Article

Interrelation of Ecophysiological and Morpho-Agronomic Parameters in Low Altitude Evaluation of Selected Ecotypes of Sweet Potato (*Ipomoea batatas* [L.] Lam.)

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Abstract: Sweet potato is a crop with a wide capacity to adapt to adverse conditions. To study the tolerance of the sweet potato to a low-altitude environment, 34 genotypes comprising three groups from different altitude conditions ranging from 18–599, 924–1298, 1401–2555 meters above sea level were evaluated. These genotypes were evaluated through ecophysiological parameters: net photosynthetic rate (P_n), stomatal conductance (G_s), transpiration (E), leaf internal CO_2 (ICO_2), vapor pressure deficit (VPD) and leaf internal temperature (LT). Subsequently, water use efficiency (WUE) and carboxylation efficiency index (CEI) were estimated. Simultaneously, morpho-agronomic characterization of the genotypes was conducted including descriptors and morpho-colorimetric parameters. A wide ecophysiological variability was found among genotypes from high, intermediate and low altitudes, when those were evaluated under low altitude conditions. The genotypes that presented major soil coverage efficiency and leaf size showed greater P_n , WUE and CEI, and Low VPD and E , aspects that benefited the ability to form roots under the low-altitude environment. The altitudinal origin of the genotypes influenced the ecophysiological response under low altitude conditions. The capacity of certain sweet potato genotypes to tolerate low altitude conditions were due to different mechanisms, such as certain morphoagronomic traits that allowed them to adjust their physiological processes, especially those related to photosynthesis.

Keywords: tolerance; sweet potato; ecophysiology; morpho-agronomic parameters; yield

1. Introduction

Sweet potato (*Ipomoea batatas* (L.) Lam.) is a crop that generates edible energy in the form of storage roots with high nutritional content, mainly from carbohydrates [1]. Unlike other crops, where the development of the aerial part is important for productivity, in sweet potato, the determining morpho-physiological processes are mainly in the formation and development of storage roots that depend directly on the carbohydrates translocation from the leaves to the roots [2–4], although in some countries the aerial part is also consumed [5].

The ontology of storage roots is determined by the process of cell division that generates an increase in cell number of this organ and by starch accumulation that represents 50–80% of the dry matter [2,6,7], possibly related to photosynthetic efficiency in the production of carbohydrates and, consequently, in the production of storage roots [4,8,9].

Different environmental factors affect photosynthetic efficiency in sweet potato, such as CO₂ concentration [10] and water availability [9,11]. Sweet potato, as a C3 plant, has the advantage of responding positively to an increase of CO₂ concentration in the environment, mainly due to its direct effect on photosynthesis and stomata physiology, generating in response a higher yield of storage roots [10]; however, this behavior is modulated by the availability of water.

Water deficit stress can have negative impacts on the photosynthetic efficiency of plants [12]. This process generates a decrease in the assimilation of CO₂, a response that is associated with physiological parameters such as the net photosynthetic rate (Pn), stomatal conductance (Gs), transpiration (E) and intracellular CO₂ (Ci) [1,9–11]. The roots are the first organ of the plant to perceive these signals, limiting the absorption and translocation of water from the sink to the source [2,4,9], directly affecting the mobilization of carbohydrates to the sink, causing a decrease in the formation of storage roots, and consequently, a decrease in crop yield [1,9].

The high plasticity of sweet potato plant is evidenced in its adaptation to several conditions; including adaption at different altitudes, from 0 to 3000 m above sea level (masl) [13,14]. This adaptation to contrasting environmental conditions is a trait of great interest due to its cultivation potential in various agro-ecological zones and at different ultraviolet-B radiation intensities [13,15–17]. The influence of altitude on the quality and quantity of radiation can affect photosynthetic efficiency [17,18], and possibly, starch storage in roots. The behavior of plants at different altitudes is conditioned by some environmental factors, such as accumulation of CO₂ and ultraviolet-B radiation, which directly influence the photosynthetic process [19].

The sweet potato plant presents high rusticity and wide adaptation to adverse environmental conditions [20]. At the morphological level, a higher photosynthetic efficiency has been found in leaves with a low leaf surface area and a lower efficiency when the leaf blade increases in size [21]. At the genetic level there is a potential for obtaining genotypes with the ability to generate favorable responses under stress conditions [6,21–24], showing that the behavior of the sweet potato cannot be generalized and will depend on the cultivar, environment and plant morphology and architecture. The objective of this research was to evaluate the tolerance of sweet potato genotypes from different altitudinal conditions to a low altitude environment. Their responses were estimated from ecophysiological, phenotypic (architecture and morphology) and agronomic parameters.

2. Materials and Methods

2.1. Plant Material

The plant material consisted of 34 sweet potato genotypes from 11 departments of Colombia, and whose collection site was between 18–2555 m above sea level (masl) (Table 1), belonging to the AGROSAVIA work collection. Genotypes that have been previously cultivated in the low altitude conditions, Agrosavia Ambarina and Aurora, were used as checks. The genotypes were grouped by three altitude intervals, High altitude (1401–2555 masl), Intermediate altitude (924–1298 masl) and Low altitude (18–599 masl).

Table 1. Ecotypes of sweet potato and description of site of origin.

