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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, where it is traditionally cultivated in the three continental regions: Amazonia, the Coast and in the valleys of the Sierra. The purpose of this study is 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). Four morphological groups and three ecogeographic groups were identified. Morphological variability was evidenced mainly in descriptors related to the leaves, stems, and inflorescences. In addition, it was possible to identify accessions that appear capable of growing under extreme conditions of drought and poor soils. These accessions could be used for improvement.

Keywords: variability; adaptation; GIS

1. Introduction

Cassava (*Manihot esculenta* Crantz) is an important subsistence and commercial 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 marginal climatic and soil conditions [4–7]. This species is native to South America, and is currently widely cultivated in the tropics as a result of the selection and domestication by indigenous peoples who have played an essential role in the composition and diversity of cassava [8–10]. 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 seasonal crop with the largest surface area at the national level, 13,601 hectares and annual production of 69,863 metric tons [11]. Cassava has traditionally been cultivated most frequently in the Amazonia region, followed by the Coast and valleys of the Sierra [12]. Amazonian ethnic groups recognize around 200 types of cassava, classifying them

as bitter and sweet [13]. In the province of Manabí (Coast Region), in addition to self-consumption, it also generates economic income through the commercialization of fresh and/or processed cassava as flour [14].

Morphological characterization has been used for several purposes, including identifying duplicates, studies of variation, and correlation with characteristics of agronomic importance [15,16]. 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 [17–20]. For example, the EMBRAPA-Brazil Corporation established 75 morphological descriptors for cassava [21]; these descriptors have allowed morphological validation of 26 ethno-varieties in Peru [22], 116 elite genotypes collected in Benin, Africa [23], 47 traditional varieties in Brazil [24], 159 accessions conserved in the field in Côte d'Ivoire, Africa [25], and in Mexico 40 accessions were characterized from a germplasm bank [26].

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 [27,28]. For example, Mezghani et al. [29] 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 the environmental conditions and associated biotic and abiotic factors to which plant species have adapted, as in a study carried out on teosinte [30]. At present, programs have been developed that use geographic information systems, such as CAPFITOGEN [31]. This program uses ecogeographic analysis tools to carry out several ecogeographic crop studies in Ecuador, e.g., maize (*Zea mays* L.) [32], capulin (*Prunus serotina* Ehrh. subsp. *capuli* (Cav. ex Spreng.) McVaugh) [33], and ulluco (*Ullucus tuberosus* Caldas) [34].

The purpose of this study is 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 is cultivated under environmental conditions that are frequently or only rarely encountered.

2. Materials and Methods

2.1. Cassava Collection

The collection of landraces was carried out in 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 [35]. As only cultivated materials were collected, no 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—incl. members of local ethnic communities, 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.

2.2. Morphological Characterization

The 195 accessions of the Ecuadorian collection were planted at the Central Amazonia 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 [21] in order to develop a dendrogram of the local cultivated materials (Figure 1.). Quantitative descriptors were recorded based on the average value obtained from five randomly selected plants within each accession. Quantitative descriptors included the length and width of the middle 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 (i) initial vigor, i.e., growth rate of the plant (height of plant in cm and distance to the 1st branch in cm); (ii) the color of apical leaves; (iii) pubescence on apical leaves; (iv) shape of the central leaflet; (v) petiole color; (vi) leaf color; (vii) color of stem epidermis; (viii) flowering; (ix) color of end branches of adult plant; (x) plant earliness, i.e., precocity of production of tuberous roots; (xi) the shape of the plant; (xii) root constrictions; (xiii) texture of the root epidermis; (xiv) the length of the root peduncle; (xv) color of the root cortex; (xvi) color of the root pulp (parenchyma); (xvii) cortex, i.e., ease of peeling, i.e., accessions with a smooth texture are easier to peel than those with a rough texture according to Torres Vargas [36] and Del Rosario-Arellano et al. [37]; and (xviii) shape of the root. The different states scored for each character examined are given in Appendix (Table A3).

