was used for ACY determination. A 5-g sample and 15 mL of solvent (85:15 95% ethanol–1.5 mol L−1 HCl) were homogenized as described above and left at 4°C for 24 h before filtration. A 2-mL volume of extract was transferred to a graduated cylinder and anthocyanin solvent was added to obtain a final volume of 100 mL. Hexane was added to remove any carotenoids present. Spectrophotometric readings at 535 nm were taken, subtracting the absorbance at 700 nm (due to turbidity). ACY were expressed as mg cyanidin 3-glucoside equiv. g−1 fresh weight, using a molar extinction coefficient of 25 965 L mol−1 cm−1 and a molecular weight of 449 g mol−1.

**Total carotenoids (TCT)**

The method reported by Talcott and Howard was used for measuring TCT. A 2-g sample with 20 mL of acetone–ethanol (1:1) solution containing 200 mg L−1 BHT was homogenized as described above before filtration. The filtrate was transferred into a graduated cylinder and solvent added to a final volume of 100 mL. A 50-mL volume of hexane and 25 mL of H2O were added and shaken vigorously before standing for 30 min to allow separation of phases to occur. The spectrophotometer was blanked with hexane and the absorbance of the hexane phase was measured at 470 nm. β-Carotene was used as a standard for the calibration curve and TCT was expressed as µg β-carotene equiv. g−1 fresh weight.

**Betaxanthins (TBX) and betacyanins (TBC)**

The method adapted from Cai and Corke was used for measuring betalains. A 5-g sample and 20 mL of solvent (McIlvaine buffer, pH 5.2) were homogenized for 2 min as described above. Solvent was added to a final volume of 50 mL before filtration. The spectrophotometer was blanked with McIlvaine buffer. The absorbance of the extract was measured at 476 nm for betaxanthin content (orange–yellow pigment) and 536 nm for betacyanin content (purple–red pigment). The content of total betaxanthins and betacyanins was calculated using absorbity values, E1%1cm, of 750 and 1120, respectively. Results were expressed as mg TBX or TBC g−1 fresh weight.

**Determination of antioxidant capacity**

Antioxidant capacity was determined by the ABTS method adapted from Arnao et al. A 5-g sample and...
25 mL of methanol were homogenized as described above and left at 4°C for 24 h before filtration. An aliquot of this extract was taken for measuring the hydrophilic antioxidant capacity (HAC). The pellet was mixed with 25 mL of dichloromethane and shaken for 15 min before filtration. An aliquot of the yellow–orange supernatant was taken for measuring of lipophilic antioxidant capacity (LAC). A 150 µL volume of extract was mixed with 2.85 mL of ABTS solution (0.1 absorbance, 734 nm) prepared as described by Awika et al.19 This mixture was allowed to react at 20°C until a steady absorbance was reached. Simultaneously, a 150-µL aliquot of methanol was treated in the same way as the sample and used as a control. The spectrophotometer was blanked with methanol and the decrease in absorbance due to antioxidant activity was recorded at 734 nm. Antioxidant capacity was calculated from a calibration curve developed for Trolox, providing a relative antioxidant capacity of the extracts compared with this standard and expressed as µg TE (trolox equiv.) g⁻¹ fresh weight.

**Statistical analysis**
SPSS for Windows version 11.0 was used for statistical analysis. Pearson correlation at the level of α = 0.01 and analysis of variance (ANOVA) with mean comparisons using Tukey’s multiple range test at α = 0.05 were performed. Results are expressed as average ± standard deviation (SD).

**RESULTS AND DISCUSSION**
The overall average moisture content of the genotypes studied in native potatoes, mashua, oca and ulluco tubers was ~71.5 ± 3.4, 89 ± 2.2, 83 ± 1.9 and 86.7 ± 1.7%, respectively, indicating a small variation of moisture content among the genotypes studied in each crop. In general, results expressed on dry or wet basis did not alter the overall ranking for each crop in relation to TPH, ACY, TCT, HAC and LAC in this study. We consider it meaningful to present the data on a wet or fresh basis since that is the way in which these crops are consumed and the way in which most references are available in the literature.