Collection Code	Department	Altitude (masl ^z)	Latitude	Longitude
High altitude (1401–2555 masl):				
0216-243.NAR	Nariño	2555	1°34'52.278"	77°00'00.786"
0816-610.BOY	Boyacá	2191	5°37.205'	73°32.051'
0316-286.STR	Santander	2073	06°46'27.6"	072°41'37.2"
0816-587A.BOY	Boyacá	2060	5°51.331'	73°32.437'
0816-600.BOY	Boyacá	1901	5°49.330'	73°35.775'
0516-491.CLD	Caldas	1899	5°14.257'	75°09.589'
0516-515.CLD	Caldas	1883	5°23.326'	75°06.526'
0316-299.STR	Santander	1853	06°57'03.6"	072°54'53.7"
0516-503.CLD	Caldas	1749	5°19.991'	75°07.207'
0816-595.BOY	Boyacá	1718	5°50.926'	73°34.815'
0816-596.BOY	Boyacá	1717	5°50.935'	73°34.825'
0816-582.BOY	Boyacá	1690	5°52.386'	73°34.365'
0816-581.BOY	Boyacá	1689	5°52.385'	73°34.365'
0316-263.STR	Santander	1650	06°31'23.1"	073°03'16.4"
0316-251.STR	Santander	1649	06°44'44.3"	073°00'21.6"
0316-261.STR	Santander	1562	06°32'10.0"	073°06'31.2"
0316-283A.STR	Santander	1481	06°39'48.3"	072°42'18.7"
0816-615.STR	Santander	1426	6°10.193'	73°42.642'
0316-257.STR	Santander	1401	06°32'38.3"	073°19'05.1"
Intermediate altitude (924–1298 masl):				
0516-357.QND	Quindío	1298	4°28'56.952"	75°43'41.682"
0715-096.NS	Norte de Santander	1207	08°16'06.6"	073°21'57.6"
0715-099.NS	Norte de Santander	1187	08°14'12.4"	073°21'17.1"
0816-618.STR	Santander	1160	6°13.600'	73°47.308'
0715-086.CES	Cesar	1122	10°25'06.1"	073°35'12.6"
0316-300.STR	Santander	1119	06°56'22.1"	073°01'16.4"
0113-660.VAL	Valle del Cauca	1000	3°30'7"	76°21'22"
0113-668.VAL	Valle del Cauca	1000	3°30'7"	76°21'22"
0316-256.STR	Santander	924	06°32'21.4"	073°17'33.4"
Low altitude (18–599 masl):				
0715-076.CES	Cesar	599	10°42'15.1"	073°19'26.4"
0516-352-HUI	Huila	525	2°41'12"	75°19'32"
0816-620.STR	Santander	521	6°13.592'	73°51.154'
0715-105.CES	Cesar	224	08°14'06.9"	073°29'55.3"
Ambarina (check)	Valle del Cauca	18	3°30'7"	76°21'22"
Aurora (check)	Córdoba	18	8°45'35"	75°53'08"

^z masl: meters above sea level.

2.2. Growth Conditions and Agronomic Management

The research was performed in an experimental field at Agustín Codazzi, Cesar, Colombia, with coordinates 10°0'7" North and 73°14'51" West, with an altitude of 104 masl. Climate conditions during the evaluation period are showed in Table 2.

Table 2. Rainfall, temperature and relative humidity of the study environment.

Month	Accumulated Rainfall (mm)	Mean Temperature (°C)	Mean relative Humidity (%)
May	290.2	28.5	69.1
June	206.4	28.7	67.9
July	231.4	29.1	66.8
August	221.9	28.3	67.9
September	187.0	28.0	72.8

The experimental field has a soil with a clay-silty texture, and pH 7.57. For establishment, mechanical land preparation and manual planting were done. Weed control was chemically using

ammonium glyphosate, (5 L ha⁻¹) and halosulfuron (150 g ha⁻¹). For pest control, Fipronil (0.6 L ha⁻¹) and Thiodicarb (1 L ha⁻¹), Bayer, Colombia, were used. Supplementary fertilization was not used.

2.3. Experimental Design

A complete randomized design with three blocks was used, with each block corresponding to an experimental unit. The experimental units consisted of plots of 5 rows of 5 m length; and planting distance of 0.4 m between plants and 1 m between rows. For all sampling evaluations, three plants per genotype were used per block from the three central rows to avoid an edge effect.

2.4. Screening of Genotypes for Ecophysiological Parameters

Net photosynthetic rate (Pn), stomatal conductance (Gs), transpiration (E), internal leaf CO₂ (ICO₂), vapor pressure deficit (VPD) and internal leaf temperature (LT) were evaluated using a portable photosynthesis system (LI-COR, LI-6400XT, NE, USA) in the morning (08:00–11:00) under a fixed blue-red light-emitting diode (LED) light source. Later, the water use efficiency (WUE) was obtained through the ratio of Pn/E, and the carboxylation efficiency index (CEI) using the ratio Pn/ICO₂ [25]. Three measurements were made for genotype on a fully expanded leaf, being the 4th or 5th leaf from apical meristem, at 120 days after planting (DAP). The equipment was calibrated to the evaluation conditions, through light and CO₂ curves, obtaining the appropriate range of photosynthetically active radiation (PARi) of 1500 μmol of photons m⁻² s⁻¹ and a CO₂ reference content of 400 μmol CO₂ mol⁻¹. These curves were optimized using the genotype Agrosavia Ambarina.