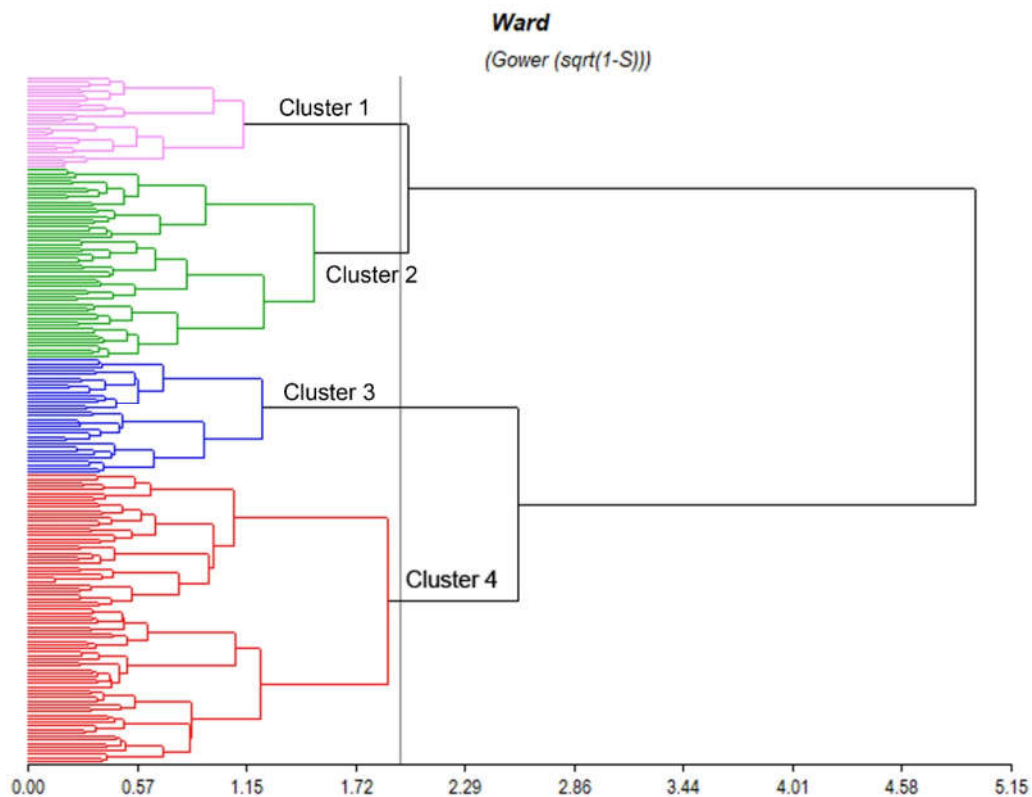


Figure 1. Dendrogram of 195 accessions of *Manihot esculenta*, indicating four groups of accessions based on quantitative morphological data using Ward's method and Gower's distance.

2.3. Ecogeographical Characterization

As mentioned before, the 195 accessions studied were collected in the Coast and the Amazonia regions of Ecuador, only a couple of accessions originated from the valleys of the Sierra among the overall 199 collected (Figure 2). Plains generally form the landscape in the Coast region, and Amazonia includes hills that originate in the eastern part of the Andes and descend toward the Amazonian plains. Humidity percentages close to 100% are found in 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 Amazonia is continuous and intense throughout the year (3000 mm average), while on the Coast, the heaviest precipitation occurs during the strong winter period from February to May and during the mild winter period from September to November. On the contrary, the dry months are July and August, and summer weather from December to January [38]. Moreover, soils on the Coast are usually floodplains that have accumulated fertile sediments from the highlands. As a result, with the much gentler slope to the east of the Sierra, the geologically older soils of the Ecuadorian Amazonia have great acidity [39].

Using the ECOGEO tool of the CAPFITOGEN program [31], the ecogeographic characterization was carried out using 55 ecogeographic variables (Supplementary Table S1). First applying ECOGEO, a grid resolution of 5 × 5 km (2.5 arc-minutes) was chosen to extract the information, and subsequently the INFOSTAT program was used (version 2018) to edit the recorded data for analysis [40].

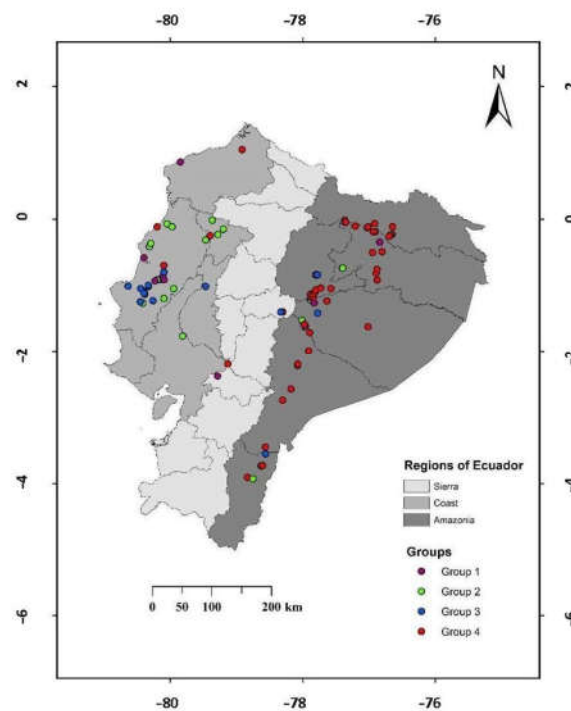


Figure 2. Distribution of 199 cassava accessions collected in Ecuador. The three continental Ecuadorian regions and morphological grouping within the regions—Figure 1—are colored accordingly.

2.4. 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 [31], the first step was to create the map with a grid cell size of 5 km by 5 km (2.5 arc-minutes) covering the Coast region

and the Amazonia 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 analyses, principal components and random forest, to identify the 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. Moreover, 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 were used to generate the ELC map.

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

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

* CV: Coefficient of Variation; SD: Standard Deviation.

2.5. Statistical Analysis

The morphological and ecogeographic characterization data were examined using the INFOSTAT program version 2018 [40]. 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 [41] 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 [38].

To establish correlations within the quantitative and qualitative descriptors, the Pearson correlation analysis [42] was performed, using INFOSTAT [40]. With the descriptors that presented the highest correlation coefficient, path analysis was carried out to evaluate the dependence between variables [43]. Statistic Z Mantel was calculated to establish correlation between the morphological and ecogeographical distance matrices [40].

