

MORPHOLOGICAL AND ECOGEOGRAPHIC STUDY OF THE DIVERSITY OF CASSAVA (*Manihot esculenta* Crantz) IN ECUADOR

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ABSTRACT

Cassava (*Manihot esculenta* Crantz) is a crop of nutritional and economic importance worldwide, cultivated in more than 100 tropical and subtropical countries including Ecuador, traditionally cultivated in its three continental regions: the Amazon, the Coast and in the valleys of the Sierra. The purpose of this study was to characterize 195 accessions from INIAP's Ecuadorian cassava collection through 1) morphological characterization with qualitative and quantitative descriptors; and 2) ecogeographic characterization to know the climatic, geophysical and edaphic conditions in which cassava grows and which environments are frequent or marginal for its cultivation. For the morphological characterization, 27 morphological descriptors were used (18 qualitative and nine quantitative), and for the ecogeographic characterization, 55 variables (41 climatic, two geophysical and 12 edaphic). As a result, four morphological groups and three ecogeographic groups were identified. In the research, morphological variability was evidenced, mainly in descriptors related to the leaf, stems and inflorescences. In addition, it was possible to identify accessions that can adapt to extreme conditions of drought and poor soils, which could be used for improvement.

KEYWORDS

Variability, adaptation, GIS

INTRODUCTION

Cassava (*Manihot esculenta* Crantz) is an important food and economical crop worldwide, grown in more than 100 tropical and subtropical countries [1–3]. In developing countries, cassava is usually cultivated by subsistence farmers since it presents easy propagation systems, high tolerance to abiotic factors such as drought and biotic factors such as insects and viruses; and, a low nutrient demand, producing reasonably well in critical climatic and soil conditions [4–7]. In South America, the highest production is in Brazil, with 17,497,115 metric tons in 2019, while Ecuador occupies the eighth place; however, cassava is the fourth temporary crop with the largest surface area at the national level, 13,601 hectares and a production of 69,863 m tons [8]. Cassava has traditionally been cultivated in the Amazon region, followed by the Coast and valleys of the Sierra [9]. Amazonian nationalities recognize around 200 types of cassava, classifying them as bitter and sweet [10]. In the province of Manabí (Coast Region), more than self-consumption, it also generates economic income through the commercialization of fresh and/or processed cassava as flour [11].

Morphological characterization has been used for several purposes, including identifying duplicates, studies of variation, and correlation with characteristics of agronomic importance [12,13]. In addition, morphological traits are helpful for preliminary assessment (pre-breeding) because they offer a quick and easy approach to assessing the extent of diversity. The registration of a sample or variety's characteristics is based on a list of morphological and agronomic descriptors, i.e. essential and useful characteristics in the description of the sample. These descriptors must be readily observable, have high discriminant action and low environmental influence [14–17]. For example, the EMBRAPA-Brazil Corporation established 75 morphological descriptors for cassava [18]; these descriptors have allowed morphologically validating 26 ethno-varieties in Peru [19], 116 elite genotypes collected in Benin, Africa [20], 47 traditional varieties in Brazil [21], 159 accessions conserved in the field in Côte d'Ivoire, Africa [22] and in Mexico 40 accessions were characterized from a germplasm bank [23].

On the other hand, ecogeographic characterization is a process that allows comparing the diversity of a species or group of species, allowing the completion of the morphological and genotypic information using the environmental information from the germplasm collection site [24,25]. For example, Mezghani et al. [26] used ecogeographic information to characterize wild relatives of carrot (*Daucus* L.) subjected to abiotic stresses of interest in crop improvement and to assess their ex-situ and in-situ conservation status in Tunisia. Likewise, it can be used to understand environmental conditions and associated biotic and abiotic factors to which plant species have adapted, as was the study carried out in teosinte [27]. At present, programs have been developed that use geographic information systems, such as CAPFITOGEN [28]. This program uses ecogeographic analysis tools to carry out several ecogeographic crop studies in Ecuador, e.g. maize (*Zea mays* L.) [29], capulin

(*Prunus serotina* Ehrh. subsp. *capuli* (Cav. ex Spreng.) McVaugh) [30] and ulluco (*Ullucus tuberosus* Caldas) [31].

The purpose of this study was to characterize 195 accessions from INIAP's Ecuadorian cassava collection through 1) morphological characterization with qualitative and quantitative descriptors; and 2) ecogeographic characterization to know the climatic, geophysical and soil conditions where cassava grows, and with environmental cultivation conditions that are either frequent or marginal.

MATERIALS AND METHODS

Cassava collection

The cassava collection encompasses 195 accessions (96 accessions collected and acquired more than two decades ago and 99 accessions collected from 2012 and 2013). The collection of landraces was carried out to representative cropping areas throughout Ecuador. Collections were performed according to standard protocols established by the National Department of Plant Genetic Resources of the National Institute for Agricultural Research INIAP, of Ecuador [32]. As only cultivated materials were collected, not special permit from the Ministry of Environment and Water was necessary for collection, which is necessary only for wild species. Passport data included information on the collector, the provider, geographical location: latitude, longitude, altitude, ecological information, soil, and uses. We collected cuttings from each accession, then watered, labelled and stored them in plastic bags until they arrived at the Experimental Station fields for planting.

Morphological characterization

The 195 accessions of the Ecuadorian collection were planted at the Central Amazon Experimental Station of INIAP, located at Via Sacha-San Carlos at 250 m a.s.l., with an average temperature of 24°C and average precipitation of 3100 mm. The cuttings were previously planted in plastic grow bags with the substrate (black soil, compost and coffee husks) where they remained for a period of 4 to 8 weeks, and then five plants per accession were transplanted into the field at a distance of 1 m between plants and 2 m between accessions. Pruning was performed after 30 days to leave a single shoot for characterization.

The collection was morphologically characterized by using 27 morphological descriptors (18 qualitative and nine quantitative) according to Fukuda and Guevara [18]. Quantitative descriptors were recorded based on the average value obtained from five random plants within each accession. Quantitative descriptors include the length of leaf lobe, the width of leaf lobe, the number of leaf lobes, the distance between leaf scars, plant height, height to first branching, total fresh weight of storage roots per plant, length of storage root, and the diameter of the storage root. The qualitative descriptors were the initial vigour of the plant, the colour of apical leaves, pubescence on apical leaves, shape of the central leaflet, petiole colour, leaf colour, colour of stem epidermis, flowering, colour of end branches of adult plant, plant earliness, the shape of the plant, root constrictions, texture of the root epidermis, the extent of the root peduncle, colour of the root cortex, colour of the root pulp (parenchyma), cortex, i.e. ease of peeling and shape of the root.

Ecogeographical Characterization

As mentioned before, the 195 accessions studied were collected in the Coast and the Amazonia regions of Ecuador. Plains generally form the landscape in the Coast region, and the Amazonia is formed by hills that originate in the eastern part of the Andes and descend towards the Amazonian plains. Humidity percentages close to 100% are found in the Amazonia throughout the year and for the Coast region during the winter period. The annual mean temperature varies between 23 and 26° C in both regions. Precipitation in the Amazonia is continuous and intense throughout the year (3000 mm average), while on the Coast, the strong winter period is from February to May and mild winter period from September to November.

On the contrary, the dry months are July and August, and summer weather from December to January [33]. Moreover, soils on the Coast are usually flood plains that have accumulated fertile sediments from the highlands. As a result, the soils of the Ecuadorian Amazon have great acidity [34].

Using the ECOGEO tool of the CAPFITOGEN program [28], the ecogeographic characterization was carried out using the 55 ecogeographic variables (Supplementary Table 1). First applying ECOGEO, a grid resolution of 5 × 5 km (2.5 arc-minutes) was chosen to extract the information, and subsequently using the INFOSTAT program (version 2018) to edit the recorded data for analysis [35].

Ecogeographical Land Characterization Map

To define the environments in which each cassava landrace is grown, a specific ecogeographic land characterization map for cassava landraces was developed for Ecuador. Using the CAPFITOGEN program and the ELC Map tool [28], the first step was creating the map with a grid cell size of 5 km by 5 km (2.5 arc-minutes) covering the Coast region and the Amazon of Ecuador. Next, the centroid of each cell was calculated, and data were extracted from 55 ecogeographic variables (41 climatic, two geophysical, 12 edaphic) compiled as GIS layers. Table 1 presents the data sources, formats, and scales or resolution of thematic layers. The variables from each module were then submitted to correlation analysis, principal components and random forest to identify redundant information. For each variable, the number of significant correlations was computed. According to this number, variables were then arranged in ascending order, and those with fewer than the median number of significant correlations were selected for further consideration. On the other hand, four Ecuadorian breeding research experts were consulted about the environmental conditions affecting the cultivation of cassava landraces. Combining the different climatic, edaphic, and geophysical clusters provided the ecogeographic categories used to generate the ELC map.

Statistical analysis

The morphological and ecogeographic characterization data was examined using the INFOSTAT program version 2018 [35]. All the quantitative variables recorded were

subjected to descriptive statistical analysis (minimum, maximum, average, standard deviation and coefficient of variation) to appreciate the variability of each trait among the cassava varieties. To identify the variables with more significant variation, the CV was calculated for quantitative variables and the index of deviation from the mode (DM) proposed by [36] for qualitative variables. The formula used to calculate DM was $1 - ((\sum_{i=1}^k (f_m - f_i) / N(k-1))$ where f_m is the frequency of the modal category, k is the number of categories, and N is the number of cases. Thus, DM ranges between 0 (no variation) when all the cases fall in a single category and 1 (maximum variation) when the cases are distributed evenly across the categories. For the multivariate analysis, Gower distance and Ward's algorithm were applied to determine the correlation among accessions [35].

RESULTS

Morphological characterization

In this study, the existence of morphological variability within the 195 accessions evaluated was evidenced.

Quantitative descriptors

Table 1 summarizes the values for nine quantitative descriptors. The range of the values produced for the total fresh weight of the storage roots per plant was from 0.84 kg to 22.00 kg, for the height at the first branch from 10.00 cm to 233.33 cm. The coefficients of variation ranged from 13.13% (length of the leaf lobe) to 61.22% (total fresh weight of storage roots per plant). Based on the nine quantitative traits, seven had high coefficients of variation ($CV > 15\%$). Only two characters have low coefficients of variation; these are the number of leaf lobes (14.18%) and the length of the leaf lobe (13.13%).

Table 1. Morphological variability with quantitative characters in cassava collection from the Ecuadorian Andes.