2.5. Morpho-Agronomical Characterization

Selected genotypes were characterized using 28 parameters describing plant architecture and morphology, which were evaluated 90 days after planting (DAP). For plant description, the parameters included: mature leaf color, immature leaf color, vine internode length, vine internode diameter, predominant vine color, secondary vine color, vine tip pubescence, mature leaf shape, leaf lobes type, leaf lobes number, shape of the central leaf lobe, mature leaf size, leaf width, petiole length, petiole pigmentation, abaxial leaf vein pigmentation, plant type, flowering habit and ground cover, length of the main vines, stem latex presence, petiole diameter, petiole pubescence and leaf pubescence; all the morphological parameters were characterized according to sweet potato descriptors [26]. Root production per plant (number and weight) was evaluated at 120 DAP.

2.6. Morpho-Colorimetric Measurements

RGB images from leaves were taken with a Canon EOS 600D camera configured with similar depth and sensor sensitivity settings for all genotypes. Light, exposition time and the distance between the specimen and the camera were controlled among the genotypes evaluated. Leaves from subapical shoot segment were dissected and photographed; shape descriptors such as area, perimeter, circularity, leaf roundness and leaf solidity were measured according to [27]. Color determination was carried out in a selected area (ROI) of the RGB images using a color measurement plug-in in image J (<https://imagej.nih.gov/ij/>).

2.7. Data Analysis

To group the genotypes according to altitude intervals, the TREE procedure of SAS software was used. To recognize the possible interaction between altitude and tuberization capacity, the genotypes were categorized in two groups, genotypes with storage roots or genotypes without storage roots. To analyze the factors (genotype, altitude and tuberization), analysis of variance was performed, with a two-way analysis with interaction effect for altitude and tuberization factors, and a one-way analysis for each factor was performed using R software. Tukey or Fisher's LSD multiple comparison test were used for mean comparison among genotypes or groups (α = 0.05). Chi-squared tests were used

for independence analysis of qualitative variables. To study the relationships between traits, linear Pearson and Spearman correlations were performed. In order to analyze simultaneously qualitative and quantitative physiological and morpho-agronomic variables, hierarchical clustering of variables was performed to reduce variable redundancy, to select and determine their correlated structure and similarity patterns through the 'hclustvar' function in the package 'ClustOfVar' compatible with the R software. A method based on the bootstrap approach was used to evaluate the stability of the partitions of variables and to determine a suitable number of clusters of variables ($B = 50$). Furthermore, six quantitative synthetic variables were established [24] and used in principal component analysis (PCA) to determine the genotype population structure based on altitude origin and tuberization capacity. PCA was performed using FactoMineR and factoextra packages of R software. R free software version 4.0.3 (R Foundation for Statistical Computing, Vienna, Austria) was used to perform all described analysis.

3. Results and Discussion

3.1. Diversity in Ecophysiological Parameters in Sweet Potato Ecotypes Evaluated under Low-Altitude Conditions

Sweet potato ecotypes collected from several altitude conditions showed a wide response in the tolerance to low altitude conditions. Genotype and altitude factors analyzed independently showed significant differences in some physiological parameters, the three intervals of altitude showed significant differences in Pn, E, VPD, WUE and CEI, while the genotype factor showed statistical differences for all ecophysiological traits (Table 3).

Table 3. Analysis of variance results for altitude and genotype factor.

Source ^z	Altitude	Genotype
DF	2	33
Pn	83.68 ** y	23.94 ***
Gs	0.025	0.22 ***
ICO ₂	224.58	349.05 ***
E	13.92 **	6.52 ***
VPD	0.4 ***	0.19 ***
LT	2.19	4.83 ***
WUE	2.46 ***	0.57 ***
CEI	0.0012 ***	0.0004 ***

^z DF: Degree freedom in ANOVA; Pn: Photosynthesis; Gs: Stomatal conductance; ICO₂: Internal CO₂; E: Transpiration; VPD: vapor pressure deficit; LT: Leaf internal temperature; WUE: Water use efficiency; CEI: Instantaneous carboxylation efficiency index. ^y Each value represents the mean square. Significance, *** $p < 0.001$; ** $p < 0.01$.

Through the categorization by altitudinal origin, the three groups presented a differential behavior. Genotypes from high altitude (1401–2555 masl) exhibited the lowest Pn, WUE and CEI, but the highest E and VPD compared with others altitude ranges. These values for physiological parameters, were possibly related to a minor tolerance to low altitude conditions (Table 4). Genotypes from the intermediate altitude range (924–1298 masl), exhibited intermediate values for Pn, WUE, CEI, E and VPD. Finally, the genotypes from the low altitude range (18–599 masl), showed the highest values for Pn, WUE and CEI, but conversely, they had the lowest values for E and VPD compared with the other altitude intervals. These results indicated that genotypes from this group presented a better physiological response under the low altitude conditions than the genotypes from the greater altitudes, possibly because they were from warm climate regions and had evolved mechanisms to tolerate low altitude conditions (104 masl). The broad adaptation of this species to different edaphoclimatic conditions [13], and the results obtained in this study, suggested that the species has wide variability to tolerate low altitude conditions and the physiological adaptation of low altitude genotypes indicated higher trait value in comparison with genotypes from other altitudinal ranges.

Table 4. Means comparison among eco-physiological parameters of several genotypes of sweet potato.