3. Results

3.1. Cassava Collection

The cassava collection encompasses 195 accessions (96 accessions collected and acquired more than two decades ago and 99 accessions collected during 2012 and 2013). The

first 96 accessions were collected mainly from mestizo farmers in the Coast and Sierra regions and the other 99 cassava accessions were collected in the Ecuadorian Amazonia in farms of Kichwa communities. Kichwa communities have a production system known as “chakra” or “chagra”, where one of the main crops is cassava, cultivated and generally managed by Kichwa women known as chakramamas or chagramamas. The production of plants in the chakra system for food, medicine, spiritual, and ornamental purposes provides food security as well as generating economic income for the families [44,45]. This system of sustainable and cultural production is based on ancestral knowledge and ecological management.

The cassava materials collected for this study were mainly sweet or white types but also some bitter yellow accessions were included. Sweet cassavas are suitable for direct consumption with only a basic preparation process (peeling and cooking), while bitter cassavas are considered toxic and must be processed before consumption, to eliminate or reduce the level of cyanide: the domestication of these two kinds of cassava probably occurred simultaneously [46]. In general, the chakra’s surplus of cassava production is sold in the local markets; however, local markets are imposing the cultivation of yellow cassava as the most profitable, resulting in the loss of white or sweet root cassava. Apparently, some bitter cassavas show better productivity or their toxicity helps them overcome pests and diseases, but their consumption predisposes to neurological diseases when bitter roots are not prepared properly; these diseases are generally endemic to African countries, but we cannot rule them out in Latin America [47]. Unfortunately, in this study we did not conduct analysis of the cyanogen content of the collected cassavas but it would be a future research topic.

3.2. Morphological Characterization

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

3.2.1. Quantitative Descriptors

Table 1 summarizes the minimum and maximum values and the coefficient of variation for nine quantitative descriptors.

3.2.2. Qualitative Descriptors

Table 2 includes the index of deviation from the mode values, i.e., the most frequent character state in the collection observed for each variable.

Table 2. Morphological variability in qualitative characters in the cassava collection from the Ecuadorian regions. The different character states recorded for each character are given in Table A3.

Variables	Index of Deviation from the Mode	Mode
Pubescence on apical leaves	0.96	Absent
Colour of apical leaves	0.88	Light green
Length 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

3.2.3. Correlations

Pearson's analysis determined that no descriptor presented a correlation greater than (0.95) 95%, indicating independence between them. The correlations of descriptors: mean weight of the root per plant and length of the root (0.49), as well as mean weight of the root per plant and diameter of the root (0.59), are those presenting higher positive correlations, which indicates that greater the length and diameter of the root, the greater the weight of the root. These variables weight and diameter of the root are positively correlated as in the study carried out by [36] and this was corroborated by the path analysis at $p < 0.0001$. The descriptors length between nodes and height of the plant presented the highest negative correlation values (−0.26).

3.3. Multivariate Analysis: Description of Clusters

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

Group 1

Group 1 comprises 26 accessions (Table A1) from four coastal provinces (Esmeraldas, Guayas, Manabí, and Santo Domingo de Los Tsáchilas) and three Amazonia provinces (Francisco de Orellana, Napo, and Pastaza). The majority originates from the Coast region (84.62%), and within that region, the accessions are mainly from the province of Manabí (69.23%) (Figure 2).

The most important statistical values for quantitative morphological variables and for qualitative characteristics are included in Table A2 and Table A3, respectively.

Group 2

Group 2 comprises 54 accessions (Table A1), which 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 the Coast region (84.62%), where the accessions collected in the Manabí province (61.11%) predominate (Figure 2).

The most important statistical values for quantitative morphological variables and for qualitative characteristics are included in Table A2 and Table A3 respectively.

Group 3

This group 3 presents 33 accessions (Table A1) collected in four provinces of the Coast (Guayas, Los Ríos, Manabí, and Santo Domingo de Los Tsáchilas), five provinces of the Amazonia (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%) (Figure 2).

The most important statistical values for quantitative morphological variables and for qualitative characteristics are included in Tables A2 and A3 respectively.

Group 4

Group 4 presents the highest number of accessions of all groups with 82 accessions (Table A1) collected in eleven Ecuadorian provinces Esmeraldas, Guayas, Manabí, and Santo Domingo de Los Tsáchilas in the Coast region; Francisco de Orellana, Morona Santiago, Napo, Sucumbíos, Pastaza, and Zamora Chinchipe in the Amazonia region; and Tungurahua in the Sierra region. Most of the accessions were collected in the Amazonia 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 greatest 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 and 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 and 18.47 kg (Table A2).

Regarding the qualitative characteristics of group 4 (Table A3), most of the accessions present (i) an initial fair and reasonable plant vigor; (ii) absence of pubescence of the apical leaf; (iii) leaves with an elliptical-lanceolate or lanceolate central lobe shape; (iv) petiole color 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.

The varietal diversity of cassava in traditional agricultural systems is high, mainly due to the exchange of local varieties of cassava [48]. Another factor is that farmers often incorporate into their harvest plants originated from sexual reproduction [49]. Both processes indicate the interest of farmers in the diversity of this crop, that is, farmers eagerly acquire new local varieties [48].