Variables	CV	Min	Max	Mean±SD
Total fresh weight of storage roots per plant, kg	61.22	0.84	22.00	5.85±3.58
Height to first branching, cm	42.67	10.00	233.33	96.87±41.33
Length of storage root, cm	27.04	23.20	84.00	44.97±12.16
Plant height, cm	24.63	83.33	393.33	251.03±61.82
Diameter of storage root, cm	24.26	3.00	17.20	9.31±2.30
Distance between leaf scars, cm	19.48	0.28	0.70	0.49±0.10
Width of leaf lobe, cm	16.19	2.48	8.57	5.61±0.91
Number of leaf lobes	14.18	5.00	11.00	7.76±1.10
Length of leaf lobe, cm	13.13	11.95	29.90	20.37±2.67

Qualitative descriptors

Table 2 includes the index of deviation from the mode values, where the most frequent character in the collection is observed for each variable. Most of the descriptors presented deviation indices above 0.25. The descriptors that presented the most significant variation were Pubescence in apical leaves (0.96), the Colour of apical leaves (0.88), Extension of

the root peduncle (0.86). In the descriptors with more significant variability, most of the accessions presented absence of the apical leaf pubescence, light green apical leaves and short root peduncle.

Table 2. Morphological variability with qualitative characters in cassava collection from the Ecuadorian Andes.

Variables	Index of deviation from the mode	Mode
Pubescence on apical leaves	0.96	Absent
Colour of apical leaves	0.88	Light green
Extent of root peduncle	0.86	Short
Colour of root cortex	0.76	Purple
Initial vigour of the plant	0.70	Good
Petiole colour	0.67	Red with green
Colour of end branches of adult plant	0.62	Dark green
Plant earliness	0.62	Intermediate
Shape of central leaflet	0.56	Elliptical lanceolate
Colour of stem epidermis	0.53	Dark green
Flowering	0.52	Present
Texture of root epidermis	0.45	Rough
Shape of root	0.43	Conical-cylindrical
Root constrictions	0.38	Absent
Colour of root pulp (parenchyma)	0.26	White
Cortex: ease of peeling	0.25	Easy
Shape of plant	0.11	Umbrella
Leaf colour	0.07	Dark green

Multivariate analysis: Clusters description

Four different groups were obtained based on the multivariate grouping analysis with quantitative and qualitative morphological data (Fig. 1). The genetic relationships between the 195 accessions evaluated determine a tendency to group according to their origin. Group 1 represented 26 accessions, of which 22 accessions (84.62%) are from the Coast and four accessions (15.38%) from the Amazon. Group 2 comprises 54 accessions; 45 accessions (83.33%) are from the Coast and nine accessions (16.67%) from the Amazon. In general, group 1 and 2 are represented by the Amazon and Costa regions. Group 3 contain 33 accessions, of which 25 accessions (75.76%) are from the Coast region, seven accessions (21.21%) from the Amazon region and one accession (3.03%) from the Sierra. Group 4 includes 82 accessions, of which 67 accessions (81.71%) correspond to the Amazon region, 14 accessions (17.07%) from the Coast and one accession from the Sierra with 1.22%. In general, groups 3 and 4 are represented by the three regions: Costa, Sierra and Amazonia. It is important to note that the province of Tungurahua, located in the Sierra Region, includes two accessions, one in Group 3 and the second in Group 4. However, when reviewing the passport data, these two accessions were collected in Rio Verde located in the eastern Andean mountain slopes bordering the Amazonian Pastaza province.

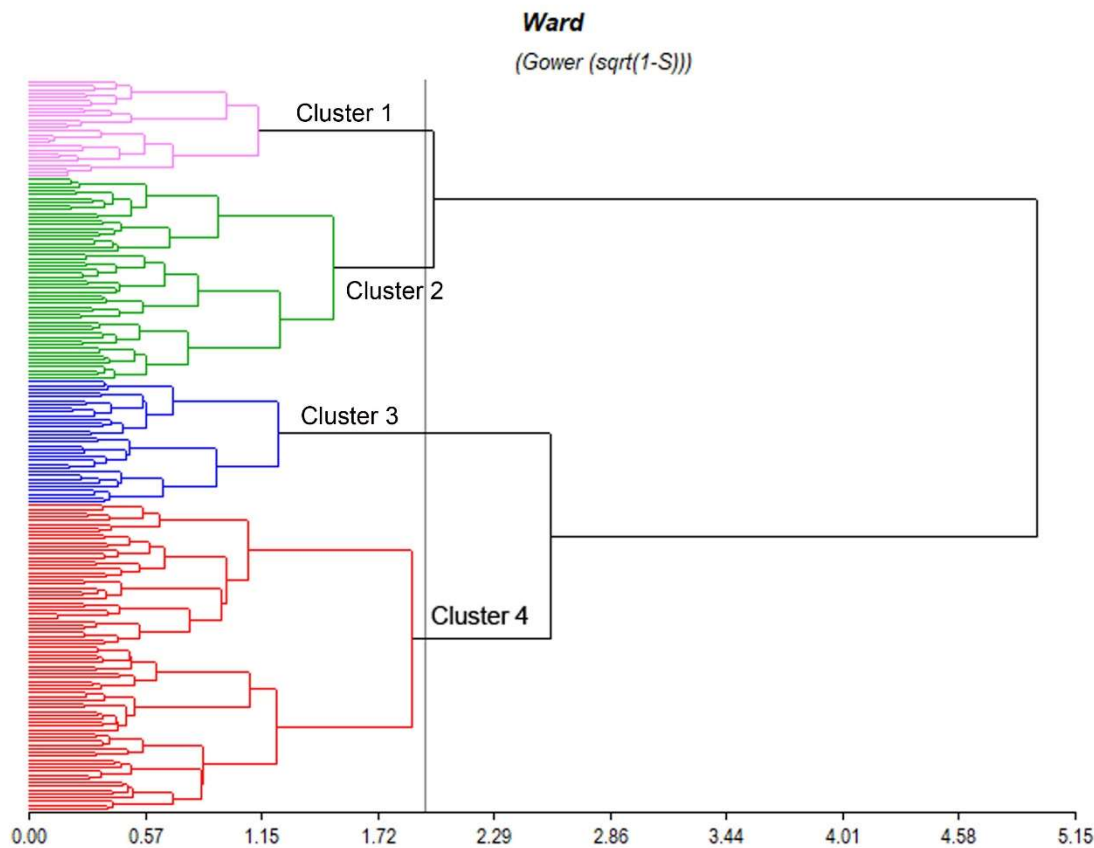


Figure 1. Dendrogram of 195 accessions of *Manihot esculenta*, indicating four groups of accessions based on quantitative morphological data using according to Ward's method and Gower's distance.

Group 1

Group 1 amounts to 26 accessions (Appendix 1) from four coastal provinces (Esmeraldas, Guayas, Manabí and Santo Domingo de Los Tsáchilas) and three Amazon provinces (Francisco de Orellana, Napo and Pastaza). The majority originates from the Coast region (84.62%), and within the region, the accessions are mainly from the province of Manabí (69.23%).

The quantitative morphological variables with the most significant variation for this group were mean root weight (CV 60.78%), the height of the first branch (CV 42.84%), plant height (CV 31.01%), length root (CV 20.75%) and internode distance (CV 20.69%). Thus, the accessions of this group present three characters with wide ranges, plant height between 98.00 cm and 350.00 cm, height at the first branch between 10.00 cm to 210.00 cm, and root length registered 29, 92 cm to 58.00 cm (Appendix 2).

Regarding the qualitative characteristics, group 1 (Appendix 3), the majority of individuals presented i. good initial vigour of the plant; ii. presence of pubescence of the apical leaf; iii.

leaves with lanceolate central lobe shape; iv. the petiole colour red with a bit of green; v. dark green stem epidermis; vi. no flowering; vii. dark green terminal branches; viii. intermediate earliness; ix. short root peduncle; x. purple root bark, and xi. white root pulp.

Group 2.

Group 2 presents 54 accessions (Appendix 1), these were collected in the coastal regions (Esmeraldas, Guayas, Manabí and Santo Domingo de Los Tsáchilas provinces) and Amazonia (Francisco de Orellana, Napo, Pastaza and Zamora Chinchipe provinces). Most of them belong to In the Cost region (84.62%), where the accessions collected in the Manabí province (61.11%) predominate.

The quantitative morphological variables with the greatest variation for this group were: Mean root weight (CV 68.76%), height of the first branch (CV 36.92%), root length (CV 28.56%), plant height (CV 24.59%), and root diameter (CV 24.14%). The accessions of this group present, like group 3, three characters with wide ranges, plant height between 127.00 cm and 330.00 cm, height at the first branch between 30.00 cm to 200.00 cm, and root length recorded 23.20 cm to 82.33 cm (Appendix 2).

Regarding the qualitative characteristics, group 2 (Appendix 3) presented i. good and regular initial vigour of the plant; ii. presence of pubescence of the apical leaf; iii. leaves with elliptical-lanceolate central lobe shape; iv. petiole colour red with a little green; v. dark green epidermis of the stem; vi. presence of flowering; vii. dark green terminal branches; viii. late maturing; ix. short root peduncle; x. purple root bark, and xi. white root pulp.

Group 3.

This group 3 presents 33 accessions (Appendix 1) collected in four provinces of the Coast (Guayas, Los Ríos, Manabí and Santo Domingo de Los Tsáchilas), five provinces of the Amazon (Francisco de Orellana, Napo, Sucumbíos, Pastaza and Zamora Chinchipe) and Sierra (Tungurahua). Most accessions in this group were collected in the Coast region (75.76%) and mainly originate in the province of Manabí (60.61%).

The quantitative morphological variables with the most significant variation for this group were: Mean root weight (CV 56.05%), the height of the first branch (CV 43.08%), plant height (CV 22.94%), and root diameter (CV 22.23%). Thus the accessions of this group have a wide range of plant height between 83 cm and 350 cm, the height at the first branch between 24.67 cm to 166.67 cm, root length registered 35.00 cm to 62.67 cm, and the mean root weight between 1.00 kg to 22.00 kg (Appendix 2).

Regarding the qualitative morphological characteristics, group 3 (Appendix 3) presents i. good and regular initial vigour of the plant; ii. pubescence of the apical leaf; iii. leaves with an elliptic-lanceolate central lobe; iv. red coloured petiole with a bit of green; v. light green stem epidermis; vi. presence of flowering; vii. light green terminal branches, viii. intermediate earliness; ix. absent root peduncle, x. pink root bark, and xi. white root pulp.

