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Basic morphology and bromatology of *Oxalistuberosa* tubers from the ex situ collection of "oca" cultivarsat Yachay Botanical Garden, Ecuador

Trabajo de integración curricular presentado como requisito para la obtención del título de Bióloga

Autora:
Hidalgo Bermeo, Nataly Eliseth

Tutor:
Dr. Romero Saltos, Hugo Geovanny

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A Dios y a mi familia.

Nataly Hidalgo Bermeo

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RESUMEN

La "oca", *Oxalis tuberosa* Molina, es un cultivo icónico de América del Sur cuya importancia histórica como alimento básico en los Andes es innegable. La especie presentan muchas variedades de tubérculos, caracterizados por formas y patrones de color distintivos. Sin embargo, en la actualidad, algunas de las variedades están desapareciendo debido a la pérdida de cultura en su producción y consumo. En esta tesis, se describe la morfología y bromatología básica de los morfotipos (variedades) de *O. tuberosa* presentes en la colección ex situ que se mantiene en el Jardín Botánico Yachay (JBY), como parte de los esfuerzos de conservación y revalorización de este emblemático tubérculo andino en Ecuador.

En base a patrones de color y tamaño, se identificaron 10 morfotipos distribuidos en todo el Ecuador, siendo las provincias de Azuay, Chimborazo, Imbabura y Tungurahua las de mayor diversidad (7 morfotipos en cada una). Al contrastar estos resultados con investigaciones previas, se evidencia que las variedades de *O. tuberosa* han ido cambiando su importancia relativa en diferentes provincias a través de los años. Además, al examinar el tamaño de los tubérculos, se sugiere que la longitud del tubérculo parece estar más controlada por factores genéticos que por factores ambientales.

Nueve de los 10 morfotipos de *O. tuberosa* fueron analizados bromatológicamente mediante protocolos AOAC e NTE INEN 1334-2. Se midieron algunos macronutrientes (Ca, K, Mg y Na) y micronutrientes (Cu, Fe, Mn y Zn), además de cenizas, acidez, humedad, grasa, proteína, carbohidratos y energía. No se observó mayor diferencia en el contenido nutricional entre los morfotipos analizados. Además, se realizó una comparación de los contenidos nutritivos de los tubérculos de *O. tuberosa* con respecto a alimentos con alto valor nutritivo, comunes en la dieta humana. Como resultado de este análisis, se concluyó que los tubérculos de *O. tuberosa* no constituyen una fuente importante de Ca ($\overline{X} = 0.0047\%$); destacan como una fuente significativa de Fe ($\overline{X} = 0.001\%$); tienen elevada acidez ($\overline{X} = 0.07\%$) atribuible a la concentración relativamente alta de ácido oxálico; son una alternativa saludable por su baja concentración de grasa ($\overline{X} = 0.9\%$); y pueden aportar una cantidad razonable de proteínas ($\overline{X} = 5.2\%$) y carbohidratos ($\overline{X} = 10.1\%$).

En conclusión, los datos obtenidos en este estudio pueden ayudar a garantizar la soberanía alimentaria del Ecuador, pero para lograrlo es necesario emprender proyectos de conservación in situ y ex situ de germoplasma de todas las variedades de *O. tuberosa*. ¡Incluyamos a *O. tuberosa* en nuestra dieta diaria!

Palabras Clave:

Oxalis tuberosa, conservación, morfotipos, bromatología, Ecuador.

ABSTRACT

The "oca", *Oxalis tuberosa* Molina, is an iconic South American crop whose historical importance as a staple food in the Andes is undeniable. The species present many tuber cultivars, characterized by distinctive shapes and color patterns. However, nowadays, some of the cultivars are disappearing due to the loss of culture in their production and consumption. In this thesis, I describe the basic morphology and bromatology of the *O. tuberosa* morphotypes (cultivars) present in the ex situ collection that is maintained at Yachay Botanical Garden (YBG), as part of the conservation and revaluation efforts of this emblematic Andean tuber in Ecuador.

Based on color and size patterns, 10 morphotypes distributed throughout Ecuador were identified, with the provinces of Azuay, Chimborazo, Imbabura and Tungurahua having the greatest diversity (7 morphotypes in each). When contrasting these results with previous research, it is evident that *O. tuberosa* varieties have been changing their relative importance in different provinces throughout the years. In addition, by examining tuber size, it is suggested that tuber length seems to be more controlled by genetic factors than by environmental factors.

Nine of the 10 *O. tuberosa* morphotypes were analyzed bromatologically using AOAC and NTE INEN 1334-2 protocols. I measured some macronutrients (Ca, K, Mg and Na) and micronutrients (Cu, Fe, Mn and Zn), in addition to ash, acidity, moisture, fat, protein, carbohydrates and energy. No major difference in nutritional content was observed among the morphotypes analyzed. In addition, I compared the nutritional content of *O. tuberosa* tubers with respect to highly nutritive foods common in the human diet. As a result of this analysis, it was concluded that *O. tuberosa* tubers are not an important source of Ca ($\overline{X} = 0.0047\%$); stand out as a significant source of Fe ($\overline{X} = 0.001\%$); have high acidity ($\overline{X} = 0.07\%$) attributable to the relatively high concentration of oxalic acid; are a healthy alternative given their low fat concentration ($\overline{X} = 0.9\%$); and can provide a reasonable amount of proteins ($\overline{X} = 5.2\%$) and carbohydrates ($\overline{X} = 10.1\%$).

In conclusion, the data obtained in this study can help to ensure Ecuador's food sovereignty, but to achieve this it is necessary to undertake in situ and ex situ germplasm conservation projects of all *O. tuberosa* cultivars. Let us all include *O. tuberosa* in our daily diet!

Keywords:

Oxalis tuberosa, conservation, morphology, bromatology, Ecuador.

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INTRODUCTION

OXALIS TUBEROSA: AN ICONIC ANDEAN TUBER

Oxalis tuberosa Molina (Oxalidaceae) (Molina, 1782), locally known as “oca”, is a native species from the Andes, distributed from Colombia to Argentina, occurring at altitudes ranging from 1500 m to 4000 m. There are also ex situ cultivars in New Zealand, Tasmania, México, United States, and Europe (GBIF, 2023). Tubers of *O. tuberosa* have been a staple crop for millennia (Hawkes, 1989). In fact, just 70 years ago, it was considered the second most important tuber in the Andes, after the potato (Hawkes, 1989). Nowadays, however, migration of young labor from rural areas to the city, along with devaluation of some native cultivars, have drastically reduced production, consumption, and diversity of *O. tuberosa* cultivars in Ecuador (Barrera et al., 2004).

Botanically, according to NRC (1989), *O. tuberosa* is described as an annual tuberous herb with a height variation of 30–80 cm; leaves are alternate, trifoliolate, with petioles 2–11 cm long; cyme inflorescences are organized in groups of 4–5 flowers each; each flower is composed by a calix of 5 sepals and by a corolla of 5 petals basally connated; petals are yellow with irregular margins and purple to red longitudinal lines; fruit is a capsule with 5 loci, each with 1–3 seeds (**Figure 1**).

EVOLUTIONARY ORIGIN AND DOMESTICATION OF *OXALIS TUBEROSA*

The origin of *O. tuberosa* is still debatable given the incongruence among the results of different studies (e.g., Emshwiller & Doyle, 2002; Emshwiller et al., 2009). The most accepted theory is that it probably originated from the hybridization between *Oxalis picchensis* and an unknown *Oxalis* from the Andes of Peru or Bolivia (Hawkes, 1989; Emshwiller & Doyle, 2002; Pearsall, 2008). This domestication event probably happened at least 7500 years ago (Smith, 1980), when Neotropical agriculture started to become established (Piperno, 2011). As a result, an octaploid was presumably created (2n=8x=64; Emshwiller et al., 2009), although other ploidies are also reported in the literature (e.g., Emshwiller & Doyle, 2002). Even those *Oxalis* species that do not produce tubers cannot be excluded from the artificial origin of *O. tuberosa* (Emshwiller et al., 2009). To a good extent, these uncertainties about the origin of this species are caused by an incomplete

sampling of all *Oxalis* taxa (Emshwiller et al., 2009) and to the limited variability of the molecular markers used (Emshwiller & Doyle, 2002).

Throughout millennia, as part of the domestication process, traditional farmers have created dozens of phenotypically different cultivars, which historically have been appreciated and commercialized (Espinosa et al., 1996; Rosero, 2010). In Ecuador, according to Espinosa et al. (1996), the cultivars that are the most produced and sold in the local markets of Ecuador are: (1) the white ("blanca") cultivar because it apparently has better production at high altitudes and can be preserved longer; and (2) the yellow-cream ("chaucha") cultivar because it can adapt to lower altitudes (e.g., 2800 m), has a shorter growing period, and is relatively sweet.

GENETIC DIVERSITY OF *OXALIS TUBEROSA*

Morphological variation

Tubers of *O. tuberosa* present a great phenotypic variation in terms of shape, size, color (from white to dark purple) and texture. To a least degree, shape, size and color of stems, leaves and flowers also vary among cultivars (pers. obs.). This phenotypic variation certainly is the result of the artificial selection pressure throughout the domestication history of *O. tuberosa* in the Andes. For example, in the Candelaria area, Bolivia, approximately 30 cultivars have been detected, from which 18 have been described in detail (Cadima et al., 2004). Over time, this high phenotypic variation of tubers has allowed the selection of cultivars better adapted to certain climatic conditions, or particular agro-industrial or culinary applications (e.g., Sánchez, 2022; Miranda, 2013).

In Ecuador, a few studies on the morphological characterization of *O. tuberosa* have been conducted. Normally, in order to systematically describe *O. tuberosa* germplasm, one must characterize the distribution of different colors on the tuber epidermis and pulp, along with tuber shape, stem color, leaf color, plant stature, crop productivity, among other parameters (IPGRI/CIP, 2001). In this context, Tapia et al. (1996) recognized 31 cultivars of *O. tuberosa* at the ex situ collection that is maintained in vitro at the germplasm bank of the National Institute for Agropecuary Research (Instituto Nacional de Investigaciones Agropecuarias, INIAP), south of Quito. Almost a decade later, using

the same ex situ collection, Tapia et al. (2004) only recognized 20 morphotypes which were separated into three groups: (1) low-stature plants with good tuber productivity and low disease incidence; (2) plants with intermediate morphological characteristics (in relation to groups 1 and 3); and, (3) relatively tall plants but with low tuber productivity. In a more recent report, Navarrete-Mier et al. (2017) recognized 11 morphotypes/cultivars based on a general analysis of 259[1] accessions of *O. tuberosa* collected throughout Ecuador, maintained at Yachay Botanical Garden (YBG).

Allelic and genotypic variation

O. tuberosa presents an auto-incompatibility system, which is why sexual reproduction is not common (Pissard et al., 2008). Under this scenario, genetic diversity is diminished and vegetative (asexual) reproduction by tubers becomes more common. Given the limited sexual reproduction, new *O. tuberosa* genotypes could only appear by: (1) somatic mutation; (2) crossing among preexistent cultivars; or, (3) hybridization with non-domesticated relatives (wild relatives) (Pissard et al., 2006).

At the molecular level, there are several studies that have assessed the genetic diversity of *O. tuberosa* populations. Inter-Simple Sequence Repeat (ISSR) markers showed that *O. tuberosa* populations from the central and southern Andes had low genetic distance among them, although the populations from Perú constituted a distinctive group of high diversity (Pissard et al., 2006). In Ecuador, using Random Amplified Polymorphic DNA (RAPD) markers, about 20 *O. tuberosa* genotypes were identified (Piedra, 2002). However, although Amplified Fragment-Length Polymorphisms (AFLP), ISSR and RAPD markers can solve relations between species or individuals closely related, they have the disadvantage of being dominant and that their fragments are anonymous (D. Harpke, pers. comm.). Modern molecular biology techniques avoided this problem by using data based on Genome-wide Single Nucleotide Polymorphisms (SNPs) which represent a larger part of the genome. These data can be obtained by sequencing DNA associated to restriction sites (RAD-Seq: Restriction Site Associated DNA Sequencing; Miller et al., 2006; Baird et al., 2008), in particular by applying the Genotyping-by-Sequencing technique (GBS) (Elshire et al., 2011). In this technique, SNPs are found

[1] By early 2020, 339 accessions had been collected for the ex situ *O. tuberosa* collection at YBG (H. Romero-Saltos, pers. com.).

sequencing short DNA regions that are adjacent to the cutting sites of certain restriction enzymes. More precisely, by using enzymes sensible to methylation, the sequences obtained by GBS correspond to sub-methylated DNA regions which most probably associate to codifying regions (Elshire et al., 2011). Among other applications, this type of data can be used to clearly identify hybridization (Eaton & Ree, 2013) and the parental geographic origin of polyploids (Raca et al., 2023).

CHEMICAL COMPOSITION OF *OXALIS TUBEROSA* TUBERS

Tubers of *O. tuberosa* possess a variety of biological compounds such as proteins, carbohydrates, fiber, lipids, minerals (macro- and micronutrients), vitamins, and a significant amount of oxalic acid (e.g., Espín et al., 2001; King & Gershoff, 1987). They also contain secondary metabolites (e.g., phenolics) with antioxidant and anti-inflammatory properties (e.g., Chirinos et al., 2009; King & Gershoff, 1987; León et al., 2011; Zhu & Cui, 2019). The nutritional and bioactive composition of *O. tuberosa* tubers vary depending on the cultivar and crop conditions, and thus it can be influenced by abiotic factors such as climate or soil fertility (Valdivia et al., 1999). Below, I present a brief literature review about the chemical composition of *O. tuberosa* tubers, based on bromatological data compiled from 19 studies in six countries (Argentina, Perú, Ecuador, Colombia, México and USA). A preliminary succinct review of this compiled data, based on 16 studies, was presented by Hidalgo-Bermeo et al. (2022) during a local scientific event.

Primary metabolites

Regarding **carbohydrates**, the literature reports highly variable data. This high variability may be caused by different biotic or abiotic factors during pre-harvest, harvest or post-harvest periods. These may include factors such as tuber maturity, sun exposure (Yenque et al., 2008), or the use of different analytical methods. Indeed, carbohydrates have been reported to vary from 10.41% (León et al., 2011) to 88.8% (King & Gershoff, 1987), while starch has been reported to vary from 7.2% (Cajamarca, 2010) to 99.21% (Valcárcel-Yamani et al., 2013).

Regarding **lipids**, it is worth mentioning that tubers of *O. tuberosa* are low in fat, varying from 0.4% (Reyes et al., 2009) to 1.1% (Reyes et al., 2009), while for **proteins,**

tubers of *O. tuberosa* can have a concentration up to 9.8% (Cajamarca, 2010). In addition, tubers of *O. tuberosa* have a variety of **vitamins** important for human metabolism, such as vitamin C, vitamin A and vitamin B. Vitamin C is relatively concentrated, varying from 0.0009% (Reyes et al., 2009) to 0.23% (Duke, 2001), while vitamin A and vitamin B complex—including thiamin (B1), riboflavin (B2) and niacin (B3)—occur in relatively low concentrations (<0.001%; Collazos et al., 1952; León et al., 2011).

Secondary metabolites

Secondary metabolites are organic compounds that are not essential for plant development. During plant development, these complex chemical compounds modify certain properties such as smell, color, taste, texture, among others. They function as pathogen or herbivores deterrents, as pollinator attractants, or as mediators to cope with stressful biotic or abiotic factors (Bennett & Wallsgrove, 1994). In this sense, secondary metabolites have important functions for plant adaptation and survival (Cisneros-Zevallos, 2003).

Campos et al. (2006) described the following secondary metabolites in *O. tuberosa*: (1) phenols (0.71–1.32 mg/g), which had higher concentration in purple tubers than in yellow tubers; (2) anthocyanins (0.14–1.3 mg/g), which were also more highly concentrated in purple tubers; and, (3) carotenoids (2–25 µg β-carotene/g), which tended to correlate with the yellow color intensity of the pulp. The higher concentration of phenols in purple tubers implies that they have good antioxidant capacity.

Minerals (nutrients)

For plants, minerals are those elements from the periodic table that are essential for their metabolism. These minerals, called "nutrients", are needed in relatively low amounts and are classified in two categories depending on the amount they are needed: (1) macronutrients (N, P, K, Ca, Mg, Na, Cl, S); and (2) micronutrients (Fe, Zn, Se, Cu, I, Mn, Cr). For tubers of *O. tuberosa*, the nutrients most commonly reported in the literature are Ca, Fe and P (Hidalgo-Bermeo et al., 2022). [Ca] can vary from 0,002% (Tapia, 1990) to 0,052% (Reyes et al., 2009); [Fe] can vary from 0,0008% (Duke, 2001) to 0,013% (León et al., 2011); and [P] can vary from 0,028% (León et al., 2011) to 0,21% (Duke, 2001). Other elements that have been measured in tubers of *O. tuberosa*, although

sporadically, are Mg, K, Na, Zn, Cu, Mn and I. Plant nutrients contribute to our health because they play important roles in different biological processes, such as bone formation and maintenance, cardiac rhythm regulation, blood oxygen transport, among others (Luna et al., 2003).