3.4. 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 (Figure 3) based on a combination of 41 bioclimatic variables, two geophysical and 12 edaphic.

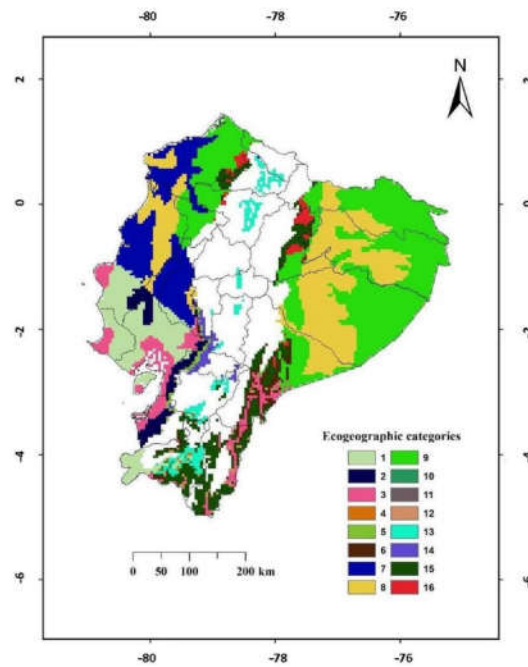


Figure 3. Map of specific ecogeographic characterization in continental Ecuador, where the accessions included in this study were collected.

The ecogeographic categories from which accessions were most frequently collected were categories 8 (21%) and 9 (31.6%). In combination, these two categories add up to 52.6% of the Ecuadorian territory where cassava is produced.

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 of 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. and the surface soil pH was 5. The range of the sand content in the surface soil was between 11 and 29% with a mean of 19.6%. The pH range 4.5 to 6.5 with a mean of 5. In category 9, the maximum temperature of the hottest month (30.3 °C) was recorded; the minimum temperature of the coldest month was 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 were 29.8 °C and 29.7 °C, the minimum temperatures were in July and August with 19.4 °C and 19.3 °C. The mean altitude where these cassava accessions grow is 321 m a.s.l. The range of the sand content in the surface soil was between 26 and 88% with a mean of 39.3% and the surface soil pH range was from 4.0 to 6.5 with a mean of 4.9.

For categories 8 and 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 surface 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: Total of exchangeable bases in the surface soil showed the greatest 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	State/Type (Mode)
Slope	0.28	Flat
Total exchangeable 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 soil	0.59	Very high
Reference of the apparent density * of the surface soil	0.48	Volcanic soil horizons
Apparent density * reference of the subsoil	0.28	Volcanic soil horizons
pH of the surface soil in a water and soil solution	0.79	Slightly acidic
pH of the subsoil in a water and soil solution	0.68	Slightly acidic
Base saturation in the surface soil	0.72	A very acidic soil

* Note: The “apparent density” is measured as follows: 1 turbid horizons 0.25; 2 horizons of volcanic soils 0.85; 3 clay horizons with structure 1.05 to 1.10; 4 mean value 1.35; 5 sandy horizons 1.45 to 1.60; 6 compact horizons 1.90 to 1.95.

3.5. Multivariate Analysis: Description of Groups

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

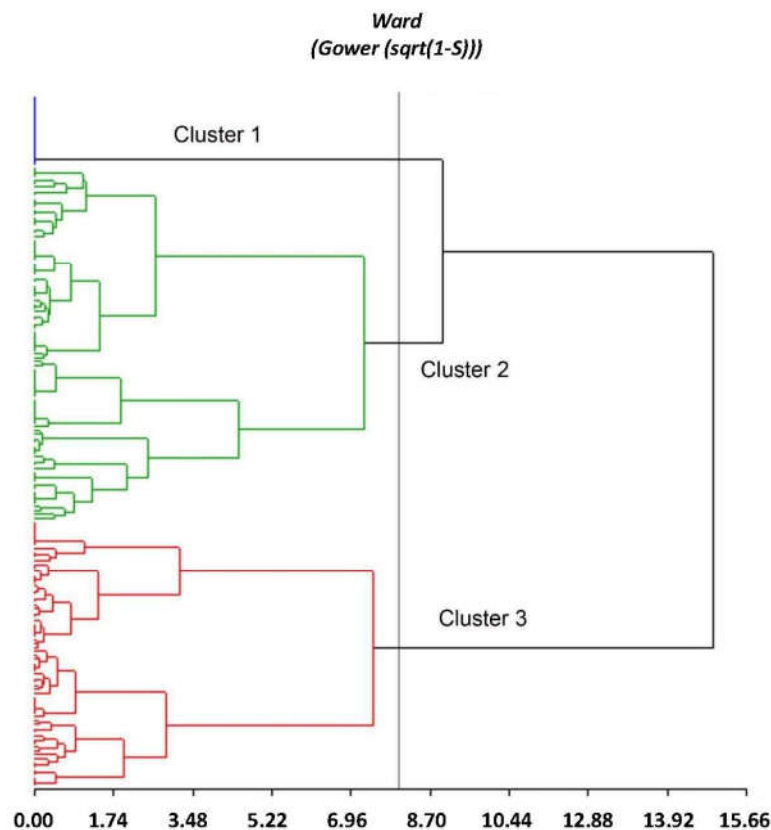


Figure 4. Dendrogram of the Ecuadorian cassava collection indicating three groups of accessions based on quantitative ecogeographic data using Ward's method and Gower's distance.