Group 4.

Group 4 presents the highest number of accessions of all groups with 82 accessions (Appendix 1) collected in eleven Ecuadorian provinces Esmeraldas, Guayas, Manabí and Santo Domingo de Los Tsáchilas in the Cost region; Francisco de Orellana, Morona Santiago , Napo, Sucumbíos, Pastaza and Zamora Chinchipe in the Amazon region; and Tungurahua in the Sierra region. Most of the accessions were collected in the Amazon

region (81.71%), the majority in the province of Sucumbíos (21.95%), followed by the provinces of Napo, Francisco de Orellana and Pastaza, each with 15.85%.

The quantitative morphological variables with the most significant variation for this group were: total fresh weight of storage roots per plant (CV 52.32%), height to first branching (CV 44.99%), length of storage root (CV 27.20%), diameter of storage root (CV 23.86%), plant height (CV 22.63%), and distance between leaf scars (CV 21.25%). The accessions of this group present a wide range of plant height between 90 cm and 393 cm, the height at the first branch between 20.00 cm to 233.33 cm; root length registered 23.67 cm to 48.00 cm, Leaf lobe length ranged from 11.95 cm to 29.90 cm and mean root weight between 1.00 kg to 18.47 kg (Appendix 2).

Regarding the qualitative characteristics of group 4 (Appendix 3), most of the accessions present i. an initial fair and reasonable plant vigour; ii. absence of pubescence of the apical leaf; iii. leaves with elliptical-lanceolate and lanceolate central lobe shape; iv. petiole colour red, red with little green and purple; v. stem epidermis dark green; vi. the presence of flowering; vii. terminal branches green with light, dark and purple hues; viii. intermediate earliness, ix. intermediate root peduncle, x. purple root bark; and, xi. white root pulp.

Ecogeographic characterization

Distribution of the diversity of Ecuadorian cassava

Seven life zones were identified (Humid Forest, Humid Forest, Very Dry Forest, Rain Forest, Dry Forest, Thorny Steppe and Thorny Mountain) where cassava diversity is growing in Ecuador, in a variation of altitude ranges and climatic conditions (Fig. 2).

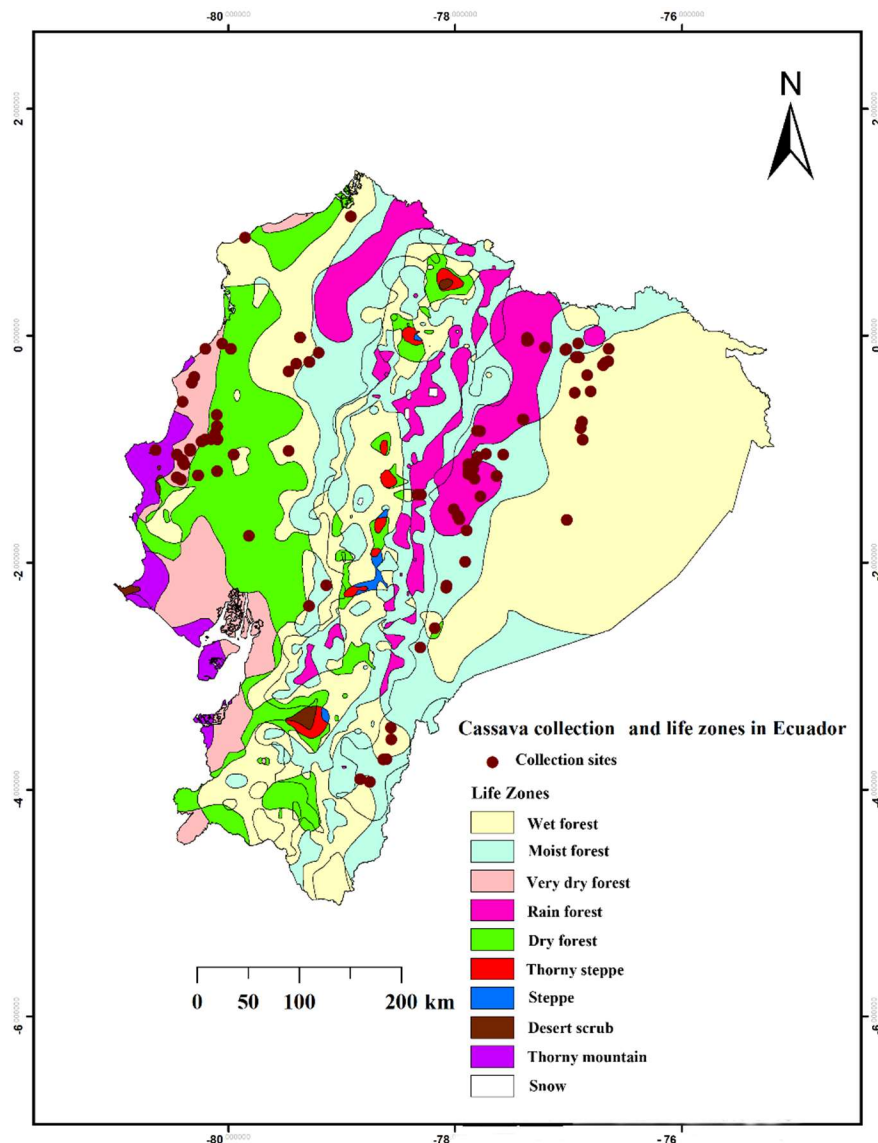


Figure 2. Distribution of 199 cassava accessions collected in Ecuador; seven life zones throughout Ecuador are coloured accordingly.

Ecogeographic characterization map of the soil

In order to define the areas in which cassava cultivation is adapted, a specific soil type characterization map was elaborated for the continental regions of Ecuador (Coast, Sierra foothills and Amazon). The ELC map was defined by 16 ecogeographic categories (Fig. 3) based on a combination of 41 bioclimatic variables, two geophysical and 12 edaphic.

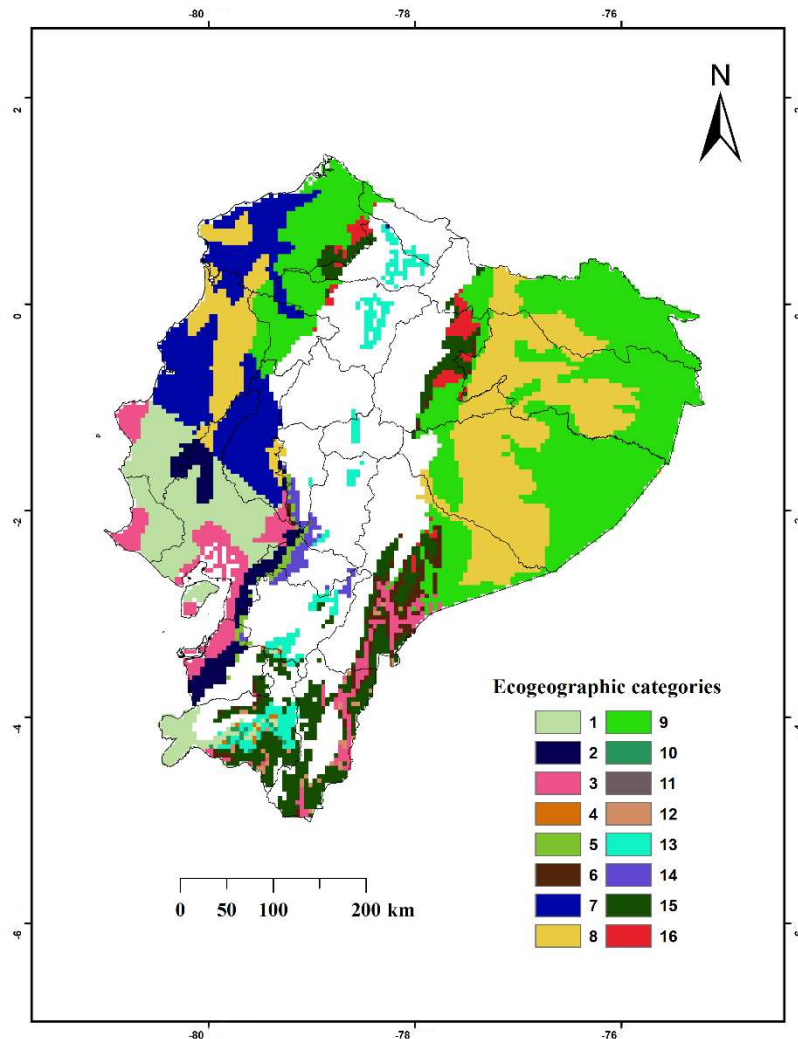


Figure 3. Map of specific ecogeographic characterization in continental Ecuador, where the local varieties of cassava are developed.

The most frequent ecogeographic categories were 8 (21%) and category 9 (31.6%), which add up to 52.6% of the Ecuadorian territory.

Category 8 presents the following characteristics: maximum temperature of the hottest month (30.2°C), minimum temperature of the coldest month (19.1°C). The highest precipitation was the month of May (273 mm), the lowest precipitation was in August (171 mm), the months of January and March were those that registered the maximum temperature 29.5°C , while the minimum temperatures corresponded to the months of July and August with 19.2°C , and the altitude was 313 m a.s.l. The sand content in the soil was 19.6%, and the soil pH was 5.

In category 9, the maximum temperature of the hottest month (30.3°C) was recorded; the minimum temperature of the coldest month (19.3°C), the highest precipitation was in May (302 mm), the precipitation in August was the lowest (200 mm). In January and March, the Maximum temperatures with 29.8°C and 29.7°C , the minimum temperatures were July

and August with 19.4° C and 19.3° C. The altitude where these cassava accessions are developing is 321 m a.s.l. The sand content in the soil is (39.3%) and the soil pH of 4.9.

The climatic variables with the greatest variation were August average precipitation, mm (CV = 101.75), October average precipitation, mm (CV = 99.89) and May average precipitation, mm (CV = 66.52). The quantitative edaphic variables with the greatest variation were: Gravel content in the subsoil, % (CV = 217.40), sand content in the subsoil, % (CV = 50.96) and sand content in the soil, % (CV = 41.64), (Table 3).

Table 3. Ecogeographic variability of quantitative traits in the Ecuador cassava collection.