<i>z</i>	Pn	Gs	ICO ₂	E	VPD	LT	WUE	CEI
High altitude (1401–2555 masl)								
Genotype								
0216-243.NAR	25.45cdefghij ^y	1.39abcde	304.05abcd	13.44abcd	1.42abcde	34.96abcd	1.89ijkl	0.0840fghijklm
0816-610.BOY	25.17cdefghij	1.63abcde	310.06ab	12.84abcdef	1.25bcde	30.54r	1.96hijkl	0.0810hijklm
0316-286.STR	30.12abcde	1.25abcde	285.11abcde	12.61abcdefg	1.45abcde	35.06abc	2.39cdefghij	0.1053abcdefg
0816-587A.BOY	27.34abcdefghi	1.91abc	308.55abc	12.91abcdef	1.14de	32.08jklmnopqr	2.12efghijkl	0.0883defghijklm
0816-600.BOY	28.03abcdefghi	1.27abcde	293.00abcde	12.58abcdefg	1.43abcde	34.74abcde	2.23efghijkl	0.0953abcdefghijklm
0516-491.CLD	22.74ghij	1.30abcde	307.27abcd	14.09abc	1.64abcd	33.35efghij	1.61l	0.0740klm
0516-515.CLD	25.20cdefghij	1.67abcde	311.26ab	13.35abcdef	1.28bcde	30.91pqr	1.90ijkl	0.0810hijklm
0316-299.STR	30.03abcde	1.32abcde	288.67abcde	12.41abcdefg	1.36abcde	34.37abcdef	2.42cdefghij	0.1040abcdefgh
0516-503.CLD	21.59ij	0.92cde	294.77abcde	12.33abcdefg	1.92abc	33.65cdefghi	1.78jkl	0.0737lm
0816-595.BOY	25.88bcdefghij	1.48abcde	309.46ab	8.74g	0.89e	33.68cdefghi	2.96abcd	0.0840fghijklm
0816-596.BOY	27.01abcdefghij	1.45abcde	300.19abcde	12.93abcdef	1.36abcde	32.45hijklmnop	2.09efghijkl	0.0900cdefghijklm
0816-582.BOY	27.64abcdefghi	1.13abcde	291.73abcde	10.95bcdefg	1.35abcde	31.67klmnopqr	2.52bcdefghi	0.0950abcdefghijklm
0816-581.BOY	28.96abcdefgh	1.59abcde	294.71abcde	14.92a	1.51abcde	33.48defghij	1.94hijkl	0.0980abcdefghijk
0316-263.STR	25.02defghij	1.54abcde	306.88abcd	14.83ab	1.49abcde	33.29efghij	1.69kl	0.0813ghijklm
0316-251.STR	27.54abcdefghi	1.44abcde	300.78abcde	11.67abcdefg	1.22cde	31.61lmnopqr	2.36cdefghijk	0.0917bcdefghijklm
0316-261.STR	25.56cdefghij	1.25abcde	301.19abcde	12.14abcdefg	1.40abcde	32.18ijklmnopq	2.11efghijkl	0.0850fghijklm
0316-283A.STR	30.83abcd	1.18abcde	281.88abcde	12.04abcdefg	1.42abcde	35.08abc	2.56bcdefghi	0.1097abcde
0816-615.STR	21.71ij	0.88de	291.78abcde	12.10abcdefg	1.96ab	33.67cdefghi	1.82jkl	0.0743jklm
0316-257.STR	30.98abcd	1.08abcde	271.01e	11.29abcdefg	1.52abcde	34.18abcdefg	2.77bcde	0.1147ab
Group mean	26.77c	1.35	297.49	12.53a	1.42a	33.20	2.16b	2.16b
Intermediate altitude (924–1298 masl)								
0516-357.QND	32.47ab	1.17abcde	276.08de	12.03abcdefg	1.44abcde	32.91fghijklmn	2.70bcdef	0.1175a
0715-096.NS	26.72abcdefghij	1.71abcd	307.03abcd	13.37abcde	1.25bcde	33.21efghijk	2.00ghijkl	0.0870efghijklm
0715-099.NS	28.73abcdefgh	1.34abcde	293.28abcde	12.80abcdef	1.38abcde	34.96abcd	2.24efghijkl	0.0980abcdefghijk
0816-618.STR	27.88abcdefghi	1.20abcde	288.94abcde	12.43abcdefg	1.44abcde	33.74bcdefgh	2.45bcdefghij	0.0963abcdefghijklm
0715-086.CES	23.54efghij	1.00abcde	293.11abcde	10.52cdefg	1.61abcd	32.08jklmnopqr	2.23efghijkl	0.0800hijklm
0316-300.STR	30.81abcd	1.06abcde	276.97cde	11.45abcdefg	1.46abcde	34.69abcde	2.69bcdef	0.1113abcd
0113-660.VAL	28.67abcdefgh	1.57abcde	304.08abcd	9.45fg	0.89e	32.84fghijklmn	3.04abc	0.0943abcdefghijklm
0113-668.VAL	29.61abcde	1.59abcde	301.74abcde	9.48efg	0.89e	32.82ghijklmn	3.12ab	0.0983abcdefghij
0316-256.STR	26.49abcdefghij	1.95a	312.32a	12.24abcdefg	1.06de	31.26opqr	2.17efghijkl	0.0850fghijklm
Group mean	28.32b	1.39	294.83	11.53b	1.26ab	33.16	2.51a	2.51a

Table 4. Cont.