**Total phenolic content (TPH)**
Our results indicate that the TPH content for native potato ranged from 0.64 to 2.32 mg g⁻¹ (Fig. 1). Genotypes 707 132, 704 463 and 705 841 had the highest TPH contents with 2.32, 2.09 and 1.9 mg g⁻¹, respectively. These values are higher than those reported previously for purple potatoes (0.76–1.27 mg g⁻¹). In mashua tubers, the TPH ranged from 0.92 to 3.37 mg g⁻¹ (Fig. 2). Genotypes ARB-5241, DP-02-24 and AGM-5109 had the highest TPH with 3.37, 3.05 and 2.75 mg g⁻¹, respectively. Purple mashua genotypes presented higher TPH values, whereas lower values of TPH were found in yellow mashua genotypes. The TPH content of ARB-5241 was comparable to that of strawberries, used as a reference (3.35 mg g⁻¹). For oca tubers, the TPH ranged from 0.71 to 1.32 mg g⁻¹ (Fig. 3). Genotypes O-018-83, MU-31 and AAQ-5477 showed the highest TPH values with 1.32, 1.31 and 1.26 mg g⁻¹.
respectively. Oca genotypes with the highest TPH were purple, whereas lower TPH values were found in yellow genotypes. Ulluco tubers had the lowest TPH content compared with the other crops studied. The TPH of ulluco tubers ranged from 0.41 to 0.77 mg g⁻¹ (Fig. 4), with genotypes U-108-84, AJA-5275 and U-09-0122 showing the highest phenolic content with 0.77, 0.63 and 0.61 mg g⁻¹, respectively. The phenolics identified previously in ulluco include rutin, narcissin and kaempferol 3-β-D-glucopyranosyl)-β-D-glucopyranoside. In general, the TPH range values for the crops studied followed the descending order mashua ≥ oca ≥ native potato.

**Total anthocyanins (ACY)**
The ACY in the pigmented native potato tubers ranged from 0.08 to 0.8 mg g⁻¹ and was only present in some genotypes (Fig. 1). Genotypes 704 463 and 707 132 showed higher levels of ACY with 0.8 and 0.59 mg g⁻¹, respectively. The ACY values were comparable to those reported previously²⁰ for purple flesh potatoes, which ranged from 0.11 to 0.6 mg g⁻¹, and higher than the ACY content in strawberries (0.4 ± 0.13 mg g⁻¹, in this study). The high ACY content of native potatoes indicates that these red and purple flesh tuber genotypes may be a novel source of natural colorants. The ACY may constitute a significant fraction of the TPH. For example, the ACY/TPH ratio was highest (~0.38) in genotype 704 463 and ranged between 0.09 and 0.38 for all pigmented native potato samples.

The ACY in mashua pigmented genotypes ranged from 0.5 to 2.05 mg g⁻¹ (Fig. 2). This ACY content is higher than those reported²² for radish cv. Fuego (0.30 mg g⁻¹), red cabbage (0.25 mg g⁻¹), strawberry (0.15–0.3 mg g⁻¹) and red raspberry (0.3–0.4 mg g⁻¹). The highest amount was found in genotype DP-02-24, which is in the range reported for blueberry,²³ 1.38–3.85 mg g⁻¹. The ACY in mashua tubers seems to be a significant component of the TPH in the pigmented genotypes. For example, the ACY/TPH fraction ranged between ~0.3 and 0.67.

For oca pigmented tubers, the ACY ranged from 0.14 to 1.3 mg g⁻¹ (Fig. 3). The highest amount was found in MU-31 and seems to be concentrated mostly in the tuber skin. For pigmented tubers, the ACY/TPH fraction ranged from 0.14 to 0.9. The ACY/TPH fraction was low (0.14) in genotype PICA-HI-92OC, owing to the relatively high TPH values, whereas for genotype MU-31, the fraction was high (0.9) owing to the high ACY content. On the other hand, our results showed that ulluco tubers do not contain anthocyanins. In general, the ACY range values of the crops studied followed the descending order mashua ≥ oca ≥ native potato. The presence or not of ACY and the differing proportions of ACY observed indicate that the genotypes studied in each type of crop would have different qualitative and quantitative phenolic profiles.

**Total carotenoids (TCT)**
The TCT in native potatoes ranged from 2 to 5 µg g⁻¹ (Table 1), these values being higher than those reported previously for commercial varieties,²⁴ ²⁵ which are in the range 0.27–3.43 µg g⁻¹. The 705 468 genotype had the highest carotenoid content with 5 µg g⁻¹. Interestingly, only one red pigmented genotype (705 024) presented carotenoids, phenolics and anthocyanins in the same tuber. In general, tubers with carotenoids tended visually to correlate with flesh yellow intensity. Violaxanthin is considered the main potato carotenoid reported in previous studies. Followed by lutein, antheraxanthin and others.²⁶ Lutein has attracted interest since high blood serum levels are correlated with a reduced risk for age-related macular degeneration in humans (AMD).²⁵ ²⁷

In mashua tubers, the TCT ranged from 1 to 25 µg β-carotene g⁻¹ (Table 2). Genotypes ARB-5576, M6COL2C and DP-0207 had the highest carotenoid contents with 25, 23 and 21 µg g⁻¹, respectively. The carotenoid content of mashua tubers is relatively high compared with commercial potatoes²⁴ ²⁵ and those found in native potatoes in this study, and also the carotenoid content in papaya²⁸ (4.08 µg g⁻¹). However, TCT in mashua are lower than those reported²⁸ for tomato (56–210 µg g⁻¹), mango (74.3 µg g⁻¹) and carrot (90 ± 16 µg g⁻¹ in this study).