Oxalic acid

Oxalic acid ($C_2H_2O_4$), a dicarboxylic acid that in plants can combine with Ca to form calcium oxalate, naturally accumulates in tubers of *O. tuberosa*, giving them a characteristic sour taste (Stevens, 2001). Oxalic acid concentration can vary depending on the *O. tuberosa* cultivar, from 80 mg/100g (Ross et al., 1999) to 221 mg/100g fresh weight (Sangketkit et al., 1999). These concentrations are equivalent to the oxalate content present in some foods common in the modern human diet: spinach or chocolate, for example (Sangketkit et al., 1999). Castañeta et al. (2022) showed that acidity (certainly correlated with oxalate content) diminished in tubers exposed to the sun for several days, but not significantly. Therefore, the sensation of acidity loss of tubers after sun exposure, that people commonly report, is probably an effect of carbohydrate accumulation masking the oxalate taste (Yenque et al., 2008).

Moisture

Moisture an important parameter, because it can influence tuber quality and durability. For tubers of *O. tuberosa*, average moisture content is high (83 ± 1.9%; Campos et al., 2006), which makes them prone to decomposition during storage, thus affecting their nutritional quality and commercial value.

JUSTIFICATION AND HISTORICAL CONTEXT

Tubers of *O. tuberosa* are disappearing in Ecuador and are in risk of genetic erosion (Pozo, 2000). Efforts to conserve this species and its cultivars must not only have a socio-economic focus, but also an ethical focus that values the ancestral practices that led to the creation of many *O. tuberosa* cultivars through millennia. Because genetic diversity has an intrinsic value that is incommensurable, Yachay Botanical Garden (YBG), in alignment with its mission, created from 2015 to 2020 an ex situ collection (*in vivo* germplasm bank) of *O. tuberosa* cultivars from Ecuador. This long-term initiative is led

by Dr. Hugo Romero-Saltos and has been supported by his many collaborators throughout the years, including several professionals and students. In total, 339 *O. tuberosa* accessions donated by ca. 190 farmers have been collected from the provinces of Carchi, Imbabura, Pichincha, Cotopaxi, Tungurahua, Chimborazo, Bolívar, Cañar, Azuay and Loja. At the moment, approximately 60 accessions survive at the YBG ex situ collection.

OBJECTIVE OF THIS STUDY

One particularly strategy to promote the conservation of *O. tuberosa* is to reconsider the nutritional value of their tubers in the context of a healthy diet. Yet, this initiative first needs an assessment of the geographic distribution of *O. tuberosa* cultivars still present in Ecuador, along with their corresponding morphological characterization. In this context, the objective of this thesis is to characterize the basic morphology (e.g., color, shape, etc.) and bromatology (food science chemical analysis) of the *O. tuberosa* tubers (accessions) present at the YBG ex situ collection, and compare the results to other studies. The ultimate goal is to prevent the disappearance of the *O. tuberosa* cultivars in Ecuador and promote their agricultural production and consumption, revaluing our autochthonous food products.

METHODS

MORPHOLOGICAL ANALYSES

Photo shooting of tubers

Description of the general morphology of *Oxalis tuberosa* tubers was based on photos (with scale) taken, throughout the years, from the tubers that were part of the YBG ex situ *O. tuberosa* collection. One photo was taken for each accession. Natural variation within each *O. tuberosa* accession was properly represented by including in each photo tubers of different sizes. In most cases, the photos analyzed corresponded to those tubers that arrived directly from the field, i.e., tubers recently collected that represented well the color, shape and size of *O. tuberosa* tubers under natural agricultural conditions. In the case of *O. tuberosa* accessions that arrived as plants (not as tubers), their growth cycle was completed at YBG, and the *O. tuberosa* tubers thereby harvested were photographed (grown under ex situ conditions). In total, 262 accessions were photographed; the remaining 77 accessions could not be photographed because they did not adapt to the ex situ conditions at YBG, and died.

Morphotype delimitation based on tuber photos

The distinction among *O. tuberosa* cultivars maintained at the YBG collection was based on the external morphological appearance of tubers. In the present study, I use the term "morphotype" to refer to a cultivar (variety) at the YBG ex situ collection of *O. tuberosa*, as defined morphologically (not genetically). To facilitate comparison across studies, I will use from now on the term "morphotype" to refer to a given cultivar.

I characterized the color of *O. tuberosa* tubers using the accessions' photos and classifying them according to the primary (main) color of the tuber epidermis, as well as secondary colors that may appear at the tuber nodes or internodes (a tuber is a modified stem). Slight variations in color hue were not given much weight during the classification process; in other words, to create a new morphotype based on color, the *O. tuberosa* tuber had to be ostensibly different.

Although tuber shape or size can also somehow change depending on the *O. tuberosa* morphotype, I underestimated their importance because, after analyzing hundreds of

photos, I noticed that there can be a lot of internal variation of tuber shape and size within the same accession, and even among tubers from the same plant! An example of this phenomenon is shown in **Figure 2**.

In summary, I applied conservative criteria regarding color and shape to separate accessions into different morphotypes.

Geographic distribution of morphotypes in Ecuador

A geographic distribution analysis of the different morphotypes across Ecuador was conducted using the field-collected data of each *O. tuberosa* accession, and the morphotype assignation given to each of the 262 accessions that were photographed. To increase the spatial resolution of this geographic analysis, I assigned a putative morphotype to the unphotographed accessions by comparing the common name of the photographed accession to the common name given to the unphotographed accession by the farmer who donated it. As a result, 64 out of the 77 accessions that were not photographed (and thus had not been assigned a morphotype) were assigned a putative morphotype; the remaining 13 accessions could not be assigned a putative morphotype because of lack of sufficient information to match the common name with the morphotype in a given county. To reduce ambiguity during this extrapolation process of morphotype names, the analysis was conducted for each province independently. To represent the output of this analysis, I designed a map of Ecuador showing the geographic distribution of morphotypes, a pie chart depicting the number of accessions per morphotype, and a pie chart depicting the number of morphotypes per province. Finally, the distribution of *O. tuberosa* morphotypes according to this study was compared with other related studies from Ecuador.

Assessment and data analyses of tuber size by morphotype

To analyze tuber size, 1 to 13 representative tubers, subjectively selected depending on the morphological variation observed, were selected from each photo (accession) (see section “Photo shooting of tubers”). The number of tubers most commonly analyzed per photo (mode) was three.

Using ImageJ®, the following variables were measured for each tuber: length (cm), width (cm) and “frontal view area” (cm^2) according to the photo. In total, 990 tubers were

individually measured. For each photo (accession), the raw data of length (cm), width (cm) and area (cm^2) from each tuber were averaged to obtain a unique value for each of these variables, and for each accession.

To assess any potential morphometric differences among morphotypes, a statistical test was conducted using the average values calculated for each accession. For a given variable, these values were first tested for normality using the Shapiro-Wilk test. This helped to decide which test, parametric or non-parametric, was the most appropriate to conduct pairwise comparisons among morphotypes (i.e., Tukey vs. Mann-Whitney, respectively). Morphotypes with <10 accessions were excluded from this analysis because of their small sample size. Because of the multiple pairwise comparisons, *P* values were Bonferroni corrected. To control for any statistical bias related to large sample size, I randomly resampled the data five times with a fixed sample size of N=20 accessions, and conducted the corresponding analyses for each resampling round.

The classification of morphotypes of the present study was compared with morphotype classifications reported in other studies, not only from Ecuador but also from other countries. This literature search was mainly supported by Google Scholar.

BROMATOLOGICAL ANALYSES

Origin of plant material analyzed

Using the germplasm from the YBG ex situ *O. tuberosa* collection (**Figure 3a**), representative *O. tuberosa* accessions were cultivated during the first months of 2022 at El Cercado community, in Cotacachi county, Imbabura province (**Figure 3b**). A sample of tubers of each accession were cultivated, using 2–3 tubers per planting. At harvest, only 27 accessions were selected for the bromatological analyses because of financial reasons. These represented as many counties and provinces of the country as possible. In addition, eight accessions harvested from the YBG collection were also chemically analyzed. Therefore, in total, 35 accessions were chemically analyzed, each composed of several *O. tuberosa* tubers. For data analyses, these 35 accessions were classified into their corresponding morphotypes.

Bromatological parameters measured

The bromatological analyses were conducted at the Chemical Engineering and Bromatology Laboratories at the Universidad Técnica Particular de Loja (UTPL). This was required given the external funding from Corporación Ecuatoriana para el Desarrollo de la Investigación y la Academia (CEDIA) that supported these analyses. The following protocols, certified by the Association of Official Agricultural Chemists (AOAC, 2005), were used:

Macro- and micronutrients: method AOAC 999.11

Concentrations of those elements that act as nutrients were measured by Atomic Absorption Spectroscopy (AAS), switching the AAS lamp depending on the mineral, using the methos AOAC 999.11. Among all nutrients, in the present study only Calcium (Ca), Potassium (K), Magnesium (Mg), Sodium (Na), Copper (Cu), Iron (Fe), Manganese (Mn) and Zinc (Zn) were measured.

In preparation for the AAS analysis, accessions were first dehydrated for 24 hours at 50 °C, and then ground to fine and homogenous powder. For each accession, 0.5 g of the sample powder was weighed and digested by 10 ml of concentrated nitric acid during 2 hours in a microwave. Once this was completed, the digested sample was cooled down and filtrated in glass balloons, and distilled water was added until a volume of 0.05 L (50 ml) was reached.

To create the calibration curve, standards of each element diluted to different concentrations were prepared by digestion with 5% nitric acid. Sometimes, a second calibration curve had to be developed if the measured value for a given element was out of range in the first calibration curve. However, this rarely happened because the typical concentration ranges of the different elements in plants are relatively well known.

Sample concentration as measure in the AAS instrument was given in $\frac{m}{L}$. This value was transformed to $\frac{m}{g}$, using the following formula:

$$N \qquad \left(\frac{m}{g}\right) = \frac{C_i * V * D}{W_d}$$

where:

$$C_i = \text{Concentration given by AAS instrument } \left(\frac{m}{L}\right)$$

$$V = \text{Volume of the digestion } (L)$$

$$D = \text{Dilution factor}$$

$$W_d = \text{Weight of dry sample } (g)$$

For data analysis, this calculated concentration $\left(\frac{m}{g}\right)$ was transformed to $\left(\frac{m}{1\ g}\right)$ and to percentage (% = g/100g).

Ash: method AOAC 940.26

Ash concentration was measured using the method AOAC 940.26. This method consists in the full combustion of an organic sample under high temperatures until pure ash is obtained.

Accessions were first dehydrated for 24 hours at 50 °C, and then ground to fine and homogenous powder. Sample crucibles were first cleaned by burning them in a muffle furnace at 500–550 °C for one hour in order to eliminate any residual from past experiments, and were then cooled down in a glass vacuum desiccator. For each accession, 2 g of the ground sample were weighed in a clean crucible (previously weighed empty). Samples in the crucibles were then burned on an electric coil burner, until no dark smoke remained, and were then placed in a muffle furnace for 24 hours at 500–550 °C in order to obtain a completely gray ash. Sample crucibles were then cooled down in a glass vacuum desiccator for 30 minutes and then weighed. Ash concentration (%) was calculated as:

$$A\ h\ (\%) = \frac{W_a - W_e}{W_d} * 100$$

where:

$$W_a = \text{Weight of crucible with ash after full combustion (g)}$$

$$W_e = \text{Weight of empty crucible (g)}$$

$$W_d = \text{Weight of dry sample (g)}$$

Acidity: method AOAC 942.15

Acidity concentration was measured using method AOAC 942.15. For this test, a sample of 10 g of fresh *O. tuberosa* was mixed, ground and homogenized with 10 ml of

distilled water. Afterwords, three drops of phenolphthalein were added this mixture, and titrated with 0.1 N sodium hydroxide (NaOH). Acid concentration (%) was calculated as:

$$A \quad (\%) = \frac{V_N \quad * N_N \quad * Eq_{lc} * 100}{1000 * W_f}$$

where:

V_N = Volume of NaOH used to titrate the sample

N_N = Normality of NaOH used to titrate

E_{lc} = Chemical equivalent of lactic acid

W_f = Weight of fresh sample

Moisture: method AOAC 920.151

Moisture content (%) of fresh tubers was measured using the method AOAC 920.15. This method consists of drying fresh samples until a stable dry weight is reached.

Sample crucibles were first cleaned and dried at 100 °C in an oven for one hour, and then were cooled down in a glass vacuum desiccator for 30 minutes. For each accession, 2 g of fresh *O. tuberosa* sample were weighed in a clean crucible (previously weighed empty). Sample crucibles were then dried in an oven at 100 °C. For 8 hours, cooled down afterwords in a desiccator for 30 minutes and weighed for the first time. Sample crucibles were then dried in the oven again for 2 more hours and subsequently weighed. This process was repeated until a stable weight was reached (typically at around 12 hours). Moisture content (%) was calculated as:

$$M \quad (\%) = \frac{(W_e + W_f) - W_f}{W_f} * 100$$

where:

W_e = Weight of empty capsule (g)

W_f = Weight of fresh sample (g)

W_f = Final weight of sample crucible (g)

Fat: method AOAC 954.02

Fat concentration was determined using the method AOAC 954.02 which consists in extracting fat with diethyl ether in a Goldfish equipment, following the Soxhlet method.

This method is based on the continuous extraction of fat by an organic solvent, which is heated, volatilized and condensed through the sample repeatedly, so that fat is collected by dripping.

Accessions were previously dehydrated for 24 hours at 50 °C, and then ground to fine and homogenous powder. The extraction procedure consisted in weighing 5 g of *O. tuberosa* powder on an extraction thimble with some cotton, and adding 50 ml of diethyl ether in the goldfish flask. Fat concentration was determined by weight loss of the sample, using the following formula:

$$F \quad (\%) = \frac{W_d - W_f}{W_d} * 100$$

where:

$$W_d = \text{Weight of dry sample (g)}$$

$$W_f = \text{Final sample weight after fat extraction (g)}$$

Proteins: method AOAC 920.152

Proteins concentration was measured using the method AOAC 920.152. This method measures total nitrogen concentration, and then uses a conversion factor of 6.25 to transform to protein (%). The method can basically be divided into three steps: digestion or mineralization, distillation and titration.

Accessions were previously dehydrated for 24 hours at 50 °C, and then ground to fine and homogenous powder. For the digestion process, 1 g of sample was weighed in a heat-resistant glass tube and mixed with one Kjeldahl tablet + 10 ml of concentrated sulfuric acid (H_2SO_4). The digestion lasted 180 minutes at 420 °C. The distillation process used 40 ml of distilled water + 45 ml of 32% sodium hydroxide (NaOH) + 60 ml of 2% boric acid (H_3BO_3). Distillation time was set to 150 seconds. For the titration process, the distilled sample was mixed with 3 drops of methyl orange and titrated with 0.1 N hydrochloric acid (HCl). Nitrogen concentration (%) was calculated as:

$$N \qquad (\%) = \frac{(V_d - V_b) * N_H \quad * M_N}{W_d}$$

where:

$$V_d = \text{Volume of HCl used to titrate the distilled sample}$$

V_b = Volume of HCl used to titrate a blank sample (distilled water)

N_H = Normality of HCl used to titrate

M_N = Nitrogen molecular weight

W_d = Weight of dry sample

Proteins concentration was calculated using the following formula:

$$P \quad (\%) = N \quad (\%) * 6.25$$

Carbohydrates: method by difference

In a plant sample, most living biomass is basically composed of carbohydrates, protein, fat, moisture and minerals. Therefore, if we were able to measure the amount of protein, fat, moisture and minerals (as ash) in a given biomass, most of what remains should be carbohydrates (on a wet weight basis). In this sense, carbohydrate concentration (%) can be simply calculated as:

$$C \quad hy \quad (\%) = 100 - [A \ h \ (\%) + M \quad (\%) + F \quad (\%) + P \quad (\%)]$$

Energy: method NTE INEN 1334-2

Energy was measured applying norm NTE INEN 1334-2, item 4.3.1 (INEN, 2011). In this item, energy conversion factors (in kcal/g) for fat, protein and carbohydrates are given. By convention, 1 g of fat gives 9 kcal; 1 g of protein gives 4 kcal; and 1 g of carbohydrate gives 4 kcal. Note that, in bromatology, the amount of calories that a food type has is commonly expressed with the term “Cal” to refer to 1000 cal (1 kcal). Note the use of uppercase in “Cal” as opposed to the use of lowercase in “cal” (this last word meaning *calorie* in the classical sense of its physical definition).

To calculate the total amount of energy of a sample, first we must remember that a concentration expressed as % is the same as a concentration expressed as g/100g. Therefore, we can calculate the total amount of energy as:

$$E \quad \left(\frac{k}{100g}\right) = [F \quad (\%) * 9] + [P \quad n \quad (\%) * 4] + [C \quad hy \quad (\%) * 4]$$

Data analyses of tuber bromatology

For each bromatological parameter measured, an average (mean ($\overline{X}$) ± 1 standard deviation, SD) concentration was calculated for the accessions in each *O. tuberosa* morphotype. No statistical analyses were conducted to compare the bromatological parameters between morphotypes because sample size for each morphotype was too low (≤10 accessions chemically analyzed). In other words, any attempt to detect patterns was simply based on visual trends.