^z	Pn	Gs	ICO ₂	E	VPD	LT	WUE	CEI
Low altitude (18–599 masl)								
0715-076.CES	33.04a	1.34abcde	279.65bcde	12.50abcdefg	1.35abcde	35.27ab	2.65bcdefg	0.1183a
0516-352-HUI	29.56abcdef	1.69abcd	299.22abcde	12.82abcdef	1.20cde	33.24efghij	2.31defghijk	0.0990abcdefghi
0816-620.STR	28.80abcdefg	1.95ab	303.61abcd	13.27abcdef	1.18de	32.01jklmnopqr	2.17efghijkl	0.0950abcdefghijklm
0715-105.CES	28.53abcdefg	1.17abcde	286.38abcde	12.39abcdefg	1.51abcde	34.30abcdefg	2.31defghijk	0.0997abcdefg
Ambarina	31.10abcd	1.46abcde	294.78abcde	8.74g	0.86e	33.10fghijkl	3.56a	0.1057abcdef
Aurora	29.26abcdefg	1.60abcde	301.74abcde	10.73cdefg	1.00de	32.75ghijklmno	2.72bcdef	0.0970abcdefghijkl
Group mean	30.04a	1.53	294.23	11.74b	1.18b	33.44	2.62a	2.62a

^z Pn: Photosynthesis, Gs: Stomatal conductance; ICO₂: Internal CO₂; E: Transpiration; VPD: vapor pressure deficit; LT: Leaf internal temperature; WUE: Water use efficiency; CEI: instantaneous carboxylation efficiency index. ^y Each value represents the mean. Different letters represent significant differences between genotypes at $p \leq 0.05$ (Tukey's test) and significant differences between groups at $p \leq 0.05$ (LSD test).

Regarding the ecophysiological diversity of the characterized genotypes, net photosynthetic rate (P_n) had a range between 21 and 33 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. The genotypes 0715-076.CES (599 masl), 0516-357.QND (1298 masl) and Agrosavia Ambarina (18 masl) presented the highest values, with 33.04, 32.47 and 31.09 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, respectively (Table 4), while 0816-615.STR (1426 masl) and 0516-503.CLD (1749 masl), genotypes from high altitude, presented the lowest averages (21 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). Most of the values among genotypes were within the range reported for C3 plants [28,29]; however, the wide range in this study associated with differences between sweet potato ecotypes used in the study. Previous studies observed P_n values below 20 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, in sweet potato genotypes subjected to water stress [9,11,30]. The values found in our study showed that the evaluation conditions guaranteed an optimal physiological state of the evaluated ecotypes. High values of P_n in genotypes from low and intermediate altitudes may indicate a high potential of tolerance to low altitude conditions and possibly to low water availability, since these conditions cause stomatal closure, reduction of P_n and affect the translocation of assimilates to roots. The growth habit of the plant in certain genotypes allowed it to maintain humidity in the soil, a morphological adaptation that, in turn, would allow it to improve the water status of the plant, modifying the opening and closing of stomata, transpiration and assimilation [31,32].

Stomatal conductance (G_s) is a parameter that relates the number and degree of stomatal opening [33]. A range of variation for G_s was between 0.88–1.95 $\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$. The genotypes 0316-256.STR (924 masl), 0816-620.STR (521 masl) and 0816-587A.BOY (2060 masl) presented an average higher than 1.90 $\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$, while the genotypes 0816-615.STR (1426 masl) and 0516-503.CLD (1749 masl) showed an average lower than 0.92 $\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$. The values found were similar to those exhibited in genotypes subjected to a level of humidity close to the field capacity, since less soil humidity induces the closure of stomata and the values found under these conditions are below 0.8 $\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$ [34,35]. However, certain sweet potato genotypes are capable of controlling the osmotic potential in the leaves through different mechanisms that regulate stomatal opening through an increase in proline levels, thus, avoiding a decrease in P_n and G_s [9,36] and unnecessary water loss through transpiration. Although a broad response was found in the stomatal conductance of the evaluated ecotypes, their adequate tolerance was evidenced regardless of their altitudinal origin.

The concentration of intercellular CO_2 fixed by plants (ICO_2) influences photosynthesis. The genotypes evaluated presented values between 271.01–312.32 $\mu\text{mol CO}_2 \text{ mol}^{-1}$, some being congruent with previous studies [37], which described values between 231 and 296 $\mu\text{mol CO}_2 \text{ mol}^{-1}$. The genotypes that exhibited the highest ICO_2 values may indicate a greater capacity for CO_2 entry, due to a greater stomatal conductance. However, this result did not generate any increase in P_n , probably because C3 species can have a saturation effect on Rubisco, decreasing its activation state and equilibrium [10,36,37].