Group 1

Regarding the qualitative characteristics (Table A5), group 1 accessions develop mainly on flat slopes, surface soil with low fertility for exchangeable bases, low carbon content in the surface soil, low cation exchange capacity of the surface soil, medium cation exchange capacity of the clay fraction, volcanic soil horizons as an indicator 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 (Table A1) collected in a single province of the Ecuadorian Coast region, 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%, and in the subsoil 20%, while the gravel content in the subsoil was 1% (Table A4; note that unfortunately we were unable to establish the minimum and maximum contents). The quantitative ecogeographic variables do not show variation for this group since the accessions were collected under similar conditions (Table A5).

Regarding the qualitative ecogeographic characteristics, group 1 (Table A5) 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 cation exchange capacity of the clay fraction; (vi) volcanic soil horizons as a

reference of apparent density in surface and subsoil soil; (vii) moderately acidic pH in soil and subsoil, and medium base saturation in the soil.

Group 2

Group 2 presents 95 accessions (Table A1) mainly from provinces of the Coast region: Esmeraldas, Manabí, Santo Domingo, Los Ríos, Guayas, Cañar, and Azuay to more than seven accessions from the Amazonia province of Francisco De Orellana. Once again, the provinces of Cañar and Chimborazo are known as Sierra region (highlands). However, the collection sites in this region are from lowland areas (La Troncal) or foothills of the western mountain range (Cumandá), respectively.

The quantitative ecogeographic variables with the greatest 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 grow in a warm environment (23.5 °C to 26 °C); however, 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, i.e., based on means over 50 years' records, 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 soils where sand content in both the surface soil and the subsoil varies from 18 to 70% (Table A4), while the sand content in the subsoil was from 18 to 70% (Table A4).

Regarding the qualitative ecogeographic characteristics, group 2 (Table A5) 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 (viii) soil saturated in bases.

Group 3

The third group comprises 81 accessions (Table A1) mainly from the Ecuadorian Amazonia region, from the provinces of Sucumbíos, Napo, Francisco de Orellana, Pastaza, Morona Santiago, Zamora Chinchipe, and Tungurahua. The latter province is known as an Andean province; however, the region of the Tungurahua province named "Baños", located in the foothills of the Andes, is known as the door of the Ecuadorian Amazonia toward 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 were collected from a broad altitudinal range between 255 m a.s.l. and 1566 m a.s.l. and may present a wide range of adaptation. They tolerate minimum temperatures between 12.9 °C and 19.5 °C. 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 and 470 mm, average rainfall for August between 118 mm and 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% (Table A4).

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, as explained above in Table 4, in surface and subsoil soil; (vii) slightly acidic pH for soil, subsoil; and (viii) soil saturated in bases (Table A5).

Mantel correlation analysis between the morphological and ecogeographical distance matrices showed a coefficient of ($r = 0.37$), which means that only 13% (r^2) of the morphological diversity is explained by the ecogeographical diversity. Values closer to 1 would mean higher correlation between these two matrices.

4. Discussion

4.1. Morphology

4.1.1. Descriptors of the Aerial Part

Shape of the central lobe of the leaf was usually elliptical-lanceolate (50% of accessions) or lanceolate (40%), respectively, of the total accessions. In this study, the lanceolate lobe shape occurs in almost all the accessions studied, in agreement with [24,50] but in contrast to the results of Meneses et al. [26] who, when characterizing 40 accessions, did not show variation in this characteristic. Similarly, Marin et al. [51] 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 color in the following order: light green, dark green, and purple-green. In this regard, [52] mention that the light green color 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 [36,53]. The results obtained are in agreement with those of Meneses et al. [26], who indicate that most of the 40 accessions presented a light green color in the apical bud, followed by dark green. Moreover, [54] indicate that the apical leaf color presented to be dark purple and light green. It is important to note that the color of the apical shoot developed purple-green and purple coloration as a distinguishing characteristic. Ceballos and de la Cruz [53] mention that it is common to observe purple shoots, but as the leaves grow and develop, they change to a greenish coloration.

Of the total accessions, 52% did not have apical leaf pubescence and 48% were pubescent. These results differ from those indicated by Meneses et al. [26], 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 [36] reported a 78.0% presence of pubescence and an absence of 22.0%, while [24] observed a presence in 100% of the accessions evaluated.

About the color of the epidermis of the stem, 57% were observed with dark green color and 26% with light green color. These results do not agree with those obtained by Meneses et al. [26], who indicated that 90% of the accessions evaluated presented a light brown color followed by a cream color. Koefender et al. [24] observed that the light brown color appeared in 51.06% of the evaluated accessions. This descriptor, according to Ramos [54], 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 [24]. On the other hand, the color of the terminal branch of the adult plant developed in the collection was dark green (49%) and light green (31%). Results were different from those found by Torres [36], who found that of the 37 accessions, 32 were green, four were green, and one was purple; and Meneses et al. [26] who indicate a purplish-green (57.5%) and green (42.5%) color.