The bromatological data obtained in this study were compared with those from other studies, not only from Ecuador but also from other countries. In addition, bromatological value of typical foods that are consumed on a daily basis were compared to the data from this study. The literature search was based on journal articles, books, theses, technical reports, or other documents found through searches in Google Scholar and online libraries, or by consulting professional contacts.

RESULTS

MORPHOLOGY

Delimitation of morphotypes

The 326 accessions analyzed were classified into 10 tuber morphotypes of *O. tuberosa* (**Figure 4**), following the codification criteria (**Table 1**) which describe color variations of the epidermis, including colors at the nodes. These colors can be variations of white, yellow, fuchsia and purple. Out of the 326 accessions, the most collected morphotype in the ex situ germplasm bank was Y.1.0 (81 accessions; **Table 1**), while the morphotypes least collected were Y.2.1, P.0.4, F.0.3 and YF.0.1 (5, 5, 3 and 2 accessions, respectively; **Table 1)**. The rest of morphotypes were represented by 29 to 59 accessions (**Table 1**).

Note that color patterns are not always immutable. For example, as can be observed in **Figure 4**, and it is explained in **Table 1**, the following considerations should be noted: (1) In morphotypes Y.1.1 and YF.0.1, sometimes there is no color at the nodes in all tubers; (2) In morphotype Y.2.0, sometimes the fuchsia secondary color of the epidermis is not too obvious or does not appear in all tubers; (3) In morphotype FP.0.0, the *O. tuberosa* tends to have a purple hue as it matures, even at the nodes; and, (4) In morphotype FP.0.2, the epidermis of small immature ocas were almost completely pink, while mature ocas were clearly purple. The rest of the morphotypes were relatively well defined and do not show much variation with respect to their colors, within the context of the conservative criteria applied.

With respect to tuber shape, as already explained in the Methods section (**Figure 2**), the variation within a morphotype could be extreme as shown, for example, in tubers from accessions 126 and 085 of the morphotype W.1.0 (white) which show high variation in size (**Figure 2**).

Geographic distribution

The morphotypes of the 326 accessions were amply distributed in the Andes of Ecuador, with some morphotypes occurring in many provinces (**Figure 5a**). Out of the 10 Andean provinces, six had 5–7 morphotypes, while two had 3–4 morphotypes only (**Figure 5b**). High concentration of morphotypes was not restricted to any specific

geographic area of the Ecuadorean Andes, although small provinces tended to have few morphotypes (e.g., Carchi and Cañar; **Figure 5b**).

Regarding the distribution of each morphotype along the geography of the Ecuadorian Andes (**Figure 5a**), it is worth mentioning that four of the 10 morphotypes occurred in almost all provinces (**Figure 5c**): Y.1.1 (10 provinces), Y.2.0 (9 provinces), FP.0.2 (9 provinces) and Y.1.0 (8 provinces). Note that three of these four broadly distributed morphotypes are yellowish. On the other hand, also four of the 10 morphotypes occurred in just a few provinces (**Figure 5c**): Y.2.1 (2 provinces), YF.0.1 (2 provinces), F.0.3 (1 province) and P.0.4 (1 province).

Morphometry of tubers: length, width and frontal view area

As explained in Methods, those morphotypes with low sample size (<10 accessions) were excluded from any statistical analysis to avoid bias in the conclusions: these were morphotypes Y.2.1, YF.0.1, F.0.3, and P.0.4. The remaining morphotypes comprised a sample of N=249 accessions. According to the Shapiro-Wilk test (W), length, width and "frontal view area" were not normally distributed (for length: W=0.98, P=0.003; for width: W=0.99, P=0.034; and for frontal view area: W=0.94, $P < 0.001$), and thus I used the non-parametric Mann-Whitney test to conduct pairwise comparisons among morphotypes, for all three variables. Regarding length, the ocas of morphotype Y.1.0 tended to have significantly lower length than those from the rest of morphotypes, except those from FP.0.2 which tended to have similar length (**Figure 6a**, **Appendix 1**). Regarding width, only one pairwise comparison was significant: tubers from morphotype Y.1.1 showed a tendency to be wider than those of morphotype FP.0.2 (**Figure 6b, Appendix 1**). Besides this difference, all morphotypes showed a similar width of *O. tuberosa* tubers (**Figure 6b, Appendix 1**). Finally, for frontal area, the results were similar to those observed in the length analysis, except that this time three morphotypes showed a similar area: Y.1.0, FP.0.0 and FP.0.2 (**Figure 6c, Appendix 1**).

As explained in the Methods, the results above were re-tested by re-sampling the data five times using subsets of N=20 accessions, randomly selected (**Appendix 2**). This statistical exercise reaffirmed just a few unequivocal patterns: (1) morphotype Y.1.0 clearly had a median length and frontal view area significantly lower than morphotype W.1.0; and (2) all morphotypes had similar width.

BROMATOLOGY

Bromatological parameters

Not all chemical analyses were conducted for the 35 accessions selected (see Methods), which represented 7–9 morphotypes out of the 10 identified in this study (**Appendix 3**). The morphotype for which there was absolutely no data available was P.0.4. In addition, note that sample size for each morphotype varied depending on the chemical parameter analyzed (from *N*=1 to *N*=10; **Appendix 3**); this was because sometimes there was not enough sample remaining of a given accession to successfully conduct a chemical analysis. Also, note that (1) to facilitate comparisons, the concentrations of all parameters were expressed as % (and, in the case of nutrients, also as mg/100g); and that (2) because of low sample size in some morphotypes, no statistical analyses were conducted to compare among morphotypes. All things considered, the main visual patterns observed with regard to the different chemical parameters analyzed were (see **Figure 7**, **Figure 11** and **Appendix 3**):

(1) For all bromatological parameters analyzed, it appears that there is no obvious large difference of concentrations among morphotypes, at least considering the sample size analyzed, which is relatively limited as it only varies from *N*=1 to *N*=10 accessions. In other words, for a given parameter analyzed, all morphotypes showed relatively similar concentrations.

(2) Regarding macronutrients (Ca, Mg, Na and K; **Figure 7**), the macronutrient least concentrated was Na, on average ranging from 1.1 mg/100g (morphotype F.0.3) to 1.6 mg/100g (morphotypes YF.0.1 and FP.0.2) (**Figure 7a**). In contrast, the macronutrient most highly concentrated was K, ranging from 150 mg/100g (morphotype Y.2.0) to 260 mg/100g (morphotype F.0.3) (**Figure 7b**). The concentration of Ca was also relatively low (4.4–4.9 mg/100g), although higher than Na. Finally, Mg showed an intermediate range of concentration, ranging from 20 mg/100g (morphotype YF.0.1) to 29 mg/100g (morphotype Y.2.1) (**Figure 7a**). Raw data per accession can be consulted in **Appendix 3**.

(3) With respect to micronutrients (Cu, Fe, Mn and Zn), **Figure 8** shows that, in general, the most concentrated micronutrient was Fe, with values that ranged from 0.95 mg/100g (morphotype Y.2.1) to 1.2 mg/100g (morphotype YF.0.1).

Cu also showed, in general, relatively high concentrations (0.20–0.96 mg/100g), although lower than those of Fe. On the other hand, Zn was usually the least concentrated micronutrient, ranging from 0.24 mg/100g (morphotype FP.0.0) to 0.28 mg/100g (morphotype F.0.3). Finally, Mn concentrations showed mid-values, ranging from 0.3 to 0.85 mg/100g, in general higher than those of Zn, but lower than Cu and Fe. Raw data per accession can be consulted in **Appendix 3**.

(4) In terms of ash, its concentration ranged from 4.98% (morphotype FP. 0.0) to 6.92% (morphotype Y.2.0) (**Figure 9a**), with an overall average across morphotypes of 6.13 ± 1.05% ($\bar{x}$ ± 1SD) (**Appendix 3**).

(5) In terms of acidity, its concentration ranged from 0.07% (morphotypes FP.0.0 and FP.0.2) to 0.08% (morphotypes Y.1.1, Y.2.0 and YF.0.1) (**Figure 9b**), with an overall average across morphotypes of 0.074 ± 0.005% ($\bar{x}$ ± 1SD) (**Appendix 3**).

(6) In terms of moisture content, it ranged from 70.5% (morphotype YF.0.1) to 81.5% (morphotype Y.1.0) (**Figure 9c**), with an overall average across morphotypes of 77.7 ± 4.1% ($\bar{x}$ ± 1SD) (**Appendix 3**).

(7) With respect to the macro-biomolecules of fat, proteins and carbohydrates, **Figure 10** shows that, in general, carbohydrates (on a dry-weight basis) ranged from 5.2% (morphotype Y.1.0) to 15.4% (morphotype FP.0.2). Proteins showed lower concentrations than carbohydrates, ranging from 4.0% (morphotype FP.0.0) to 6.3% (morphotype YF.0.1). Fat was the least concentrated biomolecule, ranging from 0.4% (morphotype Y. 2.0) to 1.6% (morphotype YF.0.1). Raw data per accession can be consulted in **Appendix 3**.

(8) In terms of energy content, it ranged from 50.71 kcal/100g (morphotype Y.1.0) to 98.67 kcal/100g (morphotype YF. 0.1) (**Figure 11**), with an overall average across morphotypes of 69.2 ± 16.59 kcal/100g ($\bar{x}$ ± 1SD) (**Appendix 3**).

DISCUSSION

MORPHOLOGY

Morphotype delimitation can be subjective, but it is comparable among studies

In this study, I used conservative criteria to separate or classify *O. tuberosa* tubers into different morphotypes, mainly by their color pattern, but not much by their shape or size because I realized they can vary a lot (see **Figure 2**). High variation in shape or size could be caused by tuber maturity, herbivory pressure, soil and water conditions during growth, among other factors. I think that if a lot of importance is given to tuber shape or size, this could lead to the artificial creation of morphotypes that really belong to the same cultivar.

Considering the different criteria used in different studies to separate morphotypes, it is important to realize that comparison between studies cannot be straightforward. Anyhow, I attempted to make a comparison of morphotypes with other studies by re-classifying them using the same conservative color criteria applied in this study (**Table 2**). The results of this comparative exercise showed that several morphotypes from the other studies can be conservatively re-classified in a single morphotype of the present study, although not always.

The morphotype classification of the present study represents an update of the preliminary classification done by Navarrete-Mier et al. (2017), using the same photos of *O. tuberosa* tubers from the ex situ collection at Yachay Botanical Garden (YBG). They reported 11 morphotypes, which I re-classified into seven of the 10 morphotypes identify in the present study; i.e., three morphotypes, Y.2.1, YF.0.1 and F.0.3, were not explicitly recognized by Navarrete-Mier et al. (2017) (**Table 2**). With respect to Tapia et al. (2004), they reported 20 morphotypes from Ecuador, from which 19 were be re-classified into eight morphotypes from the present study (**Table 2**). In other words, morphotypes YF.0.1 and F.0.3 from the present study do not seem to appear in Tapia et al. (2004)´s classification, although they reported one interesting morphotype that does not seem to correspond to any of the morphotypes from the present study (**Table 2**). With respect to Cadima et al. (2004), they reported 18 morphotypes from the Candelaria zone, Perú, from which 14 were re-classified into seven morphotypes from the present study (**Table 2**). Morphotypes Y.2.1, YF.0.1 and F.0.3 from the present study do not seem to appear in

Cadima et al. (2004); although, on the other hand, they reported four morphotypes that do not seem to be present in Ecuador (**Table 2**). Note that the present study is reporting two specific morphotypes, YF.0.1 and F.0.3, that are not being reported in any study we are aware of—evidently, it is of uttermost importance to keep maintaining germplasm of these two morphotypes under in situ or ex situ conservation.

The conundrum of *O. tuberosa* classification into different morphotypes by different authors could be somehow solved by analyzing more in detail the vegetative (leaves, stems) and reproductive (flowers, fruits) characteristics of the different cultivars, in addition to genetic analyses. It might be the case, for example, that one *O. tuberosa* cultivar with fixed tuber color really contains two or more *O. tuberosa* genotypes represented by distinguishing vegetative characteristics of stems and/or leaves. Alternatively, a genetic analysis may conclude that an *O. tuberosa* cultivar with fixed vegetative and reproductive characteristics actually contains two different morphotypes genotypically distinct (although phenologically equal, i.e. "cryptic cultivars").

Over time, *O. tuberosa* cultivars have shifted their importance in different provinces

According to the field description of *O. tuberosa* accessions from the catalogue of edible roots and tubers of Ecuador (Tapia et al., 1996), there are 17 different combinations of colors in *O. tuberosa* tubers, distributed along the Ecuadorian Andes. If we assume that these combinations represent 17 different "morphotypes", it becomes possible to compare their results with those of the present study—conducted decades after—in particular with regard to the number of *O. tuberosa* cultivars (morphotypes) per province (**Table 3**). The first pattern that becomes discernible is that, just like today, Chimborazo is a province with a high number of *O. tuberosa* cultivars (8 in 1996 vs. 7 in this study); this means that the local culture in Chimborazo, where ca. 40% of the population is indigenous (INEC, 2010), still today give importance to the production and consumption of different *O. tuberosa* cultivars. On the other hand, provinces such as Cañar and Bolívar, which in 1996 had a relatively high number of *O. tuberosa* cultivars (9 and 7, respectively), today show a reduction in the number of *O. tuberosa* cultivars present in their territory (3 and 4, respectively). Yet, this reduction in the number of *O. tuberosa* cultivars in some provinces has been counterbalanced by an increase in the number of *O. tuberosa* cultivars in other provinces, such as Imbabura (from 3 cultivars in 1996 to 7 cultivars today) and Tungurahua (also increasing from 3 to 7 cultivars). These temporal

shifts in the number of cultivars observed in certain provinces probably reflect a change in the interest of the local culture for different *O. tuberosa* cultivars, besides the most commonly cultivated yellow cultivar (Y.1.0; **Figure 5c**). In those provinces where an increase in the number of *O. tuberosa* cultivars is observed (i.e., Imbabura and Tungurahua), it is possible that traditional seed fairs, and the implementation of agroecological practices, may have had a positive effect on *O. tuberosa* agrobiodiversity.

Tuber length, but not width, seems to be controlled genetically rather than environmentally

As described in the Results section, morphotype Y.1.0 clearly had a length and a frontal view area significantly lower than morphotype W.1.0 (**Figure 6a and 6c**, **Appendix 1**), and this difference was the most strongly maintained after re-sampling and statistically re-testing with a fixed sample size across morphotypes (N=20) to eliminate any bias due to sample size (**Appendix 2**). It is also interesting to note that width does not vary significantly across morphotypes—a pattern confirmed after re-sampling and re-testing the data (**Figure 6b**, **Appendix 1**, **Appendix 2**). Because the ocas were collected in different provinces, with different soil and climatic conditions, the fact that the white *O. tuberosa* morphotype tends to be larger than the most common yellow morphotype, means that *O. tuberosa* length is probably determined by a strong genetic component rather than by an environmental component. In the future, one way to test this hypothesis will be by designing common garden experiments (i.e., under the same environmental conditions), where the largest and the smallest *O. tuberosa* tubers of different morphotypes are planted, or by planting *O. tuberosa* tubers of the same size but from different morphotypes. By conducting these experiments repeatedly over several generations, it may be possible to elucidate the effect of the interaction between genetics and environment on tuber size, or other phenotypic characteristics, across *O. tuberosa* morphotypes.

BROMATOLOGY

There are many bromatological parameters that have been analyzed for *O. tuberosa* tubers in different studies since the 1950s, when the first study that included chemical analyses of *O. tuberosa* tubers was published (Collazos et al., 1952). In a recent extensive literature review by Hidalgo-Bermeo et al. (2022), it was shown that there is data of 54

bromatological parameters of *O. tuberosa* tubers dispersed in 18 studies, but that basically no study was directly comparable because of different chemical methods applied and inconsistency on the kind and number of parameters reported.

Given this context, the present Discussion only includes comparisons with those specific studies that reported any of the 15 parameters analyzed in the present study, i.e., four macronutrients (Ca, K, Mg and Na), four micronutrients (Cu, Fe, Mn and Zn), and some typical parameters that are recurrently measured in many studies (Ash, Acidity, Moisture, Fat, Proteins, Carbohydrates and Energy). Applying this filter, there are 19 studies where bromatological data from the parameters analyzed in this study are reported (**Appendix 4**). Most studies have been conducted in Ecuador and Perú, from where *O. tuberosa* is native and where there is still a local population that consumes it. The other few bromatological studies are dispersed in different countries only from the American continent, including Mexico and USA where the *O. tuberosa* was probably taken as an exotic test crop.

Depending on the bromatological parameter, there might be similarities or differences among morphotypes

In the present study, there was not an obvious difference across morphotypes for any of the bromatological parameters analyzed (**Figure 7**, **Figure 11**). This does not mean that in the future, if other bromatological parameters are analyzed, significant differences can be detected, given the same environmental conditions (a *sine qua non* condition).