Transpiration (E) corresponds to the flow of water, in the form of vapor, generated between the plant and the atmosphere [38,39]. There were wide differences in E among the genotypes, those from a high altitude 0816-581.BOY (1689 masl), 0316-263.STR (1650 masl) and 0516-491.CLD (1899 masl), presented the highest values (14.9, 14.8 and 14.1 $\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$, respectively); the lowest values were around 8.74–10.52 $\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$, in genotypes from intermediate and low altitude Agrosavia Ambarina (18 masl), 0113-660.VAL (1000 masl) and 0113-668.VAL (1000 masl). Previous studies reported values between 4 and 17 $\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$ in two varieties of sweet potato subjected to different regimes of soil moisture, the highest values with a higher soil moisture content [34]. Different humidity regimes may influence this trait [40]. The wide diversity found among evaluated genotypes was consistent with the differing responses that can be found between different genotypes [1]. However, the differential response of genotypes from high altitude showing higher values compared with the genotypes from other altitudinal intervals suggested their lower adaptation to low altitude conditions, since the adapted genotypes exhibited lower values.

Vapor pressure deficit (VPD) is high when plants close stomata to avoid excessive water loss [41], sometimes negatively affecting photosynthesis and yield, due to the increase in stomatal resistance.

0816-615.STR (1426 masl) and 0516-503.CLD (1749 masl), genotypes from a high altitude, presented the highest VPD values (1.96 and 1.92 kPa, respectively), and were the genotypes with the lowest Pn. Moreover, the genotype that presented the highest Pn (0715-076.CES, 599 masl) had an intermediate VPD value (1.35 kPa), indicating adequate adaptation of genotypes from low altitude to low altitude evaluation conditions and an ability to keep the plant water content in balance, with an intermediate conductance and transpiration.

Variable responses for leaf internal temperature (LT) was found among the genotypes, with values between 30.54–35.27 °C. Genotype 0715-076.CES (599 masl) presented the highest LT (35.27 °C), and simultaneously exhibited the highest Pn ($33.04 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). Although it has been reported that temperatures around 35 °C influence the reduction of the enzymatic capacity of Rubisco [42], the results in this investigation indicated that there was no negative effect on Pn with the increase in LT among the genotypes. This process is favorable because the plant will not invert the water reserves, under conditions of water deficit, to reduce the leaf temperature [43]. This response differs from that reported in another C3 species (cassava *Manihot esculenta*), in which an increase in leaf temperature reduced photosynthesis [43].

Water use efficiency (WUE) represents a characteristic of great interest in plants, allowing the use of this resource in a regulated way under conditions of soil water deficit [44]. The genotypes with the highest WUE exceeded the value of $1.5 \mu\text{mol CO}_2/\text{mmol H}_2\text{O}$, which corresponded to the highest value found in sweet potato genotypes in previous reports [45], indicating more efficient water use in genotypes from intermediate and low altitudes. The genotypes with the highest WUE were Agrosavia Ambarina (18 masl), 0113-668.VAL (1000 masl) and 0113-660.VAL (1000 masl). WUE was a variable that was related to E, and among the genotypes with the best response for WUE were the same genotypes with low E values, which showed the ability of these genotypes to fix the necessary CO_2 , using the available water efficiently and decreasing transpiration process.

The carboxylation efficiency index (CEI) was estimated using the relationship between Pn and ICO_2 . The genotypes from intermediate and low altitudes 0715-076.CES (599 masl) and 0516-357.QND (1298 masl) were the most efficient according to the CEI, with values of 0.1183 and 0.1175, respectively. The least efficient genotype was a genotype from high altitude, 0516-503.CLD (1749 masl) with 0.0737. Efficiency in the carboxylation process may be associated with the ability of Rubisco to increase its affinity for CO_2 fixation with respect to intracellular O_2 and, thus, reduce photorespiration rates and increase Pn [25,46]. Consistently, the genotypes that presented the highest Pn reached the highest values for CEI also. This ecophysiological characterization revealed a wide variability between the sweet potato genotypes from different altitude (18 to 2555 masl). In general, the genotypes from low and intermediate altitudes showed a better physiological response, which was confirmed by their high Pn and CEI and low VPD, while only some genotypes from higher altitudes showed such responses.

3.2. Relationship among Ecophysiological Parameters in Sweet Potato

Multivariate analysis determined relationships among physiological traits that although highly variable among the genotypes, indicated two principal components (PC) explained 78% of all variation. Consistently, a relationship among WUE, Pn and CEI was observed (Figure 1a); all of these parameters were related to the efficiency of the photosynthetic process, and including a third PC (PC3 explained 15.17%), the component matrix indicated that CEI, Pn and WUE were the most important traits for PC1 (Supplementary materials Table S1). Another potential relationship was observed between Gs and ICO_2 , and between E and VPD.

a) **b)**

Figure 1. Relationship among physiological characteristics evaluated in sweet potato. **(a)** Principal component analysis (PCA) among physiological parameters; **(b)** Pearson's linear correlations among physiological parameters. Pn: Net photosynthetic rate, Gs: Stomatal conductance, ICO₂: Internal CO₂, E: Transpiration, VPD: vapor pressure deficit, LT: Leaf internal temperature, WUE: Water use efficiency, CEI: Carboxylation efficiency index. Each value represents the coefficient of correlation. Significance: ** $p < 0.01$; ns: no significance.

The interrelations among physiological traits were confirmed by correlation analysis (Figure 1b). Consistently, Pn had a direct correlation with WUE. WUE is considered a key mechanism that allows a reduction in water loss and increase in CO₂ assimilation. Therefore, it is a desirable trait that indicates good adaptation and greater plasticity of the genotypes [47,48]. The positive significant correlation between Gs with ICO₂ confirmed the association previously described. A high content of ICO₂ is a result of an increase in Gs, and, consistently with its negative correlation, can simultaneously reduce VPD [41], Pn, WUE and CEI [47,49]. A greater Gs allows an increase in the flux of CO₂ into the plant and can affect transpiration rates and subsequently, the Pn process, as previously reported [10,47,49–51]. However, a significant reduction of ICO₂ can also reduce Pn [47].