Variables	CV	Min	Max	Mean±SD
Altitude, m a.s.l.	78.59	5.00	1566.00	360.99±283.69
Average annual temperature °C	5.09	18.40	26.00	24.04±1.22
Isothermal*, °C	4.73	7.00	9.00	8.32±0.39
Temperature seasonality**, °C	26.08	31.70	92.60	57.11±14.89
Maximum temperature for warmest month, °C	4.30	24.10	31.90	29.92±1.29
Minimum temperature for coldest month, °C	6.64	12.90	21.80	18.35±1.22
Annual temperature range***, °C	6.10	7.80	13.60	11.57±0.71
Average temperature for the coldest trimester (coldest three months), °C	5.14	17.60	25.60	23.29±1.20
Average temperature for the quarter with most rainfall (three rainiest months), °C	6.23	18.30	26.50	24.32±1.52
The average temperature for the hottest trimester (hottest three months), °C	5.42	18.70	26.50	24.72±1.34
Maximum temperature for January, °C	4.54	23.00	31.00	29.08±1.32
Maximum temperature for February, °C	4.42	23.10	31.20	29.19±1.29
Maximum temperature for March, °C	5.04	23.20	31.50	29.39±1.48
Maximum temperature for April, °C	5.37	23.30	31.90	29.44±1.58
Maximum temperature for May, °C	4.82	23.10	31.00	28.83±1.39
Maximum temperature for June, °C	4.35	22.40	30.10	27.96±1.22
Maximum temperature for July, °C	4.47	21.90	29.90	27.76±1.24
Minimum temperature for January, °C	7.29	14.00	22.60	19.62±1.43
Minimum temperature for February, °C	7.65	14.10	22.80	19.71±1.51
Minimum temperature for March, °C	7.96	14.20	22.90	19.94±1.59
Minimum temperature for April, °C	7.70	14.20	23.00	19.86±1.53
Minimum temperature for May, °C	7.05	14.10	23.00	19.62±1.38
Minimum temperature for June, °C				
Minimum temperature for July, °C	7.16	13.30	22.50	19.11±1.37
Minimum temperature for August, °C	6.93	13.00	22.20	18.61±1.29
Minimum temperature for September, °C	6.67	12.90	22.10	18.35±1.22
Minimum temperature for October, °C	6.19	13.1	21.8	18.62±1.15
Minimum temperature for November, °C	6.21	13.60	22.00	18.91±1.17
Minimum temperature for December, °C	6.13	13.80	22.30	19.32±1.18
January average temperature, °C	5.48	18.50	26.20	24.32±1.33
February average temperature, °C	5.53	18.60	26.30	24.42±1.31
March average temperature, °C	6.13	18.70	26.60	24.64±1.51
April average temperature, °C	6.22	18.70	26.80	24.62±1.53
May average temperature, °C	5.63	18.60	26.40	24.20±1.36
June average temperature, °C	5.40	17.80	26.00	23.50±1.27
July average temperature, °C	5.32	17.40	25.70	23.16±1.23
August average temperature, °C	4.90	17.80	25.70	23.41±1.15
October average temperature, °C	4.56	18.60	25.80	23.97±1.09
December average temperature, °C	4.76	18.70	26.10	24.31±1.16
Precipitation during the hottest quarter (the three hottest months), mm	40.58	193.00	1615.00	809.62±328.56
Average precipitation for May, mm	66.52	9.00	470.00	220.02±146.36
Average precipitation for August, mm	101.75	2.00	349.00	113.67±115.66
Average precipitation for October, mm	99.89	3.00	367.00	144.52±144.37
Sand content in the soil, %	41.64	11.00	72.00	27.43±13.98
Sand content in the subsoil, %	50.96	13.00	70.00	27.43±13.98
Gravel content in the subsoil, %	217.40	0.00	49.00	6.03±13.11

* (Daytime mean temperature range / annual temperature range) * 100. ** Standard deviation * 100. *** Maximum temperature for warmest month. Minimum temperature for the coldest month.

For other qualitative edaphic variables: The total of interchangeable bases in the surface soil showed the most significant variation (MD – mode deviation – = 0.82), followed by the pH of the surface soil in a soil-water solution (MD = 0.79) and base saturation in the surface soil (MD = 0.72) (Table 4).

Table 4. Ecogeographic variability with qualitative characteristics in the cassava collection from Ecuador.

Variables	Gradient/ Soil type deviation index	Type
Slope	0.28	Flat
Total interchangeable bases in the soil surface	0.82	High fertility
Organic carbon content in the soil surface	0.49	Low
Cation exchange capacity in the surface soil	0.76	Low
Cation exchange capacity of the clay in the surface	0.59	Very high
Reference of the apparent density of the soil surface soil	0.48	Volcanic soil horizons
Apparent density reference of the subsoil	0.28	Volcanic soil horizons
The pH of the surface soil in a water and soil solution	0.79	Slightly acidic
The pH of the subsoil in a water and soil solution	0.68	Slightly acidic
The saturation of the bases in the surface soil	0.72	A very acidic soil

Multivariate analysis: Groups description

Based on the multivariate grouping analysis with quantitative data, three different groups were obtained (Fig. 4).

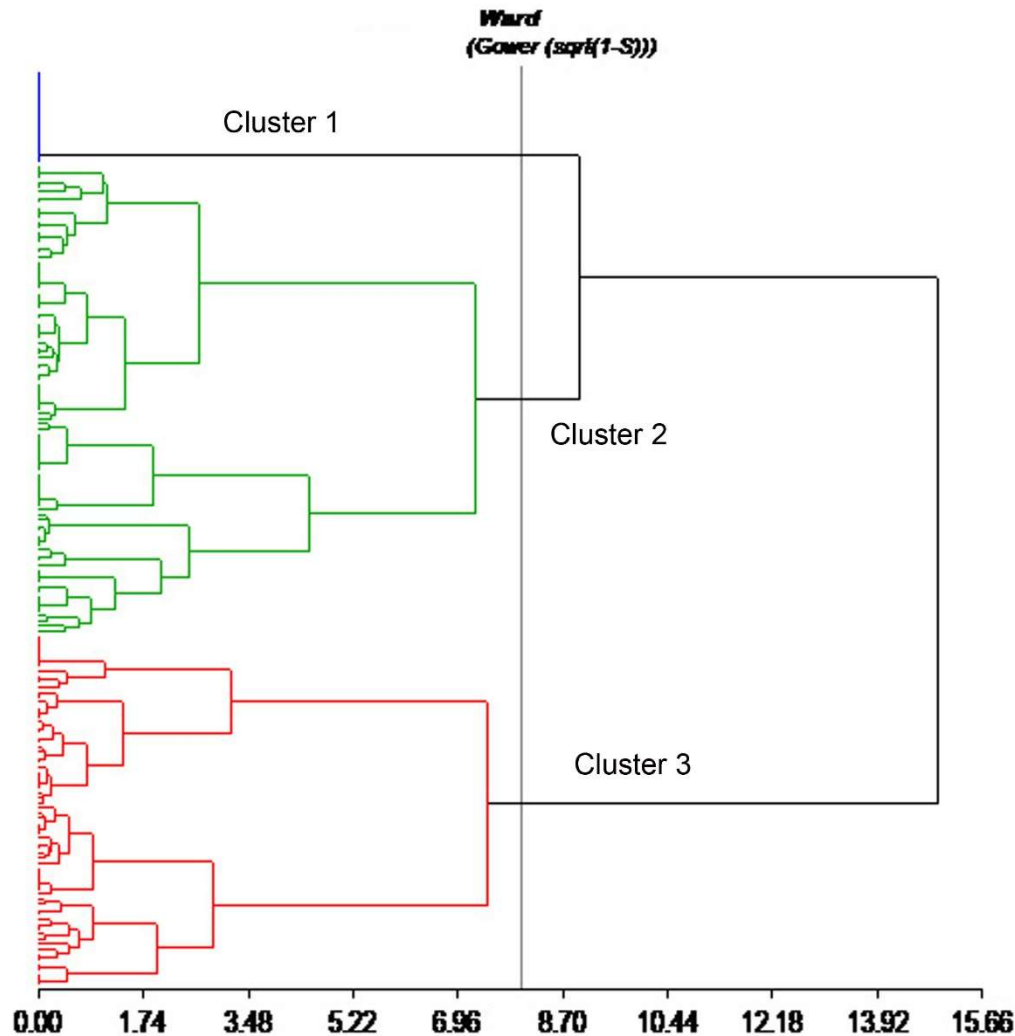


Figure 4. Dendrogram of the Ecuadorian cassava collection indicating 3 groups of accessions based on quantitative ecogeographic data using Ward's method and Gower's distance.

Group 1.

Regarding the qualitative characteristics (Appendix 5), group 1 accessions develop mainly on flat slopes, surface soil with low fertility for exchangeable bases, low carbon content on the surface, low cation exchange capacity on the soil surface, medium clay exchange capacity, volcanic soil horizons as a reference of apparent density in surface and subsoil soil, very acid pH in soil and subsoil and very acid soils for base saturation in surface soil. Group 1 presents 19 accessions (Appendix 1) collected in a single province of the Ecuadorian coast called Manabí and specifically in the Santa Ana canton. Cassava ecotypes develop in this agro-ecological zone with an altitude of 347 m a.s.l. The temperature in April, recorded as the hottest month, was 29.2° C, while the temperature in August was 17.4° C recorded as the coldest month. They are characterized by developing with rainfall of 845 mm, recorded in the hottest quarter. The sand content in the soil was 30%, in the

subsoil; it was 20%, while the gravel content in the subsoil was 1% (Appendix 4). The quantitative ecogeographic variables do not show variation for this group since the accessions were collected under similar conditions (Appendix 5).

Regarding the qualitative ecogeographic characteristics, group 1 (Appendix 5) develops on i. flat slopes, surface soil; ii. high fertility soil for exchangeable bases; iii. medium carbon content on the surface; iv. medium cation exchange capacity on the soil surface; v. very high clay exchange capacity; vi. volcanic soil horizons as a reference of apparent density in surface and subsoil soil; vii. moderately acidic pH in soil, and viii. subsoil and medium base saturation in the soil.

Group 2.

Group 2 presents 95 accessions (Appendix 1) mainly from provinces of the Costa region: Esmeraldas, Manabí, Santo Domingo, Los Ríos, Guayas, Cañar, and Azuay to more than seven accessions from the Amazon province of Fco. De Orellana. Once again, the provinces of Cañar and Chimborazo are known as Sierra region (highlands). However, the collection sites are from lowland areas (La Troncal) or foothills of the western mountain range (Cumandá), respectively.