This pattern is partially observed in other studies, in which, depending on the parameter, there could be or not be obvious differences between different morphotypes. For instance, among the four cultivars that Brito and Espín (1999) compared—"Amarilla", "Roja", "Violeta" and "Naranja"—the "Naranja" cultivar had the highest protein concentration, while the "Roja" cultivar had higher protein concentration than the "Amarilla" cultivar; however, for energy, these morphotypes did not show any clear difference. The only other study that compared among morphotypes is Araujo (2012), who studied two morphotypes: "Rojo grisáceo" and "Amarilla señorita". Although such study analyzed only a single replicate for each morphotype, Araujo (2012) detected that: (1) proteins concentration was somewhat higher in the "Rojo g." cultivar than in the "Amarilla s." cultivar (6.9% vs 4.9%), a pattern that is simile to Brito and Espín (1999);

(2) carbohydrates concentration was twice as high in the "Amarilla s." cultivar compared to the "Rojo g." cultivar (10.9% vs 5.9%): and (3) some minerals (Ca, Na, Fe, Mn) were twice as highly concentrated in the "Rojo g." cultivar than in the "Amarillo s." cultivar. Yet, for the rest of parameters, Araujo (2012) reported no strong difference.

A comparison of morphotypes of apparently the same kind between this study and another study is only possible to attempt with the study of Araujo (2012), where the "Amarillo señorita" cultivar could be comparable to the morphotype Y.1.1 of the present study[2]. Only proteins, carbohydrates and moisture in Araujo (2012) had similar values to those of the present study (4.9% vs 5.2%, 10.9% vs 10.1%, and 76.4% vs 77.7%, respectively), whereas for the other parameters the values were notably dissimilar.

In conclusion, depending on the bromatological parameter, there might be similarities or differences among morphotypes, but any pattern whatsoever detected is probably prone to sample size, the analytical method applied, crop conditions, or other technicalities. This can be explored in the future through controlled experiments.

Bromatological comparison of macro- and micronutrients across studies

For the Discussion about nutrients, I chose to focus only on those parameters that are most commonly reported in the literature, certainly because they are considered important for the human diet: the macronutrient Ca (**Figure 12a**) and the micronutrient Fe (**Figure 12c**). The rest of nutrients will be excluded from this Discussion because they are rarely reported (≤4 studies), except to note that: (1) the macronutrients Mg (**Figure 12a**), Na (**Figure 12a**) and K (**Figure 12b**) tend to show high variation (0.0065-0.0224% for Mg; 0.0015-0.0180% for Na; and 0.21-1.3% for K); and, (2) the micronutrients Cu, Mn and Zn (**Figure 12c**) consistently show very low values across studies (0.0001-0.0007% for Cu; 0.00028-0.00050% for Mn; and 0.00026-0.00180% for Zn). It is noteworthy that the data from the present study marked some of the minimum and some of the maximum values ever registered for several nutrients: for Mg and Cu, the maximum values; whereas for Na, K and Zn, the minimum values.

[2] The cultivar "Rojo grisáceo" of Araujo is comparable to the morphotype P.0.4 of this study, but there is not any bromatological data available in this study for such morphotype.

For humans, O. tuberosa is not an important source of Ca

The lowest value of Ca concentration reported in the literature is 2 mg Ca/100g dry weight (Tapia, 1990), while the highest value is 30 mg/100g (Collazos et al., 1952) (**Figure 12a**, **Appendix 4**). In this study, the average value of Ca concentration in *O. tuberosa* tubers was 4.7 mg Ca/100g dry weight (**Figure 12a**, **Appendix 4**). Chickpeas, which are well known for their high Ca concentration, can have ca. 200 mg/100g (Landi et al., 2021). This means that *O. tuberosa* tubers only represent 2.35% of the Ca concentration in chickpeas (4.7 mg Ca /200 mg Ca × 100), for the same dry weight.

A human normally needs 1300 mg Ca/day (USDA, 2005). If, for pedagogical purposes, we consider a pound of fresh *O. tuberosa* (what a family may consume in a day), we can calculate that, rounding up the data obtained in this study, there are ≈5 mg Ca/lb (≈4.7 mg Ca/448g fresh weight; see above). Considering the daily requirement for this nutrient in humans, *O. tuberosa* tubers do not seem therefore a significant source of Ca. Evidently, for a given weight, concentration of Ca will increase if the *O. tuberosa* sample is first dried (ca. 21 mg Ca/lb of *O. tuberosa* flour).

For humans, O. tuberosa is an important source of Fe

The lowest value of Fe concentration reported in the literature is 0.8 mg Fe/100g dry weight (Duke, 2001), while the highest value is 12.53 mg Fe/100g dry weight (León et al., 2011) (**Figure 12c**, **Appendix 4**). In this study, the average value of Fe concentration in *O. tuberosa* tubers was 1 mg/100g dry weight (**Figure 12c**, **Appendix 4**). Beans, which are well known for their high Fe concentration, can have ca. 5.3–8.5 mg Fe/100g dry weight (Pereira et al., 2014). This means that *O. tuberosa* tubers only represent 2.6–4.2% of the Fe concentration in beans (1 mg Fe /5.3 mg Fe × 100; 1 mg Fe /8.5 mg Fe × 100), for the same dry weight.

A human normally needs 8–18 mg Fe/day (USDA, 2005). If, for pedagogical purposes, we consider a pound of fresh *O. tuberosa* (what a family may consume in a day), we can calculate that, taking into account this study's data only, there is ≈1 mg Fe/lb (1 mg Fe/448g × 454g/lb). Considering the daily requirement for this nutrient in humans, *O. tuberosa* tubers seem therefore to be a decent source of Fe for humans.

Bromatological comparison across studies for the rest of parameters

Besides the macro- and micronutrients discussed above, it is also important to analyze the relative importance for the human diet of the rest of parameters measured in this study. Namely, I will only focus on acidity, moisture, fat, proteins, carbohydrates and energy.

High acidity in O. tuberosa tubers is related to high oxalic acid concentration

The lowest value of acidity in *O. tuberosa* tubers reported in the literature was 0.03% (Cajamarca, 2010), while the highest value was 0.4% (Palate, 2013) (**Figure 13b**, **Appendix 4**). In this study, the average value of acidity was 0.07% (**Figure 13b**, **Appendix 4**). In oca, the acidity is mostly due to the presence of oxalic acid (oxalate) which can vary from 80 mg/100g (Ross et al., 1999) to 221 mg/100g fresh weight (Sangketkit et al., 1999). To what extent this relatively high presence of oxalic acid in *O. tuberosa* can become a problem in the human diet?

To answer this question, we first need to estimate the amount of oxalic acid that a human could potentially consume. We can calculate that a pound of fresh *O. tuberosa* (what a family may consume in a day), given the data from this study, contains ≈318 mg acidity/lb (0.07 mg acidity/100mg × 454000 mg/lb). Thus, *O. tuberosa* seems to be a significant source of acidity for humans, although the concentration of oxalate in *O. tuberosa* tubers is equivalent to the oxalate content in some common foods of the modern human diet, like spinach or chocolate, among others (Sangketkit et al., 1999). Yet, an excess of oxalate in the diet may contribute to the formation of kidney stones in some people, and therefore it is recommended that the maximum amount of consumed oxalate per day should be <50 mg (Spritzler, 2017). This can be certainly achieved by boiling the tubers, as it was demonstrated by a study in which oxalate content was reduced from 30 to 87% when tubers, or other kind of food, were boiled (Chai & Liebman, 2005). Furthermore, Castañeta et al. (2022) demonstrated that acidity content can be reduced if ocas are exposed to the sun for several days, although not significantly.

Moisture values measured in this study fall within the typical range

The lowest value of moisture content in *O. tuberosa* tubers reported in the literature was 6% (Esparza et al., 2021), while the highest value was 86.8% (León et al., 2011) (**Figure 13c**, **Appendix 4**). It is strange that a few authors report very low values of

moisture content in *O. tuberosa* tubers (<14%), whereas most authors report moisture contents >68% (**Figure 13c**, **Appendix 4**). It is unknown the reason(s) for this discrepancy, but it probably reflects differences on how the sample was prepared or analyzed, or how moisture content was calculated. In this study, the average value of moisture content was 77.7%, which is closer to the values most typically reported (**Figure 13c**, **Appendix 4**). In perspective, it is important to accurately measure moisture content because it is a crucial parameter during any food processing chain, as it strongly correlates with different food quality attributes (Zou et al., 2022).

In terms of fat consumption, O. tuberosa is a healthy alternative

The lowest value of fat concentration in *O. tuberosa* tubers reported in the literature was 0.2% (Palate, 2013), while the highest value was 3.7% (Duke, 2001) (**Figure 14a**, **Appendix 4**). In this study, the average value of fat was 0.9% (**Figure 14a**, **Appendix 4**). Daily fat consumption for humans should not be above 13 g/day (AHA, 2021). A pound of *O. tuberosa* tubers, which is probably the amount consumed by a whole family, would contain 4.1 g of fat (0.9 g/100g × 454 g/1 lb). In this context, it is therefore evident that oca, as a low-fat food, is a healthy alternative in the human diet.

For humans, O. tuberosa is a reasonable source of proteins

The lowest value of proteins concentration—which, because how it is calculated (see Methods) is basically equivalent as N concentration—reported in the literature for *O. tuberosa* tubers was 0.34% (Hernández-Lauzardo et al., 2004), while the highest value was 8.92% (Esparza et al., 2021) (**Figure 14a**, **Appendix 4**). In this study, the average value of proteins concentration was 5.2% (5.2 g/100g) (**Figure 14a**, **Appendix 4**). The Andean crop known as "chocho", *Lupinus mutabilis*, which has high protein concentration, can have ca. 32.0–52.6 g/100 g dry weight (Carvajal-Larenas et al., 2016). This means that *O. tuberosa* tubers represent 16.3–9.2% of the protein concentration in "chocho" (5.2 g protein /32 g protein × 100; 5.2 g protein /52.6 g protein × 100), for the same dry weight.

A human normally needs 46–56 g protein/day (USDA, 2005). If, for pedagogical purposes, we consider a pound of fresh *O. tuberosa* (what a family may consume in a day), we can calculate that there are ≈5.3 g protein/lb (≈5.2 g protein/448g fresh weight;

see above). This value, although not very large, allows us to conclude that *O. tuberosa* seems to be a reasonable source of proteins for humans. Evidently, for a given weight, concentration of proteins will increase if the *O. tuberosa* sample is first dried (ca. 23.6 g proteins/lb of *O. tuberosa* flour).

For humans, O. tuberosa is an important source of carbohydrates

The lowest value of carbohydrates concentration reported in the literature is 8.38% (Araujo, 2012), while the highest value is 88.8% (King & Gershoff, 1987) (**Figure 14b**, **Appendix 4**). This high variation in carbohydrates concentration among different studies could be explained by different biotic or abiotic conditions during pre-harvest, harvest and post-harvest times, but also by how carbohydrate concentration is indirectly calculated by simple substraction (see Methods). For example, among other things, an *O. tuberosa* tuber harvested too young certainly may have less carbohydrate accumulated than a more mature *O. tuberosa* tuber, or an *O. tuberosa* tuber exposed to the sun for several days apparently can increase its sugar content, although this could also be explained by the decrement of moisture content (because carbohydrate concentration is not a parameter measured directly; see Methods). Indeed, Yenque et al. (2008) showed that carbohydrates concentration increased from 7.5% at harvest to 15% after 20 days of sun exposure.

In this study, the average value of carbohydrates concentration in *O. tuberosa* tubers was 10% (**Figure 14b**, **Appendix 4**). For comparison, potatoes can have ca. 17.49 g/100g (USDA, 2019). This means that *O. tuberosa* tubers represent 57.2% of the carbohydrates concentration in potatoes (10 g carbohydrate/17.49 g carbohydrate × 100), for the same weight. A human normally needs 130 g carbohydrate/day (USDA, 2005). If, for pedagogical purposes, we consider a pound of fresh *O. tuberosa*, we can calculate that there is 45.4 g of carbohydrate (10 g carbohydrate/100 g sample × 454 g/1b), which means that *O. tuberosa* is a reasonable source of carbohydrates for humans.

Finally, it is important to realize that carbohydrate content is highly and positively correlated with energy content ($Y[e\quad] = 4.3X[c\quad hy\quad] + 6.3$, $R^2 = 0.99$, P<0.001) (**Appendix 4**). This is not surprising because energy content is indirectly calculated based on the relative energy contribution of fat, protein and carbohydrates, whose relative energy contribution is standardized (see Methods). Evidently, because in

O. tuberosa tubers the concentration of carbohydrates will always be much higher than fat and protein, the energy content will always depend mostly on carbohydrates concentration.

CONCLUSION

This study characterized the basic morphology (color, length and width) and bromatology of the *Oxalis tuberosa* morphotypes present in the ex situ collection at Yachay Botanical Garden (YBG). In total, 10 *Oxalis tuberosa* morphotypes were distinguished based on 262 photographs available out of 339 accessions collected across the Andes of Ecuador, from Carchi to Loja, by the YBG research team. The level of genetic difference among morphotypes should be evaluated in future studies, along with an estimate of the level of genetic diversity contained within each morphotype and between morphotypes. Genetic mapping of those alleles related to different traits of interest can be also useful for future breeding experiments (genetic improvement).

Nine of the 10 morphotypes were chemically analyzed with regard to some macronutrients (Ca, K, Mg and Na), micronutrients (Cu, Fe, Mn and Zn), ash, acidity, moisture, fat, proteins (direct proxy of N), carbohydrates and energy. I found that all morphotypes showed similar bromatological values, and therefore they all can provide a reasonable contribution of some nutrients and energy to humans, particularly in regard to Fe, proteins and carbohydrates. Moreover, the low-fat content of *O. tuberosa* tubers make them a good alternative for a healthy diet.

For a small country like Ecuador, the presence of 10 morphotypes of *O. tuberosa* is a remarkable measure of extant agrobiodiversity. Any loss of this diversity can have unexpected and exacerbated negative effects because we are a small country with limited number of peasant communities that still cultivate oca—in this scenario, the risk of genetic erosion of this Andean tuber is higher than large countries such as Bolivia or Peru, where resilience is probably higher because of high population size and territory. To conserve *O. tuberosa* varieties, they need to be revalued as an important staple crop not only in the Andean zone, but also in the Coast and Amazon, where *O. tuberosa* consumption could be motivated by giving an added value to this tuber, known to contain essential values of some nutrients and vitamin C, and also ocatin, a protein recognized by its antimicrobial properties (Flores et al., 2002).

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TABLES

Table 1. General morphological characterization of the 10 morphotypes of *Oxalis tuberosa* tubers identified at the Yachay Botanical Garden (YBG) ex situ collection.

Morphotype No.	Morphotype code	Epidermis primary color [a]	Epidermis secondary color [a]	Node characteristics	Total accessions at YBG
1	**W.1.0**	**W.** White	**1.** Sometimes pink, but not always in all tubers from the same accession.	**0.** Same as primary color.	56
2	**Y.1.0**	**Y.** Yellow	**1.** Sometimes pink, but not always in all tubers from the same accession.	**0.** Same as primary color.	81
3	**Y.1.1**	**Y.** Yellow	**1.** Sometimes pink, but not always in all tubers from the same accession.	**1.** Fuchsia / Wine red lines	59
4	**Y.2.0**	**Y.** Yellow	**2.** Fuchsia	**0.** Same as primary color.	29
5	**Y.2.1**	**Y.** Yellow	**2.** Fuchsia	**1.** Fuchsia / Wine red lines	5
6	**YF.0.1**	**YF.** Yellow, but fuchsia when mature	**0.** Same as primary color.	**1.** Fuchsia / Wine red lines	2
7	**F.0.3**	**F.** Fuchsia	**0.** Same as primary color.	**3.** Dark purple lines / Marked white triangular stipule	3
8	**FP.0.0**	**FP.** Fuchsia, but purple when mature	**0.** Same as primary color.	**0.** Same as primary color.	30
9	**FP.0.2**	**FP.** Fuchsia, but purple when mature	**0.** Same as primary color.	**2.** Yellow stipule	56
10	**P.0.4**	**P.** Dark purple	**0.** Same as primary color.	**4.** Marked white triangular stipule	5
					326

[a] The terms “primary” and “secondary” do not mean the primary and secondary colors of the chromatic system.

Table 2. Equivalency of morphotype codes among four studies reporting a tuber classification of *Oxalis tuberosa*, organized applying the same conservative criteria as in the present study. The names, codes or numbers that appear under each column are the same as those originally reported in the different studies. Blank lines (—) indicate that a given morphotype was not reported in a given study.