One or more inflorescences were present in 144 accessions (74.0%), and there was no flowering in 51 accessions (26.0%). This observation coincides with the findings by Pincay Anchundia [55], who found that 96.45% of the accessions under study flowered and 3.5% did not flower. Koefender et al. [24] observed flowering and the presence of fruits in all

the plants they evaluated. Flowering is influenced by genetic and environmental factors and varies greatly in germplasm collections [51,56]. In this study flowering was assessed, as a qualitative descriptor (presence-absence); however, more in-depth flowering studies must be conducted in the Ecuadorian collection to be used in formal breeding; although the most common form of propagation and/or multiplication is vegetative reproduction by cuttings.

4.1.2. Root Descriptors

In cassava, the economically most important characteristic is the pulp, i.e., the root parenchyma. White pulp is one of the colors preferred in producing flours, and for sale as fresh products in local markets [53,57]. Of the 195 accessions of the cassava collection, 83.0% of the accessions presented a white pulp color and only 13.0% a cream color; in addition, in 5.0% the pulp was yellow. Meneses et al. [26] indicate opposite results for the white and cream color, but agree with the low percentage of yellow pulp. In that study, 57.5% of the accessions developed a cream pulp color while 37.5% developed white pulp; However, two accessions with yellow pulp were found (5.0%), while Koefender et al. [24] indicate contrary data, the highest frequency being presented in the cream color (47%), followed by the white color (35%) and the yellow (18%). These are not “contrary” data; color preferences simply vary, culturally and geographically. The two cited studies are from Mexico and Brazil. There are many areas in South America where yellow pulp is highly preferred, especially for making farinha. Many groups grow varieties with different pulp color for different uses [48].

Another characteristic favored for cassava sold as fresh produce is ease of peeling [58]. 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. [26], 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%).

4.1.3. Discriminant Morphological Characters

The qualitative descriptors that allowed better discrimination between the groups obtained in the statistical analysis were petiole color, the shape of the central lobe, the color of the epidermis of the stem, and the color 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 [54] and Lowe et al. [58], they correspond to descriptors of vegetative 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. [59], as in this research, the color of the terminal branches of the adult plant is pointed out as being the most significant characteristic in separating the groups. This finding means that the descriptors (i) the form of the central lobe, (ii) the color of the petiole, and (iii) the color 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 and coincided with those indicated by Lobo [20].

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; the others were 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 keeping in mind that some characters are just less variable than others are. The descriptor root length, in this study, was also considered

discriminant in the research conducted by Acosta and Alonso [52], 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 the findings by Dominguez [60], who mentions that cassava shows a wide variability and presents a high degree of intraspecific hybridization, i.e., an event not examined in the present study. The results of this study are similar to those of other studies [61,62] that used descriptors such as tuber length, epidermis color, external skin of the tuber color, the texture of the tuber surface, and the color of the pulp to document differences between groups. The quantitative descriptors that presented greatest 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 [63,64].

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 attractive plants and in the primary selection of plant material. The phenotypic identification of plants has been used in genotypic classification and taxonomic studies [65,66].

4.1.4. Environmental Adaptation Characteristics of the Cassava Collection

Ecuador is located in the tropical belt, just above the equinoctial line, i.e., celestial equator. This, in combination with its geology and its altitudinal variation, makes it very diverse in terms of climatic and edaphic conditions. In addition, the country 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, showing its wide adaptability [67]. This observation agrees with Sharkawy and Cadavid [68], who mention that cassava is grown worldwide 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; this range of conditions makes cassava suitable for adapting to climate change [69,70].

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 [71], who mentions that cassava is sown from sea level to altitudes of 2000 m a.s.l. in countries located in the tropical and subtropical range between 30° N and 30° S. The same author [68] mentions the development of cassava cultivation with annual rainfall between 500 and more than 2000 mm. The study showed 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 plants found growing at this site are resistant to drought. Drought tolerance is one of the most important adaptation characteristics of the crop [72,73], and it can be evaluated [74]. On the other hand, the annual mean temperature variation at the different collection sites ranges from 18.4 °C to 26 °C, which also indicates a considerable range of adaptation. 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 [69,70,75].

Cassava is a crop that adapts to marginal, acidic soils, enabling it to grow almost without the application of fertilizers, allowing it to adapt even to marginal areas of Africa [72,76,77]. The data indicate that in Ecuador, most of the accessions, especially in the Amazonia region (Group 1, Table A1), 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, i.e., crops whose vegetative cycle is usually less than one (1) year, with the highest production in the region [78]. In the Costa region, the crop can be grown in monoculture or mixed with maize to be commercialized [79]. 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” [80]. Furthermore, cassava in the Ecuadorian and Colombian Amazonia region has high cultural importance [81]. This type of management is similar to both the highly diverse traditional agroecosystems found elsewhere in the Americas as well as in Africa, 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 [48,82–84].

Finally, we can indicate that the applications of ecogeography and geographic information systems [28,85] 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.

Supplementary Materials: The following are available online at www.mdpi.com/2073-4395/11/9/1844/s1, Table S1: Thematic layers used in the ecogeographic characterization in cassava collection.