For oca tubers, the TCT ranged from 2 to 25 µg β-carotene g⁻¹ (Table 3). Genotypes AJA-5245 and AJA-5270 had the highest carotenoid content with 25 and 17 µg β-carotene g⁻¹, respectively. Genotype AAQ-5477 showed high ACY, TCT and TPH content among all oca genotypes studied. In the case of ulluco, the results indicate that these tubers do not contain carotenoids in the pigmented yellow tissue. According to the present results, the carotenoid content range values for the crops studied followed the descending order mashua ≥ oca ≥ native potato.

**Betaxanthins (TBX) and betacyanins (TBC)**
By using absorption spectra, the aqueous solubility properties and the response to alkaline (change to
a stable yellow color) and acidic conditions (color disappearance on boiling), 29 it was found that the pigments in ulluco correspond to betalains in the base form of betacyanins (red pigment, \( \lambda_{\text{max}} = 535–540 \text{ nm} \)) and the acid form of betaxanthins (yellow pigment, \( \lambda_{\text{max}} = 453–475 \text{ nm} \)). The results indicate that TBX in ulluco tubers ranged from 22 to 96 µg g\(^{-1} \) (Fig. 4). The highest amount was found in genotypes CLC-004 and U-09-0122 with 96 and 83 µg g\(^{-1} \), respectively. In general, these pigments have been shown to be a potential source of both natural antioxidants and natural colorants in Amaranthaceae. 30 Only genotype AQP-5454, which corresponds to a red skin ulluco tuber- presented betacyanins (TBC = 64 µg g\(^{-1} \)).

**Hydrophilic antioxidant capacity (HAC)**

The HAC obtained for native potatoes ranged from 860 to 3780 µg TE g\(^{-1} \) (Fig. 1). Genotypes 705 841, 704 463, and 702 961 showed the highest HAC values with 3780, 3369 and 2473 µg TE g\(^{-1} \), respectively. Potatoes are known to contain water-soluble phenolic antioxidants that act as radical scavengers such as quercetin and chlorogenic acid. 31 We found that a high correlation between HAC and TPH for different genotypes in a certain type of crop would only be possible if the genotypes have phenolic compounds with similar antioxidant properties (e.g. similar proton-donor properties). Since the correlation obtained is low, we hypothesize that the studied native potatoes had different phenolic profiles (qualitative,
quantitative or both) with different antioxidant properties. Furthermore, when HAC is expressed on a phenolic basis (defined as the HAC/TPH ratio in this study), this specific HAC ranged from 1066 to 2294 mg TE g⁻¹ chlorogenic acid equiv. This indicates that the phenolics present in some of the genotypes showed a higher antioxidant capacity to stabilize a greater number of free radicals than others. The specific HAC values obtained are comparable to those reported previously for blueberries (685–1966 mg TE g⁻¹ phenolics) and higher than for blackberries. When the HAC is expressed on a phenolic basis, the values obtained ranged from 729 to 3052 mg TE g⁻¹ phenolics. When the HAC is expressed on a phenolic basis, the range from 1935 to 3614 mg TE g⁻¹ phenolics) and higher than for blackberries.32

When HAC is expressed on a phenolic basis, the highest specific HAC among the ulluco genotypes was found in genotype DP-03-43 with 2322 mg TE g⁻¹ chlorogenic acid equiv. A low correlation between HAC and TPH was observed ($r^2 = 0.64, P = 0.00$), most likely due to different phenolic profiles among ulluco cultivars. In general, the trend observed was an increased antioxidant capacity for genotypes with higher phenolic content (Fig. 4). Among the phenolics present in ulluco,21 the flavonoid kaempferol has been reported to exhibit strong antioxidant activity,36,37 and to inhibit hemolysis, lipid peroxidation and superoxide radical generation.38 On the other hand, HAC and TBX were not correlated, suggesting that the TBX does not contribute to the HAC in ulluco. According to the results obtained, the HAC range values for the crops studied followed the descending order mashua $\geq$ oca $\geq$ native potato $\geq$ ulluco.

**Lipophilic antioxidant capacity (LAC)**

In native potatoes, the LAC ranged from and 115 to 361 µg TE g⁻¹ (Table 1). Genotypes 703 844, 703 286 and 707 132 showed the highest LAC values with 361, 357 and 321 µg TE g⁻¹, respectively. Interestingly, two genotypes lacking carotenoids showed LAC properties suggesting the presence of lipophilic compounds other than carotenoids with radical scavenging activity. Among the native potatoes, genotypes 705 841, 704 463 and 707 132 showed the highest total antioxidant capacity (lipophilic + hydrophilic) with 3932, 3500 and 2794 µg TE g⁻¹, respectively. The lipophilic fraction of native potatoes contributed only 3.7–24.5% of the total antioxidant capacity values.