This study (2023) ECUADOR	**Navarrete-Mier et al. (2017) ECUADOR [a]**	**Tapia et al. (2004) ECUADOR**	**Cadima et al. (2004) PERÚ**
W.1.0	11	12, 13	Pili Runtu
Y.1.0	9, 10	6, 14	Bola Kamusa K'ellu Kamusa Puka Ñawi Kamusa Zapallo Oqa
Y.1.1	6	3, 4, 7	K'ellu Qayara Pili Pintado
Y.2.0	7, 8	1, 15, 17	Sauciri
Y.2.1	—	7, 11	—
YF.0.1	—	—	—
F.0.3	—	—	—
FP.0.0	5	2, 5, 10, 18	Lari Oqa Tani
FP.0.2	2, 4	8, 9, 16	Lluch'u Oqa Titicoma
P.0.4	1, 3	19	Oqa Patria Yana Oqa
—	—	20	—
—	—	—	Kharisiri
—	—	—	Ñañu Puka Kamusa Puka Kamusa
—	—	—	Señora

[a] This was a preliminary exercise of morphotype classification of the *Oxalis tuberosa* collection at Yachay Botanical Garden (YBG), which is the same collection of the present study.

Table 3. Number of morphotypes present in the provinces of Ecuador, geographically ordered (north to south), according to Tapia et al. (1996) and this study.

Province	This study (2023) [a]	Tapia et al. (1996)
Carchi	3	4
Imbabura	7	3
Pichincha	4	5
Cotopaxi	5	3
Tungurahua	7	3
Bolívar	4	7
Chimborazo	7	8
Cañar	3	9
Azuay	7	5
Loja	5	6

[a] See also **Figure 5b**.

FIGURES

Figure 1. A typical plant of *Oxalis tuberosa* Molina, locally known as “oca”. There are different morphological variations depending on the cultivar, particularly for tubers. Photo credits: ©Yachay Botanical Garden.

Figure 2. Examples of variation in tuber size and shape within the same "white" morphotype: **a)** Photograph of accession 126; **b)** Photograph of accession 085. The different brightness of photo a) vs photo b) is simply caused by the amount of light available during photo shooting. Photo credits: ©Yachay Botanical Garden.

Figure 3. Germplasm can be protected using ex situ or in situ strategies: **a)** Ex situ germplasm bank of *Oxalis tuberosa* cultivars at Yachay Botanical Garden (YBG); **b)** In situ field crop of *Oxalis tuberosa* in Cotacachi, Ecuador. Photo credits: ©Yachay Botanical Garden.

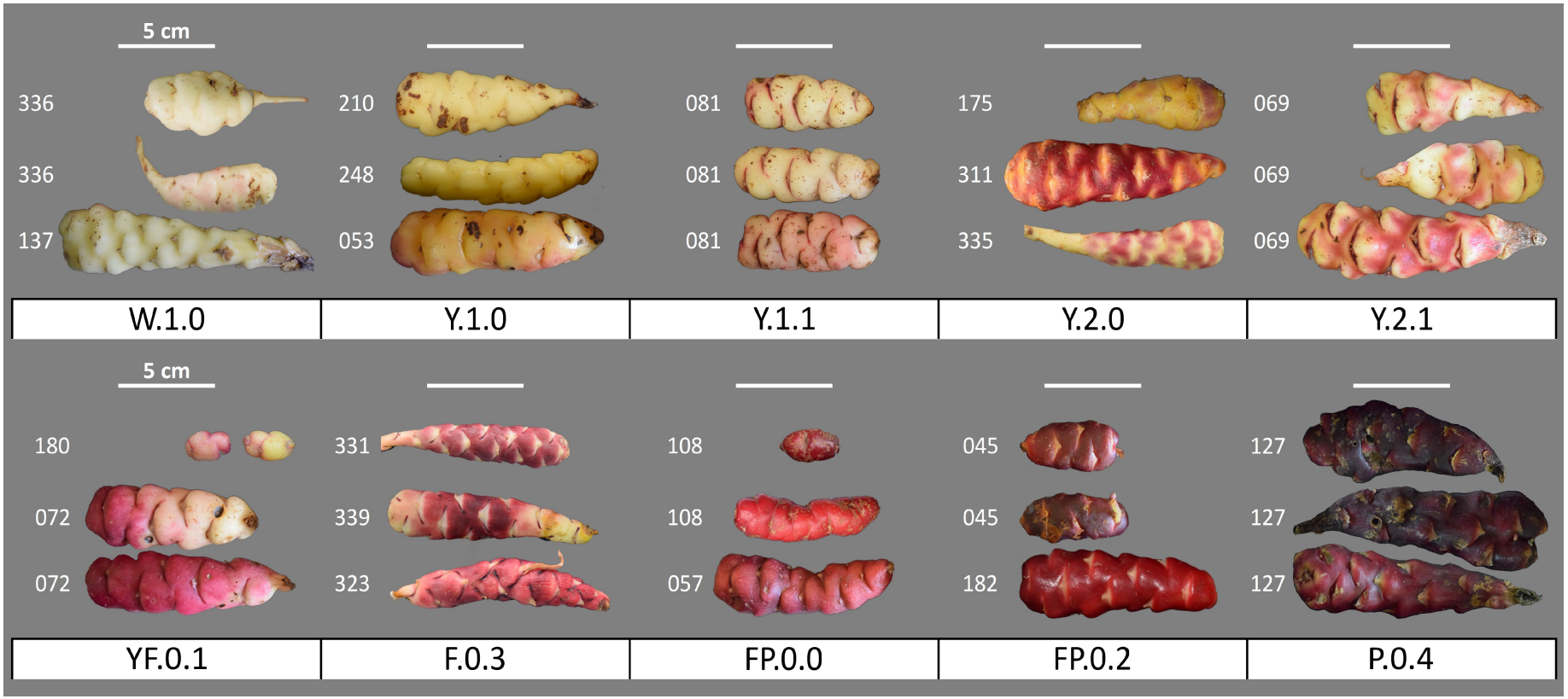

Figure 4. Representative photos of the 10 morphotypes identified and described at the ex situ *Oxalis tuberosa* collection at Yachay Botanical Garden (YBG). Morphotypes codes are explained in **Table 1**. Accession numbers appear next to each photo. White horizontal lines represent a 5 cm scale. Photo credits: ©Yachay Botanical Garden.

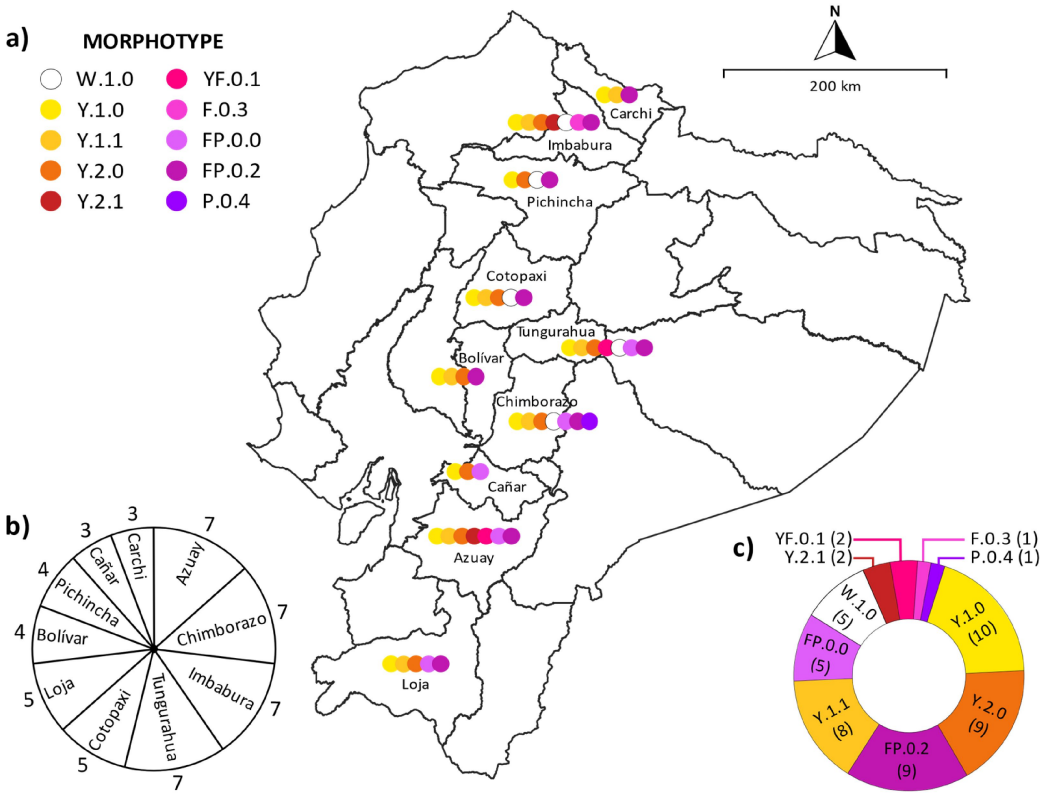

Figure 5. Geographic distribution of *Oxalis tuberosa* morphotypes in Ecuador: **a)** Map showing the distribution of morphotypes per province; **b)** Number of morphotypes per province; **c)** Number of provinces per morphotype.

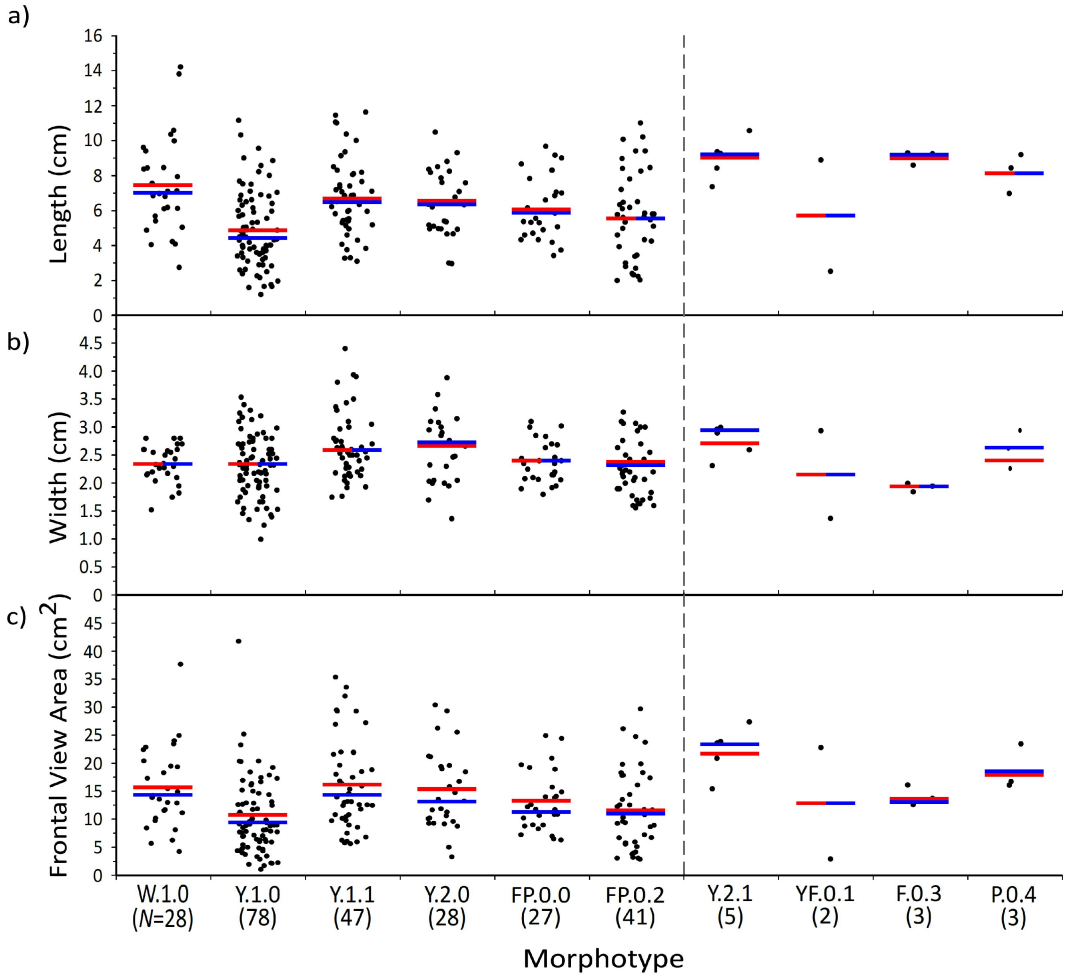

Figure 6. Morphometry of 262 accessions of *Oxalis tuberosa* at Yachay Botanical Garden, analyzed with ImageJ®: **a)** Length (cm); **b)** Width (cm); **c)** Frontal view area (cm^2). Each dot represents one accession (an average value of the ocas in that accession´s photograph). Dots have been horizontally scattered to facilitate visualization. Blue lines represent the median, while red lines represent the mean. Morphotype codes are explained in **Table 1**. *N*=sample size.

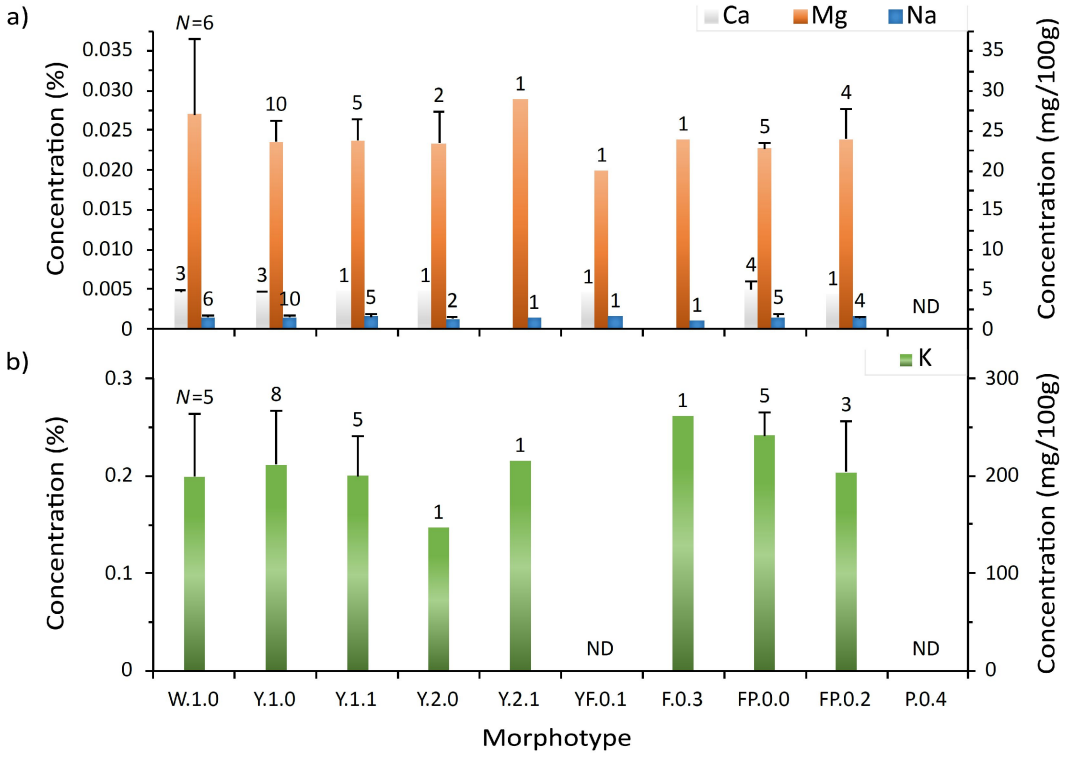

Figure 7. Concentration (in % and in mg/100g) of macronutrients for each *Oxalis tuberosa* morphotype: **a)** Ca, Mg and Na; **b)** K. Each bar represents $\bar{x}$ ± 1SD. Morphotype codes are explained in **Table 1**. Number above each bar represents sample size (*N*). "ND" indicates a morphotype with no data available.

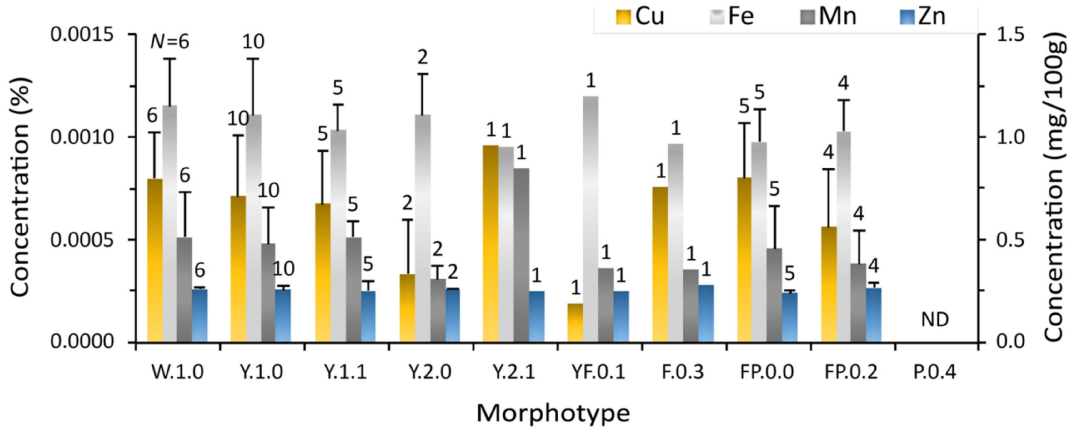

Figure 8. Concentration (in % and in mg/100g) of micronutrients for each *Oxalis tuberosa* morphotype: Cu, Fe, Mn and Zn. Each bar represents $\bar{x}$ ± 1SD. Morphotype codes are explained in **Table 1**. Number above each bar represents sample size (*N*). "ND" indicates a morphotype with no data available.