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Appendix A

Table A1. 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
	17,607; 17,615; 17,618;		17,603; 17,604; 17,605;
	18,407; 18,415; 18,419;		17,608; 17,611; 17,612;
	18,423; 18,432; 18,434;		17,614; 17,617; 17,619;
	18,440; 18,441; 18,448;		17,621; 17,623; 17,624;
	18,451; 18,452; 18,455;	17,620; 18,416; 18,422;	17,625; 17,627; 17,628;
18,414; 18,421; 18,429;	18,462; 18,466; 18,468;	18,424; 18,426; 18,427;	17,640; 18,436; 18,456;
18,435; 18,444; 18,453;	18,473; 18,476; 18,479;	18,430; 18,437; 18,439;	18,465; 18,477; 18,485;
18,459; 18,461; 18,470;	18,480; 18,483; 18,489;	18,449; 18,450; 18,460;	18,516; 18,522; 18,533;
18,472; 18,487; 18,488;	18,491; 18,495; 18,505;	18,463; 18,464; 18,486;	18,567; 18,599; 18,601;
18,497; 18,540; 18,546;	18,506; 18,510; 18,511;	18,517; 18,535; 18,543;	18,608; 18,618; 19,070;
18,564; 18,566; 18,594;	18,513; 18,523; 18,524;	18,545; 18,554; 18,556;	19,091; 19,092; 19,094;
18,597; 18,600; 18,605;	18,536; 18,539; 18,541;	18,560; 18,562; 18,571;	19,095; 19,096; 19,097;
18,616; 19,107; 19,136;	18,542; 18,547; 18,559;	18,583; 18,622; 19,071;	19,098; 19,100; 19,101;
19,149; 19,162	18,561; 18,586; 18,587;	19,108; 19,111; 19,116;	19,102; 19,103; 19,104;
	18,602; 18,607; 18,610;	19,125; 19,143; 19,148	19,106; 19,109; 19,110;
	18,615; 18,620; 18,621;		19,115; 19,117; 19,118;
	19,089; 19,113; 19,134;		19,119; 19,120; 19,121;
	19,141; 19,150; 19,454		19,122; 19,123; 19,124;

			19,126; 19,128; 19,129; 19,130; 19,131; 19,132; 19,133; 19,135; 19,137; 19,138; 19,139; 19,140; 19,142; 19,144; 19,145; 19,146; 19,147; 19,151; 19,152; 19,153; 19,154; 19,155; 19,156; 19,157; 19,158; 19,159; 19,160; 19,161
Grouping by Ecogeographical Quantitative Variables			
Group 1	Group 2	Group 3	
	17,640; 18,407; 18,414; 18,415; 18,416; 18,419; 18,421; 18,422; 18,423; 18,424; 18,426; 18,427; 18,429; 18,430; 18,432; 18,434; 18,435; 18,436; 18,437; 18,439; 18,440; 18,441; 18,444; 18,448; 18,449; 18,450; 18,451; 18,452; 18,453; 18,454; 18,455; 18,456; 18,459; 18,460; 18,461; 18,462; 18,463; 18,464; 18,465; * 18,583; 18,586; 18,587; 18,594; 18,597; 18,599; 18,600; 18,601; 18,602; 18,605; 18,607; 18,608; 18,610; 18,615; 18,616; 18,618; 18,620; 18,621; 18,622	17,603; 17,604; 17,605; 17,607; 17,608; 17,611; 17,612; 17,614; 17,615; 17,617; 17,618; 17,619; 17,620; 17,621; 17,623; 17,624; 17,625; 17,627; 17,628; 19,070; 19,071; 19,089; 19,091; 19,092; 19,094; 19,095; 19,096; 19,097; 19,098; 19,100; 19,101; 19,102; 19,103; 19,104; 19,106; 19,107; 19,108; 19,109; 19,110; 19,111; 19,113; 19,115; 19,116; 19,117; 19,118; 19,119; 19,120; 19,121; 19,122; 19,123; 19,124; 19,125; 19,126; 19,128; 19,129; 19,130; 19,131; 19,132; 19,133; 19,134; 19,135; 19,136; 19,137; 19,138; 19,139; 19,140; 19,141; 19,142; 19,143; 19,144; 19,145; 19,146; 19,147; 19,148; 19,149; 19,150; 19,151; 19,159; 19,160; 19,161; 19,162	
			19,157; 19,158

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

Table A2. 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	Mín	Max	n	Mean	SD	CV	Mín	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					
	<i>n</i>	Mean	SD	CV	Mín	Max	<i>n</i>	Mean	SD	CV	Mín	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

Table A3. 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 lobe of leaf					
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
Length 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