The quantitative ecogeographic variables with the most significant variation for this group were i. average rainfall for October (183.2%), for August (170.1%) and for May (87.68%); ii. gravel content in subsoil (121.4%), and iii. altitude (65.67%). The accessions of this group correspond to a very hot environment (23.5° C to 26° C); however, it is noteworthy that higher temperatures (28.5° C to 31.2° C) were recorded in February, (28.8° C to 31.5° C) in March, and (29.1° C to 31.9° C) in April as the highest temperature registered. In the same way, these accessions bear minimum temperatures recorded in August (17.9° C to 22.1° C), similar to the minimum temperature of September (10° C to 21.8° C) and the minimum temperature recorded in October (18.3° C to 22° C). Concerning precipitation, the average for May was 9 mm to 329 mm. It was from 2 mm to 208 mm for August, while in October, it was registered 3 mm to 310 mm. In relation to soil, this group of accessions develop in soil with a sand content of 18 at 70%, while the sand content in the subsoil was from 18 to 70% (Appendix 4).

Regarding the qualitative ecogeographic characteristics, group 2 (Appendix 5) develops i. mainly on flat slopes; ii. surface soil with low fertility for exchangeable bases; iii. low carbon content on the surface; iv. medium cation exchange capacity on the soil surface; v. very high clay exchange capacity; vi. volcanic soil horizons as a reference of apparent density in surface and subsoil soil; vii. slightly acidic pH in soil and subsoil; and, vii. soil saturated in bases.

Group 3.

The third group comprises 81 accessions (Appendix 1) mainly from the Ecuadorian Amazon region, from the provinces of Sucumbíos, Napo and Fco. De Orellana Pastaza, Morona Santiago Zamora Chinchipe and Tungurahua. The latter province is known as the Andean province; however, "Baños", located in the foothills of the Andes, is known as the door of the Ecuadorian Amazon towards the province of Pastaza.

The quantitative ecogeographic variables with the greatest variation for this group were i. gravel content in the subsoil (CV 146.4%); ii. sand content in the subsoil (CV 48.87%); iii. sand content in the soil (CV 48, 66%); iv. altitude (CV 48.43%); v. mean rainfall for August (CV 22.94%); vi. minimum temperature for June (CV 21.38%) and vii. mean

rainfall for May (CV 21.25 %). The accessions of this group present a wide range of adaptation between 255 m a.s.l. and 1566 m a.s.l., support minimum temperatures between 12.9° C to 19.5° C, the same that occurred in August. The precipitation recorded during the hottest quarter, i.e. three hottest months, was 420 mm to 1074 mm. In addition, the average rainfall for May is between 183 mm to 470 mm, average rainfall for August between 118 mm to 349 mm, average rainfall for October between 149 mm and 367 mm. The sand content in the soil is between 11% and 58%, the sand content in the subsoil between 13% and 64% and gravel content in the subsoil between 0% and 49% (Appendix 4).

Regarding the qualitative characteristics, group 3 accessions develop mainly on i. flat slopes; ii. surface soil with low fertility for exchangeable bases; iii. low carbon content on the surface; iv. low cation exchange capacity on the soil surface; v. very high capacity for clay exchange; vi. volcanic soils as a reference of apparent density in surface and subsoil soil, vii. slightly acidic pH for soil, subsoil, and viii. soil saturated in bases (Appendix 5).

DISCUSSION

MORPHOLOGY

Descriptors of the aerial part

The shape descriptor of the central lobe of the leaf was elliptical-lanceolate and lanceolate with 50.0% and 40.0% respectively of the total accessions. In this study, the lanceolate leaf form occurs in almost all the accessions studied, in agreement with [37,21] but differs from the results of Meneses et al. [23] who, when characterizing 40 accessions, did not show variation in this characteristic. Similarly, [38] report that when characterizing 19 cassava clones, they found that 13.3% of the total presented the oval-lanceolate lobe shape.

The accessions presented three shades of apical leaf colour in the following order: light green, dark green and purple-green. In this regard, [39] mention that the light green colour is an easily observable and highly heritable attribute, and it is also expressed in the same way in any environment, which contributes to better discrimination of phenotypes ([40,41]. The results obtained agree with Meneses et al. [23], who indicate that most of the 40 accessions presented a light green colour in the apical bud, followed by dark green. Also, [42] indicate that the apical leaf colour: dark purple and light green. It is important to note that the colour of the apical shoot developed purple-green and purple colouration. Ceballos and de la Cruz [40] mention that it is common to observe purple shoots, but as the leaves grow and develop, they change to a greenish colouration.

Of the total accessions, 52% did not present apical leaf pubescence and 48% presented pubescence. These results differ as indicated by Meneses et al. [23], who determined that, of 40 accessions, 87.5% had the presence of apical bud pubescence, and 12.5% did not present this characteristic. Similarly, Torres [41] reported a 78.0% presence of pubescence and an absence of 22.0%, while [21] observed a presence in 100% of the accessions evaluated.

About the colour of the epidermis of the stem, 57% were observed with dark green colour and 26% with light green colour. These results do not agree with those obtained by Meneses et al. [23], who indicated that 90% of the accessions evaluated. They presented a light brown colour followed by a cream colour. Koefender et al. [21] observed that the light brown colour appeared 51.06% in the evaluated accessions. This descriptor, according to

Ramos [42], is a characteristic that may differ between genotypes and in the different stages of plant growth; for example, in the juvenile phase, different shades may appear from light red, brown and green. In addition, it is essential to take into account that edapho-climatic factors and cultivation practices can infer in this descriptor due to the availability of nutrients in the soil and their assimilation by plants [21]. On the other hand, the colour of the terminal branch of the adult plant developed in the collection was dark green (49%) and light green (31%). Results different from those found by Torres [40], who found that of 37 accessions, 32 were green, four were green, and one was purple; and Meneses et al. [23] who indicate a purplish-green (57.5%) and green (42.5%) colour.

The inflorescence was present in 144 accessions (74.0%), and there was no flowering in 51 accessions (26.0%). This observation coincides with findings by [43], who found that 96.45% of the accessions under study flowered and 3.5% did not flower. Koefender et al. [21] observed flowering and the presence of fruits in all the evaluated plants. According to Marín et al. [38], flowering is essential for plant breeding since it allows making crosses between selected clones and thus obtaining new genetically superior individuals; the most common form of propagation and / or multiplication is vegetative reproduction by cuttings.

Root descriptors

In cassava, the economically most important characteristic is the pulp. White pulp is one of the colour preferred in producing flours, and selling as fresh products in local markets [40,44]. Of the 195 accessions of the cassava collection, 83.0% of the accessions presented a white pulp colour and only 13.0% a cream colour; in addition, 5.0% was yellow. Meneses et al. [23] indicate opposite results to the white and cream colour, but agrees with the low percentage of yellow pulp. 57.5% of the accessions developed a cream pulp colour while 37.5% white pulp; However, two accessions with yellow pulp were found (5.0%), while Koefender et al. [21] indicate contrary data, the highest frequency was presented in the cream colour (47%), followed by the white colour (35%) and the yellow (18%).

Another characteristic of the fresh market is the ease of peeling [44]. Of the total accessions studied, 88.0% presented ease of peeling, and only 12.0% presented difficulty. These results coincide with those reported by Meneses et al. [23], who indicate that only 12.0% of the accessions presented peeling difficulty of the 40 accessions. Again, this characteristic is related to texture since it was mainly found that difficult-to-peel accessions have a rough and intermediate texture (94.0%), and those easy to peel have a soft texture (6.0%).

Discriminant morphological characters

The qualitative descriptors that allowed better discrimination between the groups obtained in the statistical analysis were petiole colour, the shape of the central lobe, the colour of the epidermis of the stem, and the colour of the adult plant's terminal branches. It can be observed that there are descriptive characters for both the leaf and the stem of the plant. Furthermore, according to what is stated by Ramos [42] and Lowe et al. [45], they correspond to descriptors of vegetative and reproductive organs that are easily quantifiable and highly heritable, which are not significantly influenced by the environment. In the study carried out by Demey et al. [46], as in this research, the colour of the terminal branches of the adult plant is pointed out as the most significant characteristic in separating the groups. This finding means that the descriptors i. the form of the central lobe, ii. the

colour of the petiole and iii. the colour of the terminal branches of the adult plant could be recommended to characterize cassava accessions. Additionally, some qualitative descriptors presented more significant variability in this study coincided with those indicated by Lobo [17].

Of the nine quantitative characters, four were the most discriminating between groups; two are related to the root: root length and mean root weight per plant; and the others: height at the first branch and plant height. The descriptors mean weight of the root per plant and height of the first branch presented the highest variation, possibly due to the influence of the environment. In contrast, four of the nine descriptors evaluated, such as the number of lobes, lobe length, lobe width, and length between nodes, presented a low coefficient of variation, indicating homogeneity in the results and, therefore, the existence of good handling of the experiment. The root length descriptor, in this study, is also considered discriminant in the research conducted by Acosta et al. [39], so it can be recommended for future characterizations of cassava.

In the groupings, 27 quantitative and qualitative descriptors were used to distinguish the 195 cassava accessions in four different groups, which coincides with Dominguez [47], who mention that cassava shows a wide variability and presents a high degree of intraspecific hybridization. The results of this study are similar to other studies [48,49] that used descriptors such as tuber length, epidermis colour, external skin of the tuber colour, the texture of the tuber surface and the colour of the pulp to make a difference between groups. The quantitative descriptors that presented more variability are the total fresh weight of the storage roots per plant and height at the first branch. These morphological descriptors are influenced by the cultivar and environment interaction [50,51].

Morphological traits (qualitative and quantitative) are quite variable but helpful for preliminary evaluation (pre-breeding) and have been used by local farmers empirically to identify and in the primary selection of plant material. The phenotypic identification of plants has been used in genotypic classification and taxonomic studies [52,53].

Environmental adaptation characteristics of the cassava collection

Ecuador is located in the tropical belt, just above the equinoctial line, making it very diverse in terms of climatic and edaphic conditions, in addition also presents rich ethnic and cultural diversity. In this study, it has been determined that cassava develops in seven life zones with wide ranges of altitude, soil and climatic conditions, which shows its wide adaptability [54]. This observation agrees with Sharkawy and Cadavid [55], who mentions that cassava cultivation worldwide grows in a wide range of conditions from the humid and warm lowland tropics, through the mid-altitude tropics, to the subtropics with cold winters and summer rains; conditions that make it suitable for combating climate change [56,57].