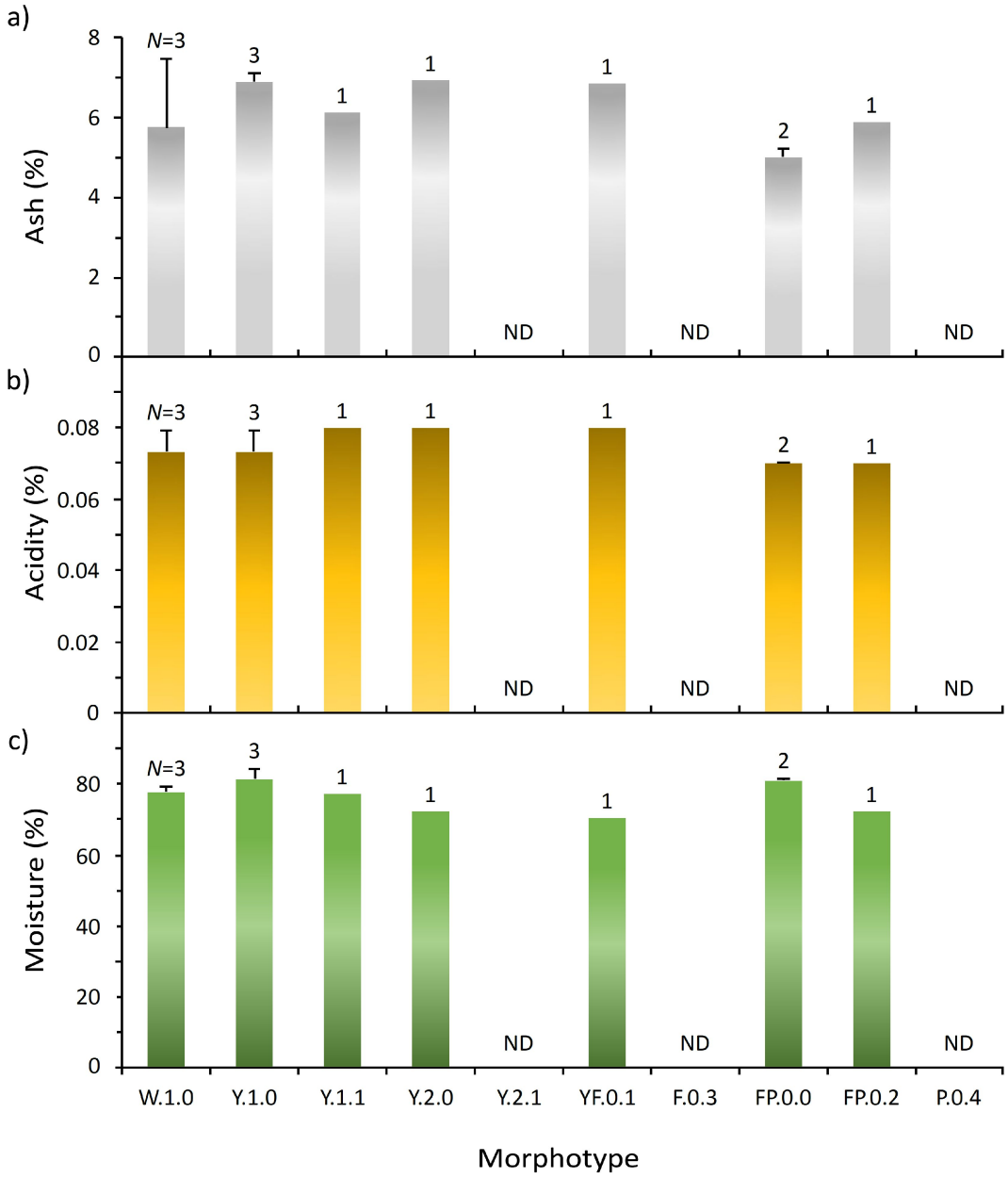

Figure 9. Concentration (%) of other bromatological parameters measured in this study for each *Oxalis tuberosa* morphotype: **a)** Ash; **b)** Acidity; **c)** Moisture content. Each bar represents $\bar{x}$ ± 1SD. Morphotype codes are explained in **Table 1**. Number under each morphotype code represents sample size (*N*). "ND" indicates a morphotype with no data available.

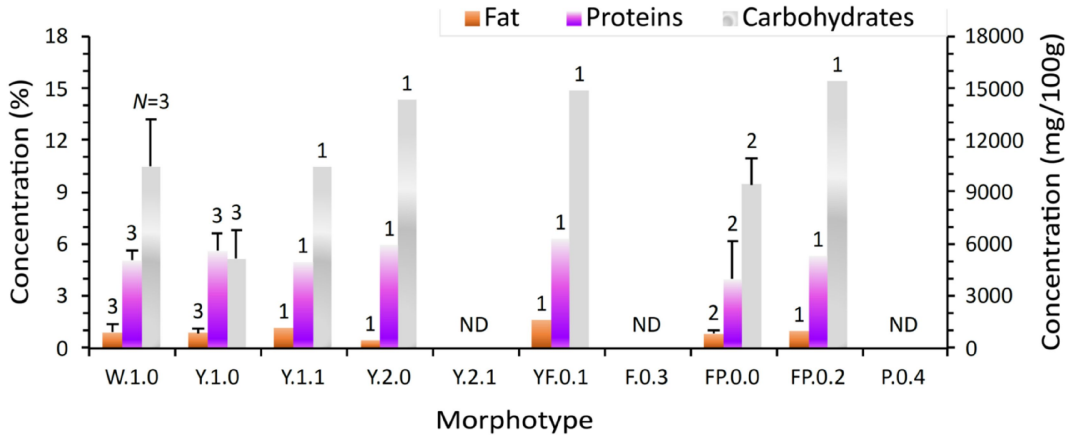

Figure 10. Concentration (in % and in mg/100g) of fat, proteins and carbohydrates for each *Oxalis tuberosa* morphotype. Each bar represents $\bar{x}$ ± 1SD. Morphotype codes are explained in **Table 1**. Number above each bar represents sample size (*N*). "ND" indicates a morphotype with no data available.

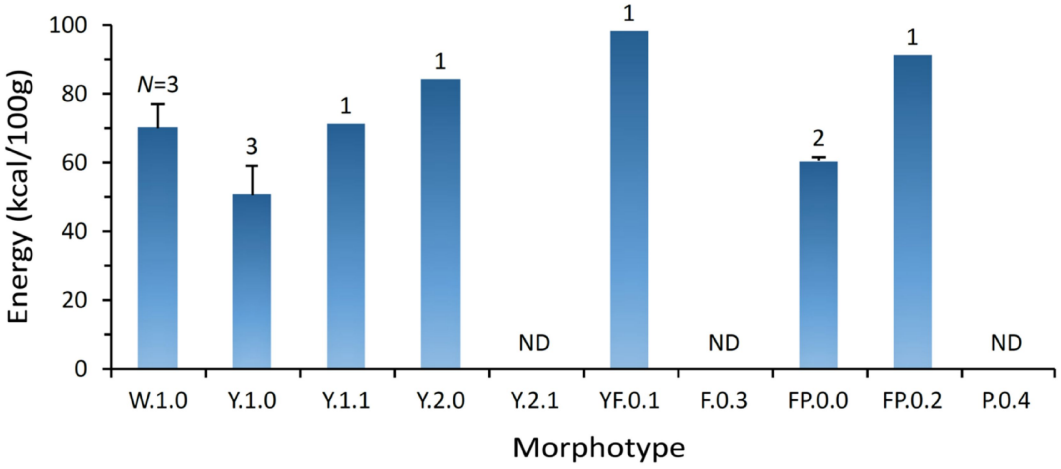

Figure 11. Energy content (kcal/100g) for each *Oxalis tuberosa* morphotype. Each bar represents $\bar{X} \pm 1SD$. Morphotype codes are explained in **Table 1**. Number above each bar represents sample size (*N*). "ND" indicates a morphotype with no data available.

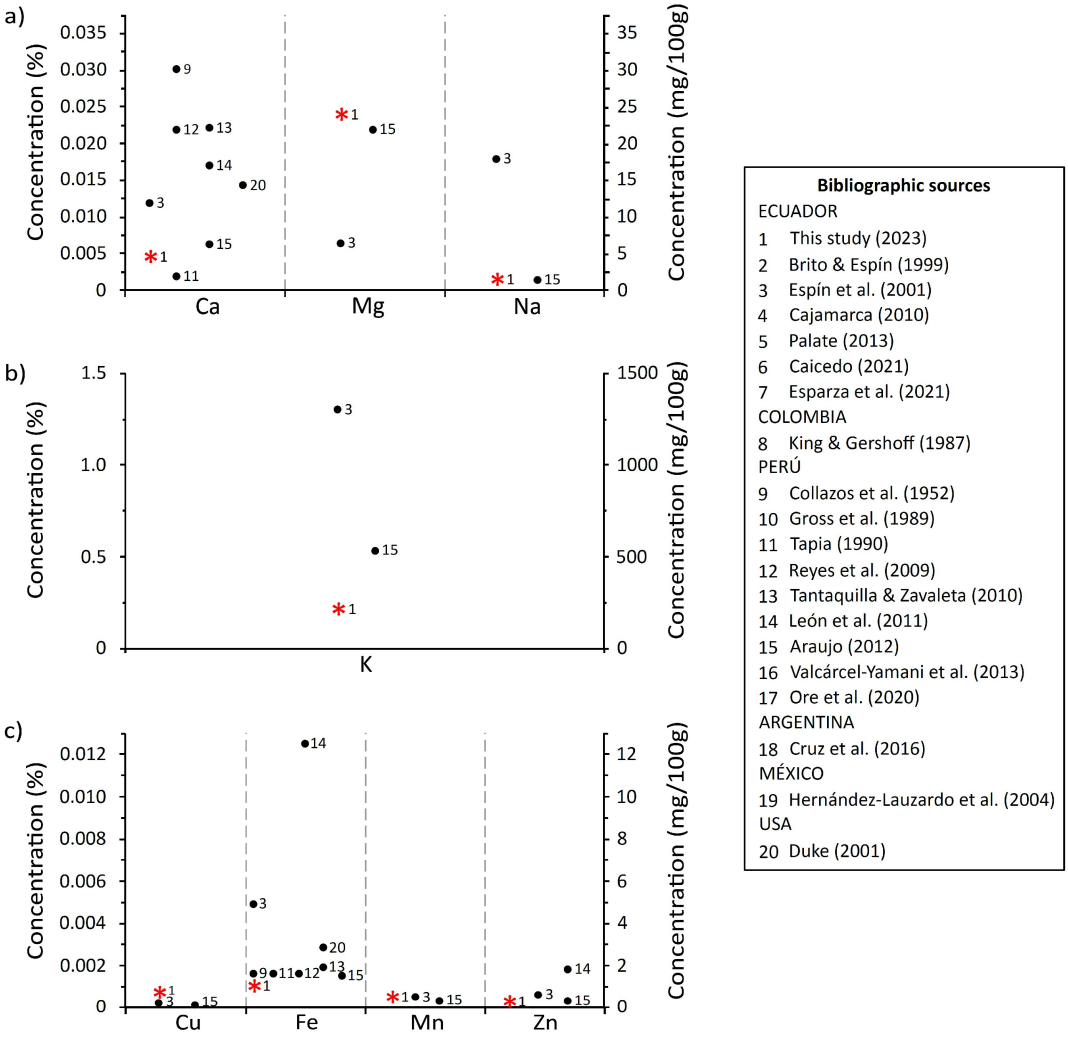

Figure 12. Concentration (in % and in mg/100g) of macronutrients and micronutrients in tubers of *Oxalis tuberosa*, as reported in the literature (black circles) and in this study (red asterisk): **a)** Macronutrients Ca, Mg and Na; **b)** Macronutrient K; **c)** Micronutrients Cu, Fe, Mn and Zn. Each study is represented by a number. Raw data is reported in **Appendix 4**.

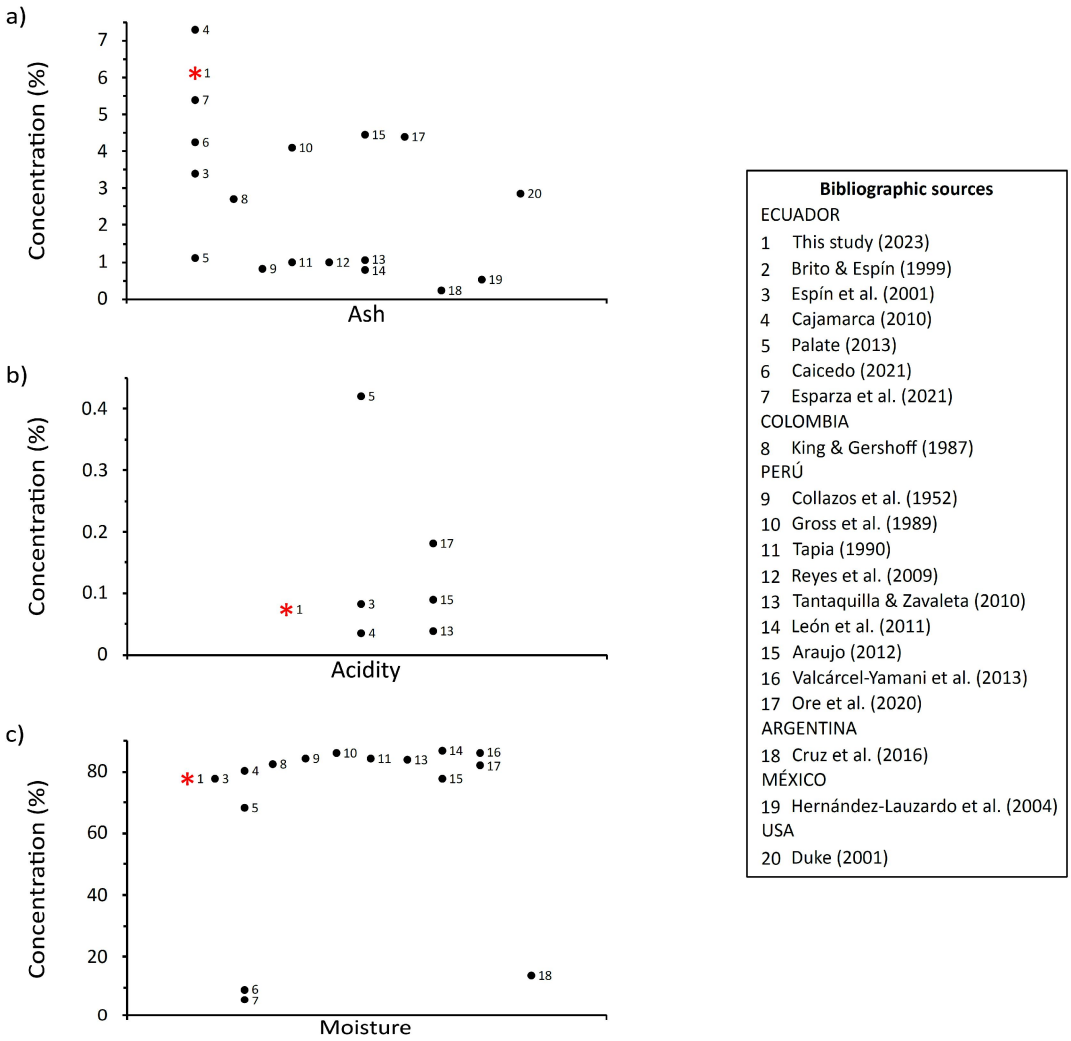

Figure 13. Concentration (%) of other bromatological parameters in tubers of *Oxalis tuberosa*, as reported in the literature (black circles) and in this study (red asterisk): **a)** Ash; **b)** Acidity; **c)** Moisture. Each study is represented by a number. Raw data is reported in **Appendix 4**.