Table A4. 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	n	Mean	SD	CV	n	Mean	SD	CV
Altitude; m a.s.l.	19	347	0	0	94	165.62	108.8	65.67	81	591	286.3	48.43
Annual average temperature; °C	19	23.5	0	0	95	24.84	0.59	2.39	81	23.22	1.3	5.6
Isothermality*; °C	19	8.3	0	0	95	8.03	0.31	3.82	81	8.66	0.22	2.59
Temperature seasonality**; °C	19	63.5	0	0	95	67.81	10.85	16	81	43.06	7.36	17.1
Maximum temperature; warmest month; °C	19	29.2	0	0	95	30.77	0.72	2.35	81	29.09	1.31	4.51
Minimum temperature; coldest month; °C	19	17.4	0	0	95	19.07	0.63	3.3	81	17.73	1.39	7.82
Annual temperature range***; °C	19	11.8	0	0	95	11.71	0.82	7	81	11.36	0.58	5.15
Average temperature; coldest quarter (3 coldest months); °C	19	22.7	0	0	95	24.02	0.59	2.45	81	22.57	1.35	6
Average temperature for the quarter with most rainfall (3 rainiest months); °C	19	24.3	0	0	95	25.51	0.61	2.41	81	22.93	1.23	5.37
Average temperature for the hottest quarter (3 hottest months); °C	19	24.3	0	0	95	25.69	0.55	2.13	81	23.68	1.32	5.59
Maximum temperature for January; °C	19	28.5	0	0	95	29.87	0.75	2.5	81	28.29	1.46	5.15
Maximum temperature for February; °C	19	28.5	0	0	95	30.02	0.64	2.14	81	28.37	1.39	4.89
Maximum temperature for March; °C	19	29	0	0	95	30.49	0.72	2.37	81	28.18	1.32	4.68
Maximum temperature for April; °C	19	29.2	0	0	95	30.68	0.83	2.71	81	28.04	1.19	4.24
Maximum temperature for May; °C	19	28.5	0	0	95	29.87	0.79	2.64	81	27.7	1.16	4.19
Maximum temperature for June; °C	19	27.4	0	0	95	28.72	0.72	2.5	81	27.19	1.27	4.67
Maximum temperature for July; °C	19	27.3	0	0	95	28.49	0.74	2.58	81	27	1.35	5.01
Minimum temperature for January; °C	19	19.4	0	0	95	20.7	0.59	2.83	81	18.4	1.29	7
Minimum temperature for February; °C	19	19.7	0	0	95	20.83	0.68	3.25	81	18.39	1.31	7.14
Minimum temperature for March; °C	19	20	0	0	95	21.17	0.61	2.89	81	18.49	1.32	7.14
Minimum temperature for April; °C	19	19.7	0	0	95	21.06	0.57	2.72	81	18.49	1.29	6.96
Minimum temperature for May; °C	19	19.2	0	0	95	20.67	0.67	3.24	81	18.49	1.22	6.59
Minimum temperature for June; °C	19	18.5	0	0	95	20.08	0.62	3.1	81	18.12	1.38	7.59
Minimum temperature for July; °C	19	17.8	0	0	95	19.45	0.62	3.17	81	17.81	1.39	7.83
Minimum temperature for August; °C	19	17.4	0	0	95	19.07	0.64	3.38	81	17.73	1.39	7.83
Minimum temperature for September; °C	19	17.5	0	0	95	19.23	0.58	3.02	81	18.17	1.37	7.56
Minimum temperature for October; °C	19	17.7	0	0	95	19.59	0.59	3.02	81	18.41	1.33	7.24
Minimum temperature for December; °C	19	18.6	0	0	95	20.09	0.54	2.67	81	18.58	1.3	6.97
Average temperature for January; °C	19	23.9	0	0	95	25.25	0.56	2.24	81	23.32	1.35	5.81
Average temperature for February; °C	19	24.1	0	0	95	25.39	0.57	2.23	81	23.35	1.32	5.66
Average temperature for March; °C	19	24.5	0	0	95	25.81	0.59	2.3	81	23.31	1.31	5.62
Average temperature for April; °C	19	24.4	0	0	95	25.85	0.64	2.47	81	23.23	1.2	5.18
Average temperature for May; °C	19	23.8	0	0	95	25.24	0.65	2.56	81	23.07	1.18	5.11
Average temperature for June; °C	19	22.9	0	0	95	24.37	0.57	2.34	81	22.62	1.32	5.85
Average temperature for July; °C	19	22.5	0	0	95	23.95	0.56	2.33	81	22.38	1.36	6.1
Average temperature for August; °C	19	22.8	0	0	95	24.03	0.6	2.49	81	22.82	1.37	5.99
Average temperature for October; °C	19	23.1	0	0	95	24.45	0.69	2.84	81	23.62	1.33	5.62
Average temperature for December; °C	19	23.8	0	0	95	24.92	0.72	2.9	81	23.73	1.34	5.64
Rainfall during the hottest quarter (3 hottest months); mm	19	845	0	0	95	784.69	441.20	56.23	81	830.6	177.7	21.39
Average rainfall for May; mm	19	117	0	0	95	124.28		87.68	81	356.5	75.75	21.25
Average rainfall for August; mm	19	8	0	0	95	29.47	50.14	170.1	81	237.2	54.42	22.94

Average rainfall for October; mm	19	9	0	0	95	43.56	79.81	183.2	81	294.7	61.23	20.77	
Sand content of soil; %	19	30	0	0	94	29.2	10.6	36.29	81	33.21	16.16	48.66	
Sand content of subsoil; %	19	20	0	0	94	23.97	11.21	4	6.77	79	33.33	16.29	48.87
Gravel content of subsoil; %	19	1	0	0	94	1.5	1.82	121.2	79	12.63	18.49	146.4	

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

Table A5. 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

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