The materials that make up the Ecuadorian collection were collected at altitudes between 5 and 1566 m a.s.l., which coincides with El-Sharkawy [58], who mention that cassava is sown from sea level to altitudes of 2,000 m a.s.l. in tropical countries located in the equatorial range between 30° north and 30° south. The same author [58] mentions the development of cassava cultivation with annual rainfall between 500 and more than 2,000 mm. Our study identified that the rainfall in the cultivation sites, during the hottest quarter

was a minimum of 193 mm and a maximum of 1615 mm, which would imply that there are materials resistant to drought. Drought is one of the most important adaptation characteristics of the crop [59,60], and it can be evaluated [61]. On the other hand, the annual mean temperature range of the collection ranges from 18.4° C to 26° C, which also indicates an important range of adaptation. In short, adaptation characteristics to changes in temperature and precipitation of cassava are highly desirable for a crop that can feed the world population in times of climate change by expanding production areas worldwide [56,57,62].

Cassava is a crop that adapts to marginal, acidic soils and enables it to grow almost without the application of pesticides, allowing it to adapt even to marginal areas of Africa [59,63,64]. The data indicate that in Ecuador, most of the accessions, especially in the Amazon region (Group 1, Appendix 1), grow in soils with low nutrient content and acidic pH. However, on the coast of Ecuador, the soils dedicated to cassava planting have high fertility, so cassava is one of the transitory crops with the highest production in the region [65]. In the Coastal region, the crop can be grown in monoculture or mixed with maize to be commercialized [66]. In contrast, in the Ecuadorian Amazon, cassava production is more dedicated to subsistence consumption, where several traditional cassava cultivars coexist in the chagra (plot) of individual farmers; as, for example, in the Kiwicha communities of Napo, where cassava is known by the generic name 'Lumu' [67]. Furthermore, cassava in the Ecuadorian and Colombian Amazon region has high cultural importance [68]. This type of management is similar to Africa's traditional agroecosystems, where farmers tend to cultivate a great diversity of varieties per crop species that can reduce the risk of crop failure due to climate impacts, diseases, pests and soil limitations [69,70].

Finally, we can indicate that the applications of ecogeography and geographic information systems [25,71] have proven essential to characterize the conditions in which cassava cultivation develops in Ecuador and identify accessions that can adapt to conditions, e.g. extreme drought and poor soils, which could be used for improvement of this important crop.

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Appendix 1. Grouping by morphological and ecogeographical quantitative characters for the Ecuadorian collection of cassava.

Grouping by morphological quantitative characters			
Group 1	Group 2	Group 3	Group 4
18414, 18421, 18429, 18435, 18444, 18453, 18459, 18461, 18470, 18472, 18487, 18488, 18497, 18540, 18546, 18564, 18566, 18594, 18597, 18600, 18605, 18616, 19107, 19136, 19149, 19162	17607, 17615, 17618, 18407, 18415, 18419, 18423, 18432, 18434, 18440, 18441, 18448, 18451, 18452, 18455, 18462, 18466, 18468, 18473, 18476, 18479, 18480, 18483, 18489, 18491, 18495, 18505, 18506, 18510, 18511, 18513, 18523, 18524, 18536, 18539, 18541, 18542, 18547, 18559, 18561, 18586, 18587, 18602, 18607, 18610, 18615, 18620, 18621, 19089, 19113, 19134, 19141, 19150, 19454	17620, 18416, 18422, 18424, 18426, 18427, 18430, 18437, 18439, 18449, 18450, 18460, 18463, 18464, 18486, 18517, 18535, 18543, 18545, 18554, 18556, 18560, 18562, 18571, 18583, 18622, 19071, 19108, 19111, 19116, 19125, 19143, 19148	17603, 17604, 17605, 17608, 17611, 17612, 17614, 17617, 17619, 17621, 17623, 17624, 17625, 17627, 17628, 17640, 18436, 18456, 18465, 18477, 18485, 18516, 18522, 18533, 18567, 18599, 18601, 18608, 18618, 19070, 19091, 19092, 19094, 19095, 19096, 19097, 19098, 19100, 19101, 19102, 19103, 19104, 19106, 19109, 19110, 19115, 19117, 19118, 19119, 19120, 19121, 19122, 19123, 19124, 19126, 19128, 19129, 19130, 19131, 19132, 19133, 19135, 19137, 19138, 19139, 19140, 19142, 19144, 19145, 19146, 19147, 19151, 19152, 19153, 19154, 19155, 19156, 19157, 19158, 19159, 19160, 19161
Grouping by ecogeographical quantitative variables			
Group 1	Group 2	Group 3	
*18583, 18586, 18587, 18594, 18597, 18599, 18600, 18601, 18602, 18605, 18607, 18608, 18610, 18615, 18616, 18618, 18620, 18621, 18622	17640, 18407, 18414, 18415, 18416, 18419, 18421, 18422, 18423, 18424, 18426, 18427, 18429, 18430, 18432, 18434, 18435, 18436, 18437, 18439, 18440, 18441, 18444, 18448, 18449, 18450, 18451, 18452, 18453, 18454, 18455, 18456, 18459, 18460, 18461, 18462, 18463, 18464, 18465, 18466, 18468, 18470, 18472, 18473, 18476, 18477, 18479, 18480, 18483, 18485, 18486, 18487, 18488, 18489, 18491, 18495, 18497, 18505, 18506, 18510, 18511, 18513, 18516, 18517, 18522, 18523, 18524, 18533, 18535, 18536, 18539, 18540, 18541, 18542, 18543, 18545, 18546, 18547, 18554, 18556, 18559, 18560, 18561, 18562, 18564, 18566, 18567, 18571, 19152, 19153, 19154, 19155, 19156, 19157, 19158	17603, 17604, 17605, 17607, 17608, 17611, 17612, 17614, 17615, 17617, 17618, 17619, 17620, 17621, 17623, 17624, 17625, 17627, 17628, 19070, 19071, 19089, 19091, 19092, 19094, 19095, 19096, 19097, 19098, 19100, 19101, 19102, 19103, 19104, 19106, 19107, 19108, 19109, 19110, 19111, 19113, 19115, 19116, 19117, 19118, 19119, 19120, 19121, 19122, 19123, 19124, 19125, 19126, 19128, 19129, 19130, 19131, 19132, 19133, 19134, 19135, 19136, 19137, 19138, 19139, 19140, 19141, 19142, 19143, 19144, 19145, 19146, 19147, 19148, 19149, 19150, 19151, 19159, 19160, 19161, 19162	

*(ECU) Gene bank codes at the National Institute for Agricultural Research (INIAP), Ecuador.

Appendix 2. Morphological variability of quantitative characters based on the three groups obtained through multivariate analysis of the Ecuadorian cassava collection.

Variables	Group 1						Group 2					
	n	Mean	SD	CV	Min	Max	n	Mean	SD	CV	Min	Max
Total fresh weight of storage roots per plant, kg	26	4.45	2.70	60.78	1.83	14.90	54	4.35	2.99	68.76	0.84	15.60
Height to first branching, cm	25	111.83	47.90	42.84	10.00	210.00	52	103.28	38.13	36.92	30.00	200.00
Length of storage root, cm	26	39.14	8.12	20.75	29.92	58.00	54	39.94	11.41	28.56	23.20	82.33
Plant height, cm	25	231.24	71.70	31.01	98.00	350.00	52	237.90	58.74	24.59	127.00	330.00
Diameter of storage root, cm	26	8.63	1.36	15.77	5.33	11.00	54	8.11	1.96	24.14	3.00	11.67
Distance between leaf scars, cm	25	0.52	0.11	20.69	0.30	0.70	54	0.53	0.10	19.61	0.30	0.70
Width of leaf lobe, cm	26	5.73	0.48	8.35	5.04	7.02	54	5.56	0.87	15.65	3.16	7.37
Number of leaf lobes	26	8.00	1.02	12.75	7.00	9.00	54	7.59	0.92	12.14	7.00	9.00
Length of leaf lobe, cm	26	22.21	1.99	8.98	18.15	25.55	54	20.29	2.74	13.48	12.83	28.35
Variables	Group 3						Group 4					
	n	Mean	SD	CV	Min	Max	n	Mean	SD	CV	Min	Max
Total fresh weight of storage roots per plant, kg	33	7.28	4.08	56.05	1.00	22.00	82	6.71	3.51	52.32	1.00	18.47
Height to first branching, cm	33	86.52	37.28	43.08	24.67	166.67	80	92.29	41.52	44.99	20.00	233.33
Length of storage root, cm	33	47.93	7.81	16.29	35.00	62.67	82	48.94	13.91	27.20	23.67	48.00
Plant height, cm	33	261.15	59.91	22.94	83.00	350.00	80	261.59	59.20	22.63	90.00	393.00
Diameter of storage root, cm	33	10.33	2.30	22.23	4.33	15.00	82	9.90	2.36	23.86	5.67	17.20
Distance between leaf scars, cm	33	0.49	0.06	13.32	0.30	0.60	82	0.46	0.10	21.13	0.30	0.70
Width of leaf lobe, cm	33	5.99	0.76	12.69	3.67	7.14	82	5.45	1.05	19.17	2.48	8.57
Number of leaf lobes	33	7.48	1.00	13.41	5.00	9.00	82	7.91	1.24	15.66	5.00	11.00
Length of leaf lobe, cm	33	20.08	2.27	11.30	13.45	24.39	82	19.97	2.77	13.89	11.95	29.90

Appendix 3. Morphological variability in qualitative characters based on the dendrogram groupings of the Ecuadorian cassava collection.