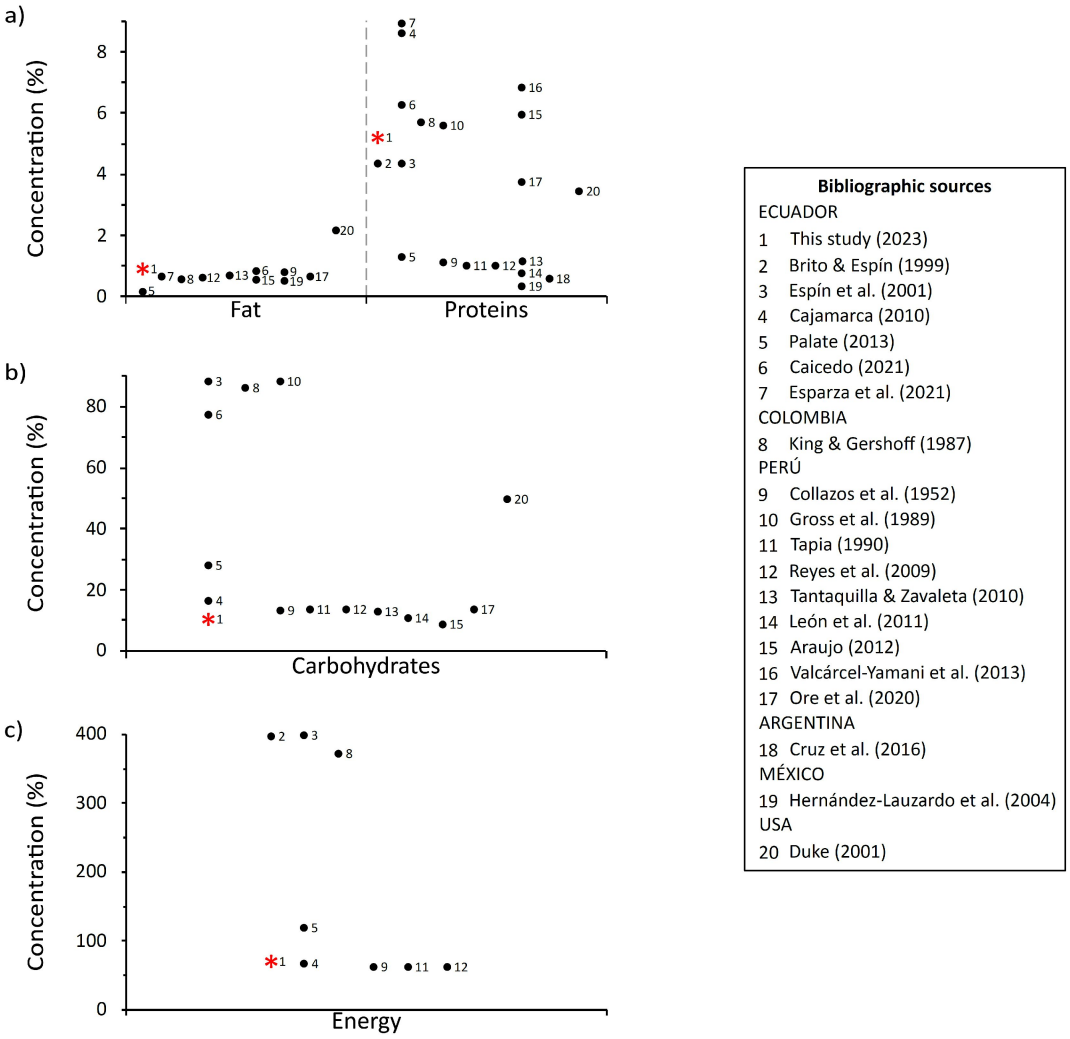

Figure 14. Concentration of macrobiomolecules (%) and energy content (kcal/100g) in tubers of *Oxalis tuberosa*, as reported in the literature (black circles) and in this study (red asterisk): **a)** Fat and Proteins; **b)** Carbohydrates; **c)** Energy. Each study is represented by a number. Raw data is reported in **Appendix 4**.

APPENDICES

Appendix 1. Mann-Whitney statistical tests conducted to compare length (cm), width (cm) and frontal view area (cm^2) of *Oxalis tuberosa* tubers from different morphotypes. The upper triangle shows Bonferroni-corrected *P* values from all pairwise comparisons (*P* values <0.05 are shaded); the lower triangle shows Mann-Whitney statistic values (*U*). To avoid statistical bias due to low sample size, only those morphotypes with a sample size >10 accessions were included in these analyses.

LENGTH

	W.1.0 (*N*=28)	**Y.1.0 (*N*=78)**	**Y.1.1 (*N*=47)**	**Y.2.0 (*N*=28)**	**FP.0.0 (*N*=27)**	**FP.0.2 (*N*=41)**
W.1.0		0.0002***	1	1	1	0.1773
Y.1.0	489		0.0002***	0.0085**	0.0422*	1
Y.1.1	577	979		1	1	0.4541
Y.2.0	316.5	610.5	602		1	1
FP.0.0	273.5	645	535	344		1
FP.0.2	367.5	1327	704	464.5	477	

WIDTH

	W.1.0 (*N*=28)	**Y.1.0 (*N*=78)**	**Y.1.1 (*N*=47)**	**Y.2.0 (*N*=28)**	**FP.0.0 (*N*=27)**	**FP.0.2 (*N*=41)**
W.1.0		1	0.8067	0.9081	1	1
Y.1.0	1048		0.1083	0.4442	1	1
Y.1.1	481.5	1305.5		1	0.684	0.0249*
Y.2.0	277	788	650.5		1	0.2982
FP.0.0	374	991	456	286		1
FP.0.2	479.5	1490.5	587	383	461.5	

FRONTAL VIEW AREA

	W.1.0 (*N*=28)	**Y.1.0 (*N*=78)**	**Y.1.1 (*N*=47)**	**Y.2.0 (*N*=28)**	**FP.0.0 (*N*=27)**	**FP.0.2 (*N*=41)**
W.1.0		0.0045**	1	1	1	0.4175
Y.1.0	587		0.0003***	0.0057**	0.1576	1
Y.1.1	656.5	1001		1	1	0.1247
Y.2.0	377	595.5	623		1	0.7264
FP.0.0	305	703.5	514.5	315.5		1
FP.0.2	393.5	1385	647.5	412	457	

Significance level: * 0.01 < P < 0.05 ** 0.001 < P < 0.01 *** P < 0.001

Appendix 2. Re-sampling results of the Mann-Whitney statistical tests conducted to compare length (cm), width (cm) and frontal view area (cm^2) of *Oxalis tuberosa* tubers from different morphotypes. In order to control for potential bias on the statistical results due to sample size, all tests were conducted with a fixed sample size of *N*=20 accessions, randomly selected. The upper triangle shows Bonferroni-corrected *P* values from all pairwise comparisons (*P* values <0.05 are shaded); the lower triangle shows Mann-Whitney statistic values (*U*).

LENGTH - Re-sampling 1

	W.1.0 (*N*=20)	**Y.1.0 (*N*=20)**	**Y.1.1 (*N*=20)**	**Y.2.0 (*N*=20)**	**FP.0.0 (*N*=20)**	**FP.0.2 (*N*=20)**
W.1.0		0.0089**	1	1	1	0.5775
Y.1.0	72.5		0.0255*	0.111	0.0232*	0.9015
Y.1.1	185	83.5		1	1	1
Y.2.0	156	100.5	167.5		1	1
FP.0.0	149.5	82.5	178	198		1
FP.0.2	123	130	142	165	164.5	

LENGTH - Re-sampling 2

	W.1.0 (*N*=20)	**Y.1.0 (*N*=20)**	**Y.1.1 (*N*=20)**	**Y.2.0 (*N*=20)**	**FP.0.0 (*N*=20)**	**FP.0.2 (*N*=20)**
W.1.0		0.0125*	1	1	1	1
Y.1.0	76		0.9017	0.2789	0.5775	1
Y.1.1	138	130		1	1	1
Y.2.0	143.5	112.5	198		1	1
FP.0.0	133	123	197	187		1
FP.0.2	135.5	161.5	180	184	193	

LENGTH - Re-sampling 3

	W.1.0 (*N*=20)	**Y.1.0 (*N*=20)**	**Y.1.1 (*N*=20)**	**Y.2.0 (*N*=20)**	**FP.0.0 (*N*=20)**	**FP.0.2 (*N*=20)**
W.1.0		0.0017**	1	1	1	1
Y.1.0	57		0.0022**	0.0006***	0.0019**	0.2892
Y.1.1	182	59		1	1	1
Y.2.0	160.5	48	181		1	1
FP.0.0	161.5	58	184	197		1
FP.0.2	157	113	179	200	193	

LENGTH - Re-sampling 4

	W.1.0 (*N*=20)	**Y.1.0 (*N*=20)**	**Y.1.1 (*N*=20)**	**Y.2.0 (*N*=20)**	**FP.0.0 (*N*=20)**	**FP.0.2 (*N*=20)**
W.1.0		0.0062**	1	1	1	1
Y.1.0	69		0.2499	0.0244*	0.0676*	1
Y.1.1	148	111		1	1	1
Y.2.0	159.5	83	186		1	1
FP.0.0	147	94.5	199	194		1
FP.0.2	139.5	140	177	170.5	172	

LENGTH - Re-sampling 5

	W.1.0 (*N*=20)	**Y.1.0 (*N*=20)**	**Y.1.1 (*N*=20)**	**Y.2.0 (*N*=20)**	**FP.0.0 (*N*=20)**	**FP.0.2 (*N*=20)**
W.1.0		0.2074	1	1	1	0.5407
Y.1.0	108.5		0.9017	0.4416	1	1
Y.1.1	165.5	130		1	1	1
Y.2.0	183	119	176		1	1
FP.0.0	147	138.5	178.5	156		1
FP.0.2	122	174	137	136	163	

Significance level: * 0.01 < P < 0.05 ** 0.001 < P < 0.01 *** P < 0.001

WIDTH - Re-sampling 1

	W.1.0 (*N*=20)	**Y.1.0 (*N*=20)**	**Y.1.1 (*N*=20)**	**Y.2.0 (*N*=20)**	**FP.0.0 (*N*=20)**	**FP.0.2 (*N*=20)**
W.1.0		1	1	0.522	1	1
Y.1.0	170.5		0.9291	0.5586	1	1
Y.1.1	147	130.5		1	1	0.1525
Y.2.0	121.5	122.5	192.5		0.7955	0.1202
FP.0.0	197.5	163.5	150.5	128		1
FP.0.2	142	192	104.5	101.5	140	

WIDTH - Re-sampling 2

	W.1.0 (*N*=20)	**Y.1.0 (*N*=20)**	**Y.1.1 (*N*=20)**	**Y.2.0 (*N*=20)**	**FP.0.0 (*N*=20)**	**FP.0.2 (*N*=20)**
W.1.0		1	1	1	1	1
Y.1.0	186.5		1	1	1	1
Y.1.1	168	185		1	1	1
Y.2.0	154	172	184.5		1	1
FP.0.0	189.5	195	173.5	168		1
FP.0.2	179.5	183	152	161	178	

WIDTH - Re-sampling 3

	W.1.0 (*N*=20)	**Y.1.0 (*N*=20)**	**Y.1.1 (*N*=20)**	**Y.2.0 (*N*=20)**	**FP.0.0 (*N*=20)**	**FP.0.2 (*N*=20)**
W.1.0		1	1	1	1	1
Y.1.0	177		0.2789	0.4263	1	1
Y.1.1	135.5	112.5		1	1	1
Y.2.0	141	118.5	184		1	1
FP.0.0	173.5	148.5	147.5	166.5		1
FP.0.2	190.5	166.5	144.5	159	194	

WIDTH - Re-sampling 4

	W.1.0 (*N*=20)	**Y.1.0 (*N*=20)**	**Y.1.1 (*N*=20)**	**Y.2.0 (*N*=20)**	**FP.0.0 (*N*=20)**	**FP.0.2 (*N*=20)**
W.1.0		1	1	0.5575	1	1
Y.1.0	184.5		1	1	1	1
Y.1.1	165	171		1	1	1
Y.2.0	122.5	146	173		1	0.4557
FP.0.0	153	171	190.5	167.5		0.769
FP.0.2	161	160.5	133	119.5	127.5	

WIDTH - Re-sampling 5

	W.1.0 (*N*=20)	**Y.1.0 (*N*=20)**	**Y.1.1 (*N*=20)**	**Y.2.0 (*N*=20)**	**FP.0.0 (*N*=20)**	**FP.0.2 (*N*=20)**
W.1.0		1	1	1	1	1
Y.1.0	176		1	0.8206	1	1
Y.1.1	164.5	138.5		1	1	0.5966
Y.2.0	144	128.5	188		1	0.3838
FP.0.0	184	172	156	146		1
FP.0.2	149	196	123.5	117	163.5	

Significance level: * 0.01 < P < 0.05 ** 0.001 < P < 0.01 *** P < 0.001

FRONTAL VIEW AREA - Re-sampling 1						
	W.1.0 (*N*=20)	**Y.1.0 (*N*=20)**	**Y.1.1 (*N*=20)**	**Y.2.0 (*N*=20)**	**FP.0.0 (*N*=20)**	**FP.0.2 (*N*=20)**
W.1.0		0.042*	1	1	1	0.7019
Y.1.0	89		0.02929	0.0546*	0.0767*	1
Y.1.1	199.5	85		1	1	0.7017
Y.2.0	180	92	173		1	1
FP.0.0	157	96	167	178.5		1
FP.0.2	126	146	126	138	144.5	

FRONTAL VIEW AREA - Re-sampling 2						
	W.1.0 (*N*=20)	**Y.1.0 (*N*=20)**	**Y.1.1 (*N*=20)**	**Y.2.0 (*N*=20)**	**FP.0.0 (*N*=20)**	**FP.0.2 (*N*=20)**
W.1.0		0.2155	1	1	1	1
Y.1.0	109		1	0.6796	1	1
Y.1.1	169.5	139		1	1	1
Y.2.0	180	125.5	190		1	1
FP.0.0	155	143	192	174.5		1
FP.0.2	151	176	176	171	183.5	

FRONTAL VIEW AREA - Re-sampling 3						
	W.1.0 (*N*=20)	**Y.1.0 (*N*=20)**	**Y.1.1 (*N*=20)**	**Y.2.0 (*N*=20)**	**FP.0.0 (*N*=20)**	**FP.0.2 (*N*=20)**
W.1.0		0.0084**	1	1	1	1
Y.1.0	72		0.0051**	0.0007***	0.0059**	0.3846
Y.1.1	198	67		1	1	1
Y.2.0	184	48.5	186		1	1
FP.0.0	175	68.5	178	183.5		1
FP.0.2	169	117	160	177	189	

FRONTAL VIEW AREA - Re-sampling 4						
	W.1.0 (*N*=20)	**Y.1.0 (*N*=20)**	**Y.1.1 (*N*=20)**	**Y.2.0 (*N*=20)**	**FP.0.0 (*N*=20)**	**FP.0.2 (*N*=20)**
W.1.0		0.0152*	1	1	1	1
Y.1.0	78		0.334	0.03356	0.1998	1
Y.1.1	172.5	115		1	1	1
Y.2.0	193	86.5	181		1	1
FP.0.0	163	108	197	180.5		1
FP.0.2	135	152	159	142.5	157	

FRONTAL VIEW AREA - Re-sampling 5						
	W.1.0 (*N*=20)	**Y.1.0 (*N*=20)**	**Y.1.1 (*N*=20)**	**Y.2.0 (*N*=20)**	**FP.0.0 (*N*=20)**	**FP.0.2 (*N*=20)**
W.1.0		0.5777	1	1	1	0.7478
Y.1.0	123		0.7714	0.1852	1	1
Y.1.1	189	127.5		1	1	0.8472
Y.2.0	189	107	187		1	0.637
FP.0.0	159	137.5	175	146		1
FP.0.2	127	177	129	124.5	158	

Significance level: * 0.01 < P < 0.05 ** 0.001 < P < 0.01 *** P < 0.001

Appendix 3. Raw bromatological data of all *Oxalis tuberosa* accessions analyzed, organized by morphotype code. The $\bar{X} \pm 1$ standard deviation (SD) per each bromatological parameter are also shown. Blank lines (—) represent parameters that could not be analyzed because not enough sample was available. All concentrations are shown as percentage (%) to facilitate comparisons among parameters. Data from tubers harvested from the demonstrative agricultural plot in Cotacachi (Imbabura) are shown in **black**, while data from tubers harvested from the ex situ collection at Yachay Botanical Garden (YBG) are shown in **red**. The Cotacachi plot was planted using the *O. tuberosa* germplasm (accessions) from YBG.