Regarding the relationship between E and VPD, the positive correlation indicated that there was an increase of E, until a maximum limit of VPD (values below 2 kpa); then, E was reduced. In fact, when the VPD increases, stomata are forced to close to protect the plant from dehydration [41]. In contrast, an inverse relation between VPD and Gs was observed; an expected response due to VPD increase, forcing the stomata to close to protect the plant from dehydration [41]. Additionally, an inverse relationship between WUE and both VPD and E was found, indicating that sweet potato plants were more efficient in the use of this resource when the Gs, E and VPD decreased due to greater stomatal resistance and lower water loss [41]. In addition, this correlation was also reported previously in related species of *Ipomoea*, in which a low water loss was found, caused by low Gs, along with the maintenance of good photosynthetic behavior, which represents an adequate WUE [47].

The positive correlation between Gs and E can be explained by a greater opening of the stomata causing E to continue along with Pn [52,53]. In respect to LT, this parameter decreased with the increase of Gs because the transpiration process is favored in the plant [44,54,55], and water release promote a cooling effect in the leaf. An inverse correlation was found for ICO₂ and LT, indicating that as the LT increased, the ICO₂ was reduced; this may be due to the stomatal closure effect generated by heating the plant canopy, to reduce the E [56], which would have caused a reduction in CO₂ availability. Similarly, the negative correlation between Pn and VPD indicated a reduction of Pn when the VPD values were high. This behavior is conditioned by the plant response, through stomatal closure mechanism, which reduces dehydration [9,41,51,57]. In this way, it is evident that when the Gs was reduced, the diffusion of CO₂ was affected, also implying an effect on Pn [25].

These associations between ecophysiological parameters demonstrated tolerance strategies in a wide variability of the sweet potato genotypes. The response of Pn, WUE and CEI in the genotypes was largely determined by the values of Gs, ICO₂ and E. These parameters defined the response of the genotypes to the evaluation conditions.

3.3. Interaction between Ecophysiological and Morpho-Agronomic Parameters Involved in Sweet Potato Tolerance to Low-Altitude Conditions

Results from morpho-agronomic and ecophysiological characterization was analyzed simultaneously to determine the interaction of these traits on the tolerance of sweet potato to low altitude conditions. Although, a wide diversity was found among genotypes, several traits were strongly related to each other, providing the same information and producing data redundancy. Therefore, to avoid this constraint, a hierarchical analysis of quantitative and qualitative variables was used for variable selection, determination of any association between them and creation of synthetic variables to improve the integral analysis of the genotypes. Thirty variables were selected, which showed higher stability of the partitions and represented several variables that were not further included, such as: secondary color of the stems, shape of the central leaf lobe, leaf solidity, red coloration, internode diameter, stem latex, petiole pubescence, mature leaf width, petiole diameter and general outline of the leaf. Six general groups were produced from the analyzed variables and were defined as synthetic variables SV1, SV2, SV3, SV4, SV5 and SV6 (Figure 2). SV1 mainly involved parameters related to the plant type, pubescence, tuberous root formation, ground cover, leaf size and leaf roundness; SV2 grouped characteristics of WUE, E and leaf area; SV3 grouped traits related to

leaf shape and pigmentation; SV4 represented Pn, CEI and mature leaf color; SV5 only represented physiological attributes such as Gs, VPD, ICO₂ and LT; finally, SV6 grouped leaf color attributes (Figure 2, Supplementary Materials Table S2). This data analysis was performed in line with previous studies which have shown that phenotypic descriptions may contain redundant variables and that variable aggregation can be used to select an optimal set of explanatory variables for an appropriate statistical model by removing multi-collinearity [58], an aspect generated by the similarity among some groups of variables that bring the same information [24].

Figure 2. Estimation of synthetic variables from ecophysiological, morphological, morphometrical and productive parameters. Pn: Photosynthesis, Gs: Stomatal conductance, ICO₂: Internal CO₂, E: Transpiration, VPD: vapor pressure deficit, LT: Leaf internal temperature, WUE: Water use efficiency, CEI: Carboxylation efficiency index.

Using these synthetic variables, the behavior of the genotypes from different altitude intervals and with differential tuberization capacity was analyzed. The multivariate analysis showed that the ecophysiological response, the morphological characteristics and the ability to produce storage roots were independent of the altitudinal origin of the sweet potato genotypes (Figure 3a). Meanwhile, genotypes with capacity to produce storage roots were associated with the synthetic variables SV2, SV4 and SV1, which grouped mainly gas exchange parameters such as Pn, WUE, E and CEI; plant type, soil cover, leaf area, leaf roundness, flowering habit and productive parameters (Figure 3b).

Figure 3. Principal component analysis (PCA) among synthetic variables. **(a)** Comparison among altitudinal intervals (high, intermediate, and low), **(b)** comparison among groups of genotypes with storage roots and without roots. Pn: Photosynthesis, Gs: Stomatal conductance, ICO_2 : Internal CO_2 , E: Transpiration, VPD: vapor pressure deficit, LT: Leaf internal temperature, WUE: Water use efficiency, CEI: Carboxylation efficiency index.