State	Group 1	Group 2	Group 3	Group 4	Total
Initial vigour of the plant					
1. Low	0.19	0.46	0.48	0.46	0.43
3. Intermediate	0.81	0.50	0.52	0.46	0.53
5. High	0.00	0.04	0.00	0.07	0.04
Total	1.00	1.00	1.00	1.00	1.00
Colour of apical leaves					
3. Light green	0.54	0.50	0.48	0.11	0.34
5. Dark green	0.27	0.20	0.18	0.30	0.25
7. Purple green	0.19	0.26	0.33	0.33	0.29
9. Purple	0.00	0.04	0.00	0.26	0.12
Total	1.00	1.00	1.00	1.00	1.00
Pubescence of apical leaves					
0. Absent	0.23	0.22	0.27	0.90	0.52
1. Present	0.77	0.78	0.73	0.10	0.48
Total	1.00	1.00	1.00	1.00	1.00
Shape of central leaflet					
0. Ovoid	0.00	0.00	0.00	0.05	0.02
1. Elliptic-lanceolate	0.00	0.63	0.85	0.44	0.50
2. Obovate-lanceolate	0.00	0.00	0.00	0.01	0.01
3. Oblong-lanceolate	0.00	0.07	0.00	0.01	0.03
4. Lanceolate	0.96	0.28	0.15	0.40	0.40
5. Straight or linear	0.00	0.00	0.00	0.04	0.02
6. Pandurate					
7. Linear-pyramidal	0.04	0.02	0.00	0.02	0.02
8. Linear-pandurate	0.00	0.00	0.00	0.01	0.01
9. Linear-hostatilobalate	0.00	0.00	0.00	0.01	0.01
Total	1.00	1.00	1.00	1.00	1.00
Petiole colour					
1. Yellowish green	0.00	0.00	0.06	0.02	0.02
2. Green	0.08	0.09	0.03	0.04	0.06
3. Reddish green	0.00	0.07	0.00	0.00	0.02
5. Greenish red	0.88	0.61	0.39	0.16	0.42
7. Red	0.00	0.15	0.15	0.22	0.16
9. Purple	0.00	0.04	0.03	0.16	0.14
10. Yellowish Green-red	0.00	0.02	0.33	0.11	0.13
11. Reddish yellow green					
12. Purplish-green					
13. Greenish-purple	0.04	0.02	0.00	0.11	0.06
Total	1.00	1.00	1.00	1.00	1.00
Leaf colour					
3. Light green	0.00	0.02	0.00	0.09	0.04
5. Dark green	1.00	0.98	1.00	0.90	0.95
7. Purple green	0.00	0.00	0.00	0.01	0.01
9. Purple					
Total	1.00	1.00	1.00	1.00	1.00
Colour of stem epidermis					
1. Greenish-yellow	0.00	0.00	0.03	0.01	0.01
2. Light green	0.04	0.02	0.88	0.24	0.26
3. Dark green	0.92	0.98	0.03	0.40	0.57
4. Purple cream					
5. Purple	0.00	0.00	0.00	0.26	0.11
6. Green with red purple stripes	0.04	0.00	0.06	0.06	0.04
7. Purple green	0.00	0.00	0.00	0.02	0.01
Total	1.00	1.00	1.00	1.00	1.00

Flowering					
0. Absent	0.85	0.33	0.12	0.09	0.26
1. Present	0.15	0.67	0.88	0.91	0.74
Total	1.00	1.00	1.00	1.00	1.00
Colour of terminal branches of adult plant					
2. Light green	0.00	0.04	0.91	0.35	0.31
3. Dark green	0.96	0.94	0.03	0.23	0.49
5. Purple green	0.04	0.02	0.03	0.23	0.11
6. Red green	0.00	0.00	0.03	0.11	0.05
7. Purple	0.00	0.00	0.00	0.07	0.03
Total	1.00	1.00	1.00	1.00	1.00
Plant earliness					
3. Early (3-6 months)	0.00	0.02	0.00	0.02	0.02
5. Intermediate (6-9 months)	0.96	0.30	0.79	0.82	0.69
7. Late (>9 months)	0.04	0.69	0.21	0.16	0.30
Total	1.00	1.00	1.00	1.00	1.00
Shape of plant					
1. Compact	0.04	0.12	0.06	0.06	0.07
2. Open	0.04	0.02	0.00	0.01	0.02
3. Umbrella	0.60	0.62	0.67	0.56	0.60
4. Cylindrical	0.16	0.13	0.12	0.20	0.16
5. Erect	0.16	0.12	0.15	0.16	0.15
Total	1.00	1.00	1.00	1.00	1.00
Root constrictions					
0. Absent	0.92	0.78	0.79	0.80	0.81
1. Present	0.08	0.22	0.21	0.20	0.19
Total	1.00	1.00	1.00	1.00	1.00
Texture of root epidermis					
3. Smooth	0.15	0.02	0.15	0.02	0.06
5. Intermediate	0.23	0.35	0.24	0.16	0.24
7. Rough	0.62	0.63	0.61	0.82	0.70
Total	1.00	1.00	1.00	1.00	1.00
Extent of root peduncle					
1. Sessile	0.42	0.11	0.39	0.10	0.19
3. Short	0.38	0.52	0.30	0.28	0.36
5. Intermediate	0.15	0.28	0.09	0.46	0.31
7. Long	0.04	0.09	0.21	0.16	0.13
Total	1.00	1.00	1.00	1.00	1.00
Colour of root cortex					
1. White	0.08	0.20	0.15	0.23	0.19
2. Cream	0.08	0.22	0.18	0.22	0.19
3. Yellow	0.08	0.06	0.03	0.07	0.06
4. Pink	0.19	0.15	0.45	0.04	0.16
5. Purple	0.58	0.37	0.18	0.44	0.39
Total	1.00	1.00	1.00	1.00	1.00
Colour of root pulp					
1. White	0.96	0.85	0.91	0.73	0.83
2. Cream	0.00	0.13	0.09	0.18	0.13
3. Yellow	0.04	0.02	0.00	0.09	0.05
4. Orange					
5. Pink					
Total	1.00	1.00	1.00	1.00	1.00
Shape of root					
1. Conical	0.23	0.28	0.12	0.16	0.19
2. Conical-cylindrical	0.73	0.63	0.82	0.63	0.68
3. Cylindrical	0.04	0.07	0.03	0.20	0.11
4. Irregular	0.00	0.02	0.03	0.01	0.02
Total	1.00	1.00	1.00	1.00	1.00
Cortex: ease of peeling					
1. Easy	0.92	0.80	0.97	0.88	0.88
2. Difficult	0.08	0.20	0.03	0.12	0.12
Total	1.00	1.00	1.00	1.00	1.00

Appendix 4. Ecogeographic variability with quantitative characters based on the three groups obtained through multivariate analysis for the Ecuadorian cassava collection.

Variables	Group 1						Group 2						Group 3					
	n	Mean	SD	CV	Min	Max	n	Mean	SD	CV	Min	Max	n	Mean	SD	CV	Min	Max
Altitude, m a.s.l.	19	347	0	0	347	347	94	165.62	108.8	65.67	5	438	81	591	286.3	48.43	255	1566
Annual average temperature, °C	19	23.5	0	0	23.5	23.5	95	24.84	0.59	2.39	23.5	26	81	23.22	1.3	5.6	18.4	24.9
Isothermality*, °C	19	8.3	0	0	8.3	8.3	95	8.03	0.31	3.82	7	8.8	81	8.66	0.22	2.59	8	9
Temperature seasonality**, °C	19	63.5	0	0	63.5	63.5	95	67.81	10.85	16	36.5	92.6	81	43.06	7.36	17.1	31.7	66.3
Maximum temperature, warmest month, °C	19	29.2	0	0	29.2	29.2	95	30.77	0.72	2.35	29.2	31.9	81	29.09	1.31	4.51	24.1	30.7
Minimum temperature, coldest month, °C	19	17.4	0	0	17.4	17.4	95	19.07	0.63	3.3	17.9	21.8	81	17.73	1.39	7.82	12.9	19.5
Annual temperature range***, °C	19	11.8	0	0	11.8	11.8	95	11.71	0.82	7	7.8	12.7	81	11.36	0.58	5.15	10.9	13.6
Average temperature, coldest quarter (3 coldest months), °C	19	22.7	0	0	22.7	22.7	95	24.02	0.59	2.45	22.6	25.6	81	22.57	1.35	6	17.6	24.3
Average temperature for the quarter with most rainfall (3 rainiest months), °C	19	24.3	0	0	24.3	24.3	95	25.51	0.61	2.41	24.2	26.5	81	22.93	1.23	5.37	18.3	24.5
Average temperature for the hottest quarter (3 hottest months), °C	19	24.3	0	0	24.3	24.3	95	25.69	0.55	2.13	24.5	26.5	81	23.68	1.32	5.59	18.7	25.4
Maximum temperature for January, °C	19	28.5	0	0	28.5	28.5	95	29.87	0.75	2.5	28.2	31	81	28.29	1.46	5.15	23	30.1
Maximum temperature for February, °C	19	28.5	0	0	28.5	28.5	95	30.02	0.64	2.14	28.5	31.2	81	28.37	1.39	4.89	23.1	30.5
Maximum temperature for March, °C	19	29	0	0	29	29	95	30.49	0.72	2.37	28.8	31.5	81	28.18	1.32	4.68	23.2	29.9
Maximum temperature for April, °C	19	29.2	0	0	29.2	29.2	95	30.68	0.83	2.71	29.1	31.9	81	28.04	1.19	4.24	23.3	29.6
Maximum temperature for May, °C	19	28.5	0	0	28.5	28.5	95	29.87	0.79	2.64	28.2	31	81	27.7	1.16	4.19	23.1	29.4
Maximum temperature for June, °C	19	27.4	0	0	27.4	27.4	95	28.72	0.72	2.5	27	30.1	81	27.19	1.27	4.67	22.4	28.8
Maximum temperature for July, °C	19	27.3	0	0	27.3	27.3	95	28.49	0.74	2.58	26.8	29.9	81	27	1.35	5.01	21.9	28.5
Minimum temperature for January, °C	19	19.4	0	0	19.4	19.4	95	20.7	0.59	2.83	19.6	22.6	81	18.4	1.29	7	14	20.1
Minimum temperature for February, °C	19	19.7	0	0	19.7	19.7	95	20.83	0.68	3.25	19.6	22.8	81	18.39	1.31	7.14	14.1	20.2
Minimum temperature for March, °C	19	20	0	0	20	20	95	21.17	0.61	2.89	19.9	22.9	81	18.49	1.32	7.14	14.2	20.3
Minimum temperature for April, °C	19	19.7	0	0	19.7	19.7	95	21.06	0.57	2.72	19.9	23	81	18.49	1.29	6.96	14.2	20.4
Minimum temperature for May, °C	19	19.2	0	0	19.2	19.2	95	20.67	0.67	3.24	19.5	23	81	18.49	1.22	6.59	14.1	20.2
Minimum temperature for June, °C	19	18.5	0	0	18.5	18.5	95	20.08	0.62	3.1	19	22.5	81	18.12	1.38	7.59	13.3	20
Minimum temperature for July, °C	19	17.8	0	0	17.8	17.8	95	19.45	0.62	3.17	18.4	22.2	81	17.81	1.39	7.83	13	19.7
Minimum temperature for August, °C	19	17.4	0	0	17.4	17.4	95	19.07	0.64	3.38	17.9	22.1	81	17.73	1.39	7.83	12.9	19.5
Minimum temperature for September, °C	19	17.5	0	0	17.5	17.5	95	19.23	0.58	3.02	18	21.8	81	18.17	1.37	7.56	13.1	19.9
Minimum temperature for October, °C	19	17.7	0	0	17.7	17.7	95	19.59	0.59	3.02	18.3	22	81	18.41	1.33	7.24	13.6	20.1
Minimum temperature for December, °C	19	18.6	0	0	18.6	18.6	95	20.09	0.54	2.67	19	22.3	81	18.58	1.3	6.97	13.8	20.5
Average temperature for January, °C	19	23.9	0	0	23.9	23.9	95	25.25	0.56	2.24	23.9	26.2	81	23.32	1.35	5.81	18.5	25.1
Average temperature for February, °C	19	24.1	0	0	24.1	24.1	95	25.39	0.57	2.23	24.2	26.3	81	23.35	1.32	5.66	18.6	25.3
Average temperature for March, °C	19	24.5	0	0	24.5	24.5	95	25.81	0.59	2.3	24.6	26.6	81	23.31	1.31	5.62	18.7	25
Average temperature for April, °C	19	24.4	0	0	24.4	24.4	95	25.85	0.64	2.47	24.5	26.8	81	23.23	1.2	5.18	18.7	24.9
Average temperature for May, °C	19	23.8	0	0	23.8	23.8	95	25.24	0.65	2.56	24	26.4	81	23.07	1.18	5.11	18.6	24.8
Average temperature for June, °C	19	22.9	0	0	22.9	22.9	95	24.37	0.57	2.34	23.2	26	81	22.62	1.32	5.85	17.8	24.4
Average temperature for July, °C	19	22.5	0	0	22.5	22.5	95	23.95	0.56	2.33	22.6	25.7	81	22.38	1.36	6.1	17.4	24.1
Average temperature for August, °C	19	22.8	0	0	22.8	22.8	95	24.03	0.6	2.49	22.5	25.7	81	22.82	1.37	5.99	17.8	24.6
Average temperature for October, °C	19	23.1	0	0	23.1	23.1	95	24.45	0.69	2.84	22.8	25.8	81	23.62	1.33	5.62	18.6	25.3
Average temperature for December, °C	19	23.8	0	0	23.8	23.8	95	24.92	0.72	2.9	23.1	26.1	81	23.73	1.34	5.64	18.7	25.6
Rainfall during the hottest quarter (3 hottest months), mm	19	845	0	0	845	845	95	784.69	441.20	56.23	193	1615	81	830.6	177.7	21.39	420	1074
Average rainfall for May, mm	19	117	0	0	117	117	95	124.28		87.68	9	329	81	356.5	75.75	21.25	183	470
Average rainfall for August, mm	19	8	0	0	8	8	95	29.47	50.14	170.1	2	208	81	237.2	54.42	22.94	118	349
Average rainfall for October, mm	19	9	0	0	9	9	95	43.56	79.81	183.2	3	310	81	294.7	61.23	20.77	149	367
Sand content of soil, %	19	30	0	0	30	30	94	29.2	10.6	36.29	23	72	81	33.21	16.16	48.66	11	58
Sand content of subsoil, %	19	20	0	0	20	20	94	23.97	11.214	6.77	18	70	79	33.33	16.29	48.87	13	64
Gravel content of subsoil, %	19	1	0	0	1	1	94	1.5	1.82	121.2	0	4	79	12.63	18.49	146.4	0	49