Morphotype Accession No.	**Ca (%)**	**K (%)**	**Mg (%)**	**Na (%)**	**Cu (%)**	**Fe (%)**	**Mn (%)**	**Zn (%)**	**Ash (%)**	**Acidity (%)**	**Moisture (%)**	**Fat (%)**	**Proteins (%)**	**Carbohydrates (%)**	**Energy (kcal/100g)**
W.1.0															
116	—	0.1589	0.02526	0.00188	0.00088	0.00097	0.000498	0.00026	—	—	—	—	—	—	—
131	0.00477	—	0.02045	0.0015	0.00035	0.00124	0.00013	0.00026	7.66	0.07	78.28	1.43	5.22	7.41	63.39
307	—	0.172	0.02064	0.00117	0.00086	0.00096	0.000785	0.00026	—	—	—	—	—	—	—
334	0.00453	0.236	0.02687	0.00112	0.00081	0.00153	0.000625	0.00027	5.21	0.08	76.32	0.55	5.49	12.43	76.63
336	0.00485	0.293	0.02266	0.00167	0.0009	0.00126	0.00044	0.00026	4.33	0.07	78.86	0.73	4.46	11.62	70.89
337	—	0.138	0.04585	0.00159	0.00098	0.00096	0.000595	0.00024	—	—	—	—	—	—	—
$\bar{X}$±1SD (*N*=sample size)	0.00472 ±0.00017 (*N*=3)	0.2 ±0.064 (*N*=5)	0.027 ±0.01 (*N*=6)	0.0015 ±0.0003 (*N*=6)	0.0008 ±0.0002 (*N*=6)	0.0012 ±0.0002 (*N*=6)	0.00051 ±0.0002 (*N*=6)	0.00026 ±0.00001 (*N*=6)	5.73 ±1.73 (*N*=3)	0.073 ±0.0058 (*N*=3)	77.82 ±1.33 (*N*=3)	0.903 ±0.465 (*N*=3)	5.057 ±0.53 (*N*=3)	10.49 ±2.7 (*N*=3)	70.303 ±6.64 (*N*=3)
Y.1.0															
54	0.00462	—	0.02051	0.00181	0.00022	0.00119	0.00052	0.00025	6.76	0.07	80.42	0.78	6.1	5.94	55.18
80	—	0.2587	0.02526	0.00103	0.00081	0.00096	0.00015	0.00026	—	—	—	—	—	—	—
203	—	0.212	0.02145	0.0016	0.00077	0.00096	0.000648	0.000245	—	—	—	—	—	—	—
239	0.0047	—	0.02088	0.00151	0.00015	0.00182	0.00055	0.00024	7.14	0.07	79.72	0.72	6.21	6.21	56.16
273	—	0.191	0.02863	0.00108	0.00099	0.00098	0.000253	0.00027	—	—	—	—	—	—	—
292	—	0.101	0.02463	0.00169	0.00088	0.00096	0.000715	0.0003	—	—	—	—	—	—	—
299	—	0.286	0.02097	0.00119	0.00069	0.00096	0.00043	0.00025	—	—	—	—	—	—	—
318	—	0.1987	0.02263	0.00158	0.0009	0.00096	0.00051	0.00027	—	—	—	—	—	—	—
319	—	0.204	0.02467	0.00158	0.00072	0.00098	0.0006	0.00021	—	—	—	—	—	—	—
320	0.00469	0.24	0.02563	0.00125	0.00098	0.0013	0.00044	0.00026	6.75	0.08	84.4	1.08	4.46	3.31	40.8
$\bar{X}$±1SD (*N*=sample size)	0.00467 ±0.00004 (*N*=3)	0.21 ±0.055 (*N*=8)	0.024 ±0.0027 (*N*=10)	0.0014 ±0.0003 (*N*=10)	0.0007 ±0.0003 (*N*=10)	0.0011 ±0.0003 (*N*=10)	0.00048 ±0.00017 (*N*=10)	0.00026 ±0.00002 (*N*=10)	6.883 ±0.22 (*N*=3)	0.073 ±0.0058 (*N*=3)	81.513 ±2.52 (*N*=3)	0.86 ±0.193 (*N*=3)	5.59 ±0.98 (*N*=3)	5.153 ±1.6 (*N*=3)	50.71 ±8.6 (*N*=3)
Y.1.1															
73	0.00475	0.159	0.02698	0.00189	0.00028	0.00125	0.00052	0.00025	6.11	0.08	77.39	1.1	4.96	10.44	71.5

Morphotype Accession No.	**Ca (%)**	**K (%)**	**Mg (%)**	**Na (%)**	**Cu (%)**	**Fe (%)**	**Mn (%)**	**Zn (%)**	**Ash (%)**	**Acidity (%)**	**Moisture (%)**	**Fat (%)**	**Proteins (%)**	**Carbohydrates (%)**	**Energy (kcal/100g)**
135	—	0.199	0.02076	0.00174	0.00093	0.00098	0.000573	0.00026	—	—	—	—	—	—	—
169	—	0.229	0.02591	0.00115	0.00082	0.00099	0.000493	0.0003	—	—	—	—	—	—	—
328	—	0.251	0.0213	0.00103	0.00055	0.00099	0.000403	0.00027	—	—	—	—	—	—	—
329	—	0.161	0.02354	0.00182	0.0008	0.00096	0.00059	0.00017	—	—	—	—	—	—	—
$\bar{X}$±1SD (*N*=sample size)	0.00475 (*N*=1)	0.2 ±0.04 (*N*=5)	0.024 ±0.0027 (*N*=5)	0.0015 ±0.0004 (*N*=5)	0.0007 ±0.0003 (*N*=5)	0.001 ±0.0001 (*N*=5)	0.0005 ±0.00007 (*N*=5)	0.00025 ±0.00005 (*N*=5)	6.11 (*N*=1)	0.08 (*N*=1)	77.39 (*N*=1)	1.1 (*N*=1)	4.96 (*N*=1)	10.44 (*N*=1)	71.5 (*N*=1)
Y.2.0															
71	—	0.147	0.0261	0.00111	0.00052	0.00097	0.000353	0.00026	—	—	—	—	—	—	—
221	0.00478	—	0.02049	0.00147	0.00015	0.00125	0.00026	0.00026	6.92	0.08	72.45	0.41	5.89	14.33	84.57
$\bar{X}$±1SD (*N*=sample size)	0.00478 (*N*=1)	0.15 (*N*=1)	0.023 ±0.004 (*N*=2)	0.0013 ±0.00025 (*N*=2)	0.0003 ±0.0003 (*N*=2)	0.0011 ±0.0002 (*N*=2)	0.0003 ±0.00007 (*N*=2)	0.00026 ±0 (*N*=2)	6.92 (*N*=1)	0.08 (*N*=1)	72.45 (*N*=1)	0.41 (*N*=1)	5.89 (*N*=1)	14.33 (*N*=1)	84.57 (*N*=1)
Y.2.1															
66	—	0.216	0.02897	0.00139	0.00096	0.00095	0.000846	0.00025	—	—	—	—	—	—	—
$\bar{X}$±1SD (*N*=sample size)	—	0.216 (*N*=1)	0.029 (*N*=1)	0.0014 (*N*=1)	0.00096 (*N*=1)	0.00095 (*N*=1)	0.00085 (*N*=1)	0.00025 (*N*=1)	—	—	—	—	—	—	—
YF.0.1															
180	0.00454	—	0.01998	0.00157	0.00019	0.0012	0.00036	0.00025	6.84	0.08	70.48	1.59	6.25	14.84	98.67
$\bar{X}$±1SD (*N*=sample size)	0.00454 (*N*=1)	—	0.02 (*N*=1)	0.0016 (*N*=1)	0.0002 (*N*=1)	0.0012 (*N*=1)	0.00036 (*N*=1)	0.00025 (*N*=1)	6.84 (*N*=1)	0.08 (*N*=1)	70.48 (*N*=1)	1.59 (*N*=1)	6.25 (*N*=1)	14.84 (*N*=1)	98.67 (*N*=1)
F.0.3															
339	—	0.262	0.02384	0.00113	0.00076	0.00097	0.000358	0.00028	—	—	—	—	—	—	—
$\bar{X}$±1SD (*N*=sample size)	—	0.26 (*N*=1)	0.024 (*N*=1)	0.0011 (*N*=1)	0.00076 (*N*=1)	0.00097 (*N*=1)	0.00036 (*N*=1)	0.00028 (*N*=1)	—	—	—	—	—	—	—
FP.0.0															
32	0.00412	0.2586	0.02269	0.00108	0.00079	0.0009	0.00016	0.00023	—	—	—	—	—	—	—
56	0.00428	0.2586	0.02269	0.00108	0.00095	0.0009	0.000695	0.00023	—	—	—	—	—	—	—
61	0.0065	0.2165	0.0233	0.00156	0.00099	0.00099	0.000543	0.00023	4.83	0.07	81.4	0.91	2.39	10.47	59.63
70	—	0.2589	0.02315	0.00188	0.00094	0.00085	0.000552	0.00026	—	—	—	—	—	—	—

Morphotype Accession No.	**Ca (%)**	**K (%)**	**Mg (%)**	**Na (%)**	**Cu (%)**	**Fe (%)**	**Mn (%)**	**Zn (%)**	**Ash (%)**	**Acidity (%)**	**Moisture (%)**	**Fat (%)**	**Proteins (%)**	**Carbohydrates (%)**	**Energy (kcal/100g)**
108	0.00475	0.212	0.02175	0.00165	0.00034	0.00125	0.00034	0.00025	5.14	0.07	80.34	0.66	5.5	8.36	61.38
$\overline{X}$±1SD (*N*=sample size)	0.00491 ±0.001 (*N*=4)	0.24 ±0.024 (*N*=5)	0.023 ±0.0006 (*N*=5)	0.0015 ±0.0004 (*N*=5)	0.0008 ±0.0003 (*N*=5)	0.00098 ±0.0002 (*N*=5)	0.00046 ±0.0002 (*N*=5)	0.00024 ±0.00001 (*N*=5)	4.985 ±0.22 (*N*=2)	0.07 ±0 (*N*=2)	80.87 ±0.75 (*N*=2)	0.785 ±0.177 (*N*=2)	3.945 ±2.199 (*N*=2)	9.415 ±1.5 (*N*=2)	60.51 ±1.24 (*N*=2)
FP.0.2															
192	—	0.197	0.02244	0.00157	0.00077	0.00098	0.00053	0.0003	—	—	—	—	—	—	—
223	—	0.259	0.02963	0.00158	0.00069	0.00095	0.000478	0.00026	—	—	—	—	—	—	—
228	0.00444	—	0.02142	0.00149	0.00015	0.00125	0.00016	0.00025	5.87	0.07	72.45	0.97	5.31	15.4	91.57
305	—	0.155	0.02224	0.00158	0.00064	0.00094	0.000368	0.00026	—	—	—	—	—	—	—
$\overline{X}$±1SD (*N*=sample size)	0.00444 (*N*=1)	0.2 ±0.05 (*N*=3)	0.024 ±0.0038 (*N*=4)	0.0016 ±0.00004 (*N*=4)	0.00056 ±0.0003 (*N*=4)	0.001 ±0.0002 (*N*=4)	0.00038 ±0.00016 (*N*=4)	0.00027 ±0.00002 (*N*=4)	5.87 (*N*=1)	0.07 (*N*=1)	72.45 (*N*=1)	0.97 (*N*=1)	5.31 (*N*=1)	15.4 (*N*=1)	91.57 (*N*=1)
P.0.4															
$\overline{X}$±1SD (*N*=sample size)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
$\overline{X}$±1SD	**0.0047 ±0.00055 (*N*=14)**	**0.21 ±0.048 (*N*=29)**	**0.024 ±0.0046 (*N*=35)**	**0.0015 ±0.0003 (*N*=35)**	**0.0007 ±0.0003 (*N*=35)**	**0.001 ±0.0002 (*N*=35)**	**0.00047 ±0.0002 (*N*=35)**	**0.00026 ±0.00002 (*N*=35)**	**6.13 ±1.049 (*N*=12)**	**0.0742 ±0.0052 (*N*=12)**	**77.71 ±4.13 (*N*=12)**	**0.911 ±0.348 (*N*=12)**	**5.187 ±1.072 (*N*=12)**	**10.063 ±3.88 (*N*=12)**	**69.2 ±16.59 (*N*=12)**

Appendix 4. Average concentrations of different bromatological parameters as reported in the literature, organized by country. Only those parameters that were also analyzed in the present study are shown. To facilitate comparison, all concentrations were converted to percentage (%). In some cases, raw data from a publication had to be reanalyzed in order to calculate the $\overline{x} \pm 1$ standard deviation (SD), and the sample size (*N*).

No.	Study	Ca (%)	K (%)	Mg (%)	Na (%)	Cu (%)	Fe (%)	Mn (%)	Zn (%)	Ash (%)	Acidity (%)	Moisture (%)	Fat (%)	Proteins (%)	Carbohydrates (%)	Energy (Kcal/100g)
	ECUADOR															
1	This study (2023)	0.0047 ±0.00055 (*N*=14)	0.21 ±0.048 (*N*=29)	0.024 ±0.0046 (*N*=35)	0.0015 ±0.0003 (*N*=35)	0.0007 ±0.0003 (*N*=35)	0.001 ±0.0002 (*N*=35)	0.00047 ±0.0002 (*N*=35)	0.00026 ±0.00002 (*N*=35)	6.13 ±1.049 (*N*=12)	0.0742 ±0.0052 (*N*=12)	77.71 ±4.13 (*N*=12)	0.911 ±0.348 (*N*=12)	5.187 ±1.072 (*N*=12)	10.063 ±3.88 (*N*=12)	69.2 ±16.59 (*N*=12)
2	Brito and Espín (1999)	—	—	—	—	—	—	—	—	—	—	—	—	4.35 ±0.45 (*N*=46)	—	396 ±0.04 (*N*=46)
3	Espín et al. (2001)	0.012	1.3	0.0065	0.018	0.0002	0.0049	0.0005	0.0006	3.39	0.0829	77.73	—	4.35 ±0.45 (*N*=46)	88.19	399
4	Cajamarca (2010)	—	—	—	—	—	—	—	—	7.3 [c]	0.0341 [c]	80.1 [c]	—	8.6 [c]	16.1 [c]	67 [c]
5	Palate (2013)	—	—	—	—	—	—	—	—	1.1	0.42	68.3	0.167	1.3	27.93	118.42
6	Caicedo (2021)	—	—	—	—	—	—	—	—	4.23	—	9.32	0.83	6.28	77.25	—
7	Esparza et al. (2021)	—	—	—	—	—	—	—	—	5.4 ±0.28 (*N*=3)	—	6.03 ±0.11 (*N*=3)	0.64 ±0.04 (*N*=3)	8.92 ±0.77 (*N*=3)	—	—
	COLOMBIA															

No.	Study	Ca (%)	K (%)	Mg (%)	Na (%)	Cu (%)	Fe (%)	Mn (%)	Zn (%)	Ash (%)	Acidity (%)	Moisture (%)	Fat (%)	Proteins (%)	Carbohydrates (%)	Energy (Kcal/100g)
8	King and Gershoff (1987)	—	—	—	—	—	—	—	—	2.7 (1.9–3.5) [a]	—	82.4 (80.2–84.6) [a]	0.55 (0.5–0.6) [a]	5.7 (3–8.4) [a]	85.9 (83–88.8) [a]	371.35 (368.7–374) [a]
	PERÚ															
9	Collazos et al. (1952)	0.03	—	—	—	—	0.0016	—	—	0.8	—	84.1	0.8	1.1	13.1	62
10	Gross et al. (1989)	—	—	—	—	—	—	—	—	4.1	—	86.2	—	5.6	87.9	—
11	Tapia (1990)	0.002	—	—	—	—	0.0016	—	—	1	—	84.1	—	1	13.3	61
12	Reyes et al. (2009)	0.022	—	—	—	—	0.0016	—	—	1	—	—	0.6	1	13.3	61
13	Tantaquilla and Zavaleta (2010)	0.0221	—	—	—	—	0.0019	—	—	1.05	0.039	83.83	0.7	1.14	12.47	—
14	León et al. (2011)	0.0172	—	—	—	—	0.0125	—	0.0018	0.78	—	86.79	—	0.77	10.41	—
15	Araujo (2012)	0.0064 (0.0046–0.0082) [b][c]	0.53 (0.48–0.58) [b][c]	0.022 (0.0215–0.022) [b][c]	0.0016 (0.0011–0.002) [b][c]	0.0001 (0.00009–0.0001) [b][c]	0.0015 (0.001–0.002) [b][c]	0.0003 (0.0001–0.0004) [b][c]	0.0003 (0.00028–0.0003) [b][c]	4.44 (4.42–4.45) [b] [c]	0.089 (0.071–0.1) [b] [c]	77.65 (76.37–78.93) [b] [c]	0.53 (0.51–0.54) [b] [c]	5.94 (4.93–6.94) [b] [c]	8.38 (5.89–10.87) [b] [c]	—
16	Valcárcel-Yamani et al. (2013)	—	—	—	—	—	—	—	—	—	—	86.23 [c]	—	6.84	—	—
17	Ore et al. (2020)	—	—	—	—	—	—	—	—	4.39 [c]	0.18 [c]	81.92 [c]	0.66 [c]	3.74 [c]	13.32 [c]	—

No.	Study	Ca (%)	K (%)	Mg (%)	Na (%)	Cu (%)	Fe (%)	Mn (%)	Zn (%)	Ash (%)	Acidity (%)	Moisture (%)	Fat (%)	Proteins (%)	Carbohydrates (%)	Energy (Kcal/100g)
	ARGENTINA															
18	Cruz et al. (2016)	—	—	—	—	—	—	—	—	0.24	—	14	—	0.58	—	—
	MÉXICO															
19	Hernández-Lauzardo et al. (2004)	—	—	—	—	—	—	—	—	0.52	—	—	0.52	0.34	—	—
	USA															
20	Duke (2001)	0.014 (0.004–0.0247) [a]	—	—	—	—	0.003 (0.0008–0.0049) [a]	—	—	2.85 (0.8–4.9) [a]	—	—	2.15 (0.6–3.7) [a]	3.45 (0.7–6.2) [a]	49.5 (13.8–85.2) [a]	—

[a] Average calculated based only on two data points reported in the original publication: the maximum and minimum values.
[b] Average calculated based on three or more data points reported in the original publication.
[c] Data reported corresponds to that most directly comparable to this study's data, in terms of sample nature (dry or wet weight, depending on the parameter).