For mashua tubers, the LAC ranged from 93 to 279 µg TE g⁻¹ (Table 2). Genotypes M6COL2C, ARV-5366 and DP-02-03 showed the highest LAC values with 279, 225 and 224 µg TE g⁻¹, respectively. In mashua, LAC was observed only in genotypes that had carotenoids. Genotypes ARB-5241 and AGM-5109 presented LAC values (1346 and 1163 µg TE g⁻¹ DW, respectively) comparable to tomato (1425 µg TE g⁻¹ DW). The correlation between LAC and TCT was very low ($r^2 = 0.14, P = 0.058$), suggesting that the carotenoid profiles between genotypes were different. In general, genotypes ARB-5241, DP-02-24 and ARV-5366 had the highest total antioxidant capacity (lipophilic + hydrophilic) with 10 002, 9309 and 8092 µg TE g⁻¹, respectively. The lipophilic fraction contributed 2–19% to the total antioxidant capacity values for mashua tubers.

The LAC of oca tubers ranged from 69 to 320 µg TE g⁻¹, with genotypes AAQ-5477, COC-537 and ATT-5466 showing the highest LAC values with 320, 268 and 219 µg TE g⁻¹, respectively (Table 3). There is no correlation between LAC and TCT in oca tubers, most likely owing to different profiles of carotenoids present in the different genotypes. Genotypes O-018–83, AAQ-5477 and MU-31 showed total antioxidant capacities (lipophilic + hydrophilic) of 4952, 4716 and 4070 µg TE g⁻¹, respectively. The lipophilic fraction

---

**Table 1.** LAC values for native potatoes.

<table>
<thead>
<tr>
<th>Genotype</th>
<th>LAC (µg TE g⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>703 844</td>
<td>361</td>
</tr>
<tr>
<td>703 286</td>
<td>357</td>
</tr>
<tr>
<td>707 132</td>
<td>321</td>
</tr>
</tbody>
</table>

---

**Table 2.** LAC values for mashua tubers.

<table>
<thead>
<tr>
<th>Genotype</th>
<th>LAC (µg TE g⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>M6COL2C</td>
<td>279</td>
</tr>
<tr>
<td>ARV-5366</td>
<td>225</td>
</tr>
<tr>
<td>DP-02-03</td>
<td>224</td>
</tr>
</tbody>
</table>

---

**Table 3.** LAC values for oca tubers.

<table>
<thead>
<tr>
<th>Genotype</th>
<th>LAC (µg TE g⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>AAQ-5477</td>
<td>320</td>
</tr>
<tr>
<td>COC-537</td>
<td>268</td>
</tr>
<tr>
<td>ATT-5466</td>
<td>219</td>
</tr>
</tbody>
</table>

---

D Campos *et al.*


DOI: 10.1002/jsfa
Antioxidants in Andean tuber crops

Figure 5. Andean tubers with high antioxidant capacity: (A) native potato 707 132; (B) mashua ARB-5241; (C) oca O-018-83; (D) ulluco U-108-84.

contributed 1.9–10.2% to the total antioxidant capacity values for oca tubers.

For ulluco tubers, our results indicate that they do not present LAC for any of the genotypes studied. In general, the LAC value ranges obtained for potatoes, mashua and oca tubers were similar. The total antioxidant capacity of these crops is mainly attributed to the phenolic compounds, which are present in higher amounts than carotenoids.

CONCLUSIONS
This survey of Andean tuber germplasm for antioxidant compounds confirms that each type of crop studied can be considered as an excellent source of dietary phytochemicals (Fig. 5). The phytochemicals responsible for the antioxidant capacity are related to the phenolics and carotenoids present in each tuber. The antioxidant values of these tuber crops are higher than or comparable to known sources of natural antioxidants, such as blueberries, indicating that these crops have the potential to be considered as important novel sources of nutraceuticals. These Andean tuber crops hold great promise for producing new and unique healthy, functional products for the benefit of producers and consumers.

ACKNOWLEDGEMENTS
Carla Rios, Daniel Segura and Katherine Alejandro are thanked for technical assistance.

REFERENCES
11 King SR and Gershoff SN, Nutritional evaluation of three underexploited Andean tubers: Oxalis tuberosa (Oxalidaceae), Ullucus tuberosus (Basellaceae) and Tropaeolum tuberosum (Tropaeolaceae). Econ Bot 41:503–511 (1987).