Appendix 5. Ecogeographic variation of qualitative characters based on the grouping of dendrograms for the Ecuadorian cassava collection.

	Group 1	Group 2	Group 3	Total
Slope				
1. Flat (0-2°)	1	0.78	0.81	0.81
2. Very smooth (2-5°)	0	0.22	0.14	0.16
3. Smooth (5-12°)	0	0	0.05	0.02
Total	1	1	1	1
Total exchangeable bases in surface soil				
1. Low fertility	0	0.24	0.53	0.34
2. Medium fertility	0	0.04	0.47	0.22
3. High fertility	1	0.71	0	0.44
Total	1	1	1	1
Organic carbon content in surface soil				
1. Very low	0	0.23	0	0.11
2. Low	0	0.54	0.89	0.63
3. Medium	1	0.22	0	0.21
4. High	0	0	0.11	0.05
Total	1	1	1	1
Cation exchange capacity in surface soil				
1. Very low	0	0.07	0.02	0.05
2. Low	0	0.19	0.98	0.5
3. Medium	1	0.73	0	0.45
Clay cation exchange capacity in surface				
2. Low	0	0	0.35	0.14
3. Medium	0	0.12	0.44	0.23
4. High	0	0	0.21	0.08
5. Very high	1	0.88	0	0.55
Total	1	1	1	1
Apparent bulk density reference in surface soil				
1. Peaty horizons	0	0	0.28	0.12
2. Volcanic soil horizons	0	0.93	0.57	0.69
3. Clay horizons with structure	1	0.07	0.15	0.2
Total	1	1	1	1
Apparent bulk density reference in subsoil				
1. Peaty horizons	0	0	0.29	0.12
2. Volcanic soil horizons	1	0.96	0.59	0.81
3. Clay horizons with structure	0	0.04	0.11	0.07
Total	1	1	1	1
Surface soil pH in a soil-water solution				
1. Very acid	0	0.01	0.49	0.21
2. Acid	0	0.27	0.41	0.3
3. Moderately acid,	0	0.16	0.1	0.12
4. Slightly acid	1	0.51	0	0.34
5. Practically neutral	0	0.01	0	0.01
6. Neutral	0	0.04	0	0.02
Total	1	1	1	1
pH in subsoil in soil-water solution				
1. Very acid	0	0.01	0.49	0.21
2. Acid	0	0.28	0.39	0.3
3. Moderately acid,	0	0.04	0.01	0.03
4. Slightly acid	1	0.62	0.1	0.44
5. Practically neutral	0	0.01	0	0.01
6. Neutral	0	0.04	0	0.02
Total	1	1	1	1
Saturation of bases in surface soil				
1. Very acidic soil	0	0.21	1	0.52
2. Medium soil	1	0.22	0	0.21
3. Soil saturated in bases	0	0.56	0	0.27
Total	1	1	1	1

Supplementary Table 1. Thematic layers used in the ecogeographic characterization in cassava collection.

Variable	Unit/category	Component*
Annual average temperature	°C	Bioclimatic
Isothermality	°C	Bioclimatic
Temperature seasonality	°C	Bioclimatic
Maximum temperature for the warmest month	°C	Bioclimatic
Minimum temperature for the coldest month	°C	Bioclimatic
Annual temperature range	°C	Bioclimatic
Average temperature for the coldest quarter (3 coldest months)	°C	Bioclimatic
Average temperature for the quarter with most rainfall (3 rainiest months)	°C	Bioclimatic
Average temperature for the hottest quarter (3 hottest months)	°C	Bioclimatic
Maximum temperature for January	°C	Bioclimatic
Maximum temperature for February	°C	Bioclimatic
Maximum temperature for March	°C	Bioclimatic
Maximum temperature for April	°C	Bioclimatic
Maximum temperature for May	°C	Bioclimatic
Maximum temperature for June	°C	Bioclimatic
Maximum temperature for July	°C	Bioclimatic
Minimum temperature for January	°C	Bioclimatic
Minimum temperature for February	°C	Bioclimatic
Minimum temperature for March	°C	Bioclimatic
Minimum temperature for April	°C	Bioclimatic
Minimum temperature for May	°C	Bioclimatic
Minimum temperature for June	°C	Bioclimatic
Minimum temperature for July	°C	Bioclimatic
Minimum temperature for August	°C	Bioclimatic
Minimum temperature for September	°C	Bioclimatic
Minimum temperature for October	°C	Bioclimatic
Minimum temperature for December	°C	Bioclimatic
Average temperature for January	°C	Bioclimatic
Average temperature for February	°C	Bioclimatic
Average temperature for March	°C	Bioclimatic
Average temperature for April	°C	Bioclimatic
Average temperature for May	°C	Bioclimatic
Average temperature for June	°C	Bioclimatic
Average temperature for July	°C	Bioclimatic
Average temperature for August	°C	Bioclimatic
Average temperature for October	°C	Bioclimatic

Average temperature for December	°C	Bioclimatic
Rainfall during the hottest quarter (3 hottest months)	mm	Bioclimatic
Average rainfall for May	mm	Bioclimatic
Average rainfall for August	mm	Bioclimatic
Average rainfall for October	mm	Bioclimatic
Elevation	m	Geophysical
Slope	1 Flat (0-2°), Very smooth (2-5°), Smooth (5-12°)	Geophysical
Surface soil pH in a soil-water solution	1 Very acid, 2 Acid, 3 Moderately acid, 4 Slightly acid, 5 Practically neutral, 6 Neutral	Edaphic
pH in subsoil in soil-water solution	1 Very acid, 2 Acid, 3 Moderately acid, 4 Slightly acid, 5 Practically neutral, 6 Neutral	Edaphic
Organic carbon content in surface soil	1 Very low, 2 Low, 3 Medium, 4 High	Edaphic
Total exchangeable bases in surface soil	1 Low fertility, 2 Medium fertility, 3 High fertility	Edaphic
Cation exchange capacity in surface soil	1 Very low, 2 Low, 3 Medium	Edaphic
Clay cation exchange capacity in surface	1 Very low, 2 Low, 3 Medium, 4 High, 5 Very high	Edaphic
Apparent bulk density reference in surface soil	1 Peaty horizons, 2 Volcanic soil horizons, 3 Clay horizons with structure	Edaphic
Apparent bulk density reference in subsoil	1 Peaty horizons, 2 Volcanic soil horizons, 3 Clay horizons with structure	Edaphic
Saturation of bases in surface soil	1 Very acidic soil, 2 Medium soil, 3 Soil saturated in bases	Edaphic
Sand content of soil,	%	Edaphic
Sand content of subsoil	%	Edaphic
Gravel content of subsoil	%	Edaphic

*Source for bioclimatic: WorldClim, <http://www.worldclim.org>, for geophysical: Shuttle Radar Mission, <http://srtm.csi.cgiar.org>, for edaphic: MAGAP, <http://geoportal.magap.gob.ec/geonetwork/srv/spa/main.home>