The results of the correlation analysis confirmed the relationship among different phenotypic characteristics (morphology and color), physiological parameters and with storage root production previously determined by cluster analysis (Supplementary materials Table S3). From a cluster that grouped the synthetic variables SV1, SV4 and SV2, ground cover, mature leaf size, and flowering habit, a positive correlation with Pn, CEI and WUE, was observed. However, abaxial leaf vein pigments, mature leaf color and leaf adaxial pubescence presented negative correlation with these physiological parameters. A cluster that grouped the synthetic variables SV3, SV6 and SV5, showed a positive correlation with leaf perimeter and Pn, as with circularity with Gs and ICO_2 , and internode length was negatively correlated with Pn, ICO_2 , E, VPD and WUE.

These results may be associated with the direct effect of leaf size, leaf maturation and amount of biomass, which correspond to parameters associated with the main photosynthetic structures, and is related to Pn, WUE and water loss by transpiration [59,60]. However, when leaves reach their maximum maturity and senescence begins, the photosynthetic capacity is reduced [61]. These morphological traits also were related to LT, CEI and WUE; however, most of the traits that were positively related to Pn were negatively associated to VPD. Flowering habit depends on cultivar and growing conditions, but there was no evidence of any relationship with photosynthetic process. Negative correlation of ecophysiological parameters (Pn, ICO_2 , E, VPD and WUE) with variables associated with leaf shape, presence of pigments in plant organs and plant architecture were found. Some plants have structural and pigmentation modifications in the leaves as protective barriers to environmental factors, which reduce their absorption of radiation, avoiding saturation of plant, but exposing the photosynthetic structures to an imbalance [62]. Furthermore, this type of barrier can reduce the absorption of photosynthetic wavelengths and affect Pn by photoinhibition [62]. On the other hand, the presence of pubescence may contribute to reduced transpiration [63], which related to stomatal closure and may imply a negative effect on Pn [64]. Adaptation to the conditions of genotype origin is given by the physiological characteristics that allow them to adapt to the environment in which they develop and stimulate the acquisition of water, light and other components for growth [65].

The characterized population presented a wide phenotypic and ecophysiological variability between and within groups categorized by different altitudinal intervals (high, intermediate and low altitude), and tuberization capacity (genotypes with storage roots and genotypes without storage roots). Variance analysis integrating altitude and tuberization factors and their interaction showed that for altitude intervals, only Pn and WUE presented statistically significant differences. Regarding tuberization the parameters Pn, WUE, CEI, root number, root weight, leaf circularity, leaf roundness and leaf solidity were statistically different, while the interaction was not statistically significant for any variable (Table 5).

Table 5. Combined analysis of variance for altitude and tuberization capacity factors for eco-physiological, morphological and productive parameters.

Source ^z	Altitude (A)	Tuberization (T)	A * T
DF ^y	2	1	2
Pn	32.61 * x	67.25 **	13.51
Gs	0.02	0.00	0.19
ICO_2	77.5	230.2	280.9
E	7.43	5.76	0.85
VPD	0.19	0.25	0.12
LT	0.90	2.70	4.09
WUE	1.14 **	1.37 **	0.12
CEI	0.0004	0.0012 **	0.0003
Root number	2.56	142.85 ***	4.42
Root weight	219,952.32	2,664,236.85 ***	227,622.92
Leaf area	1276.2	3204.2	384.5
Leaf perimeter	259.62	622.58	296.13

Table 5. Cont.

Source ^z	Altitude (A)	Tuberization (T)	A * T
Leaf circularity	0.02	0.14 *	0.06
Leaf roundness	0.0004	0.02 *	0.0079
Leaf solidity	0.02	0.11 *	0.03

^z Pn: Photosynthesis; Gs: Stomatal conductance; ICO₂: Internal CO₂; E: Transpiration; VPD: vapor pressure deficit; LT: Leaf internal temperature; WUE: Water use efficiency; CEI: Carboxylation efficiency index. ^y DF: Degree freedom.

^x Each value represents the mean square. Significance: *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$.

The genotypes presented a wide variability in morphometric and agronomic parameters within each altitudinal interval; however, between groups no significant differences were detected (Table 6). Most of the genotypes that tuberized were collected in places of low altitude, and only some genotypes of high altitude showed the ability to adapt to the evaluation conditions. The evaluated genotypes were grouped with respect to their capacity to produce storage roots, in order to determine the characteristics that allowed to guarantee better tolerance to low altitude conditions, and to be comparable to the Aurora and Ambarina varieties. Genotypes 0715-076.CES, 0316-251.STR, 0316-256.STR, 0316-283A.STR, 0316-299.STR, 0316-300.STR, 0516-352-HUI, 0816-600.BOY, 0816-618.STR and 0113-668.VAL produced storage roots at 120 DAP. The genotype 0316-299.STR presented the highest yield per plant, with 1.326 gr/plant, being comparable with the Ambarina variety (Table 6).

Table 6. Means comparison of morphometric and agronomic parameters in several ecotypes of sweet potato.

Genotypes	Number of Storage Roots per Plant	Storage Roots Weight per Plant	Leaf Area	Leaf Perimeter	Circularity	Soil Cover ^z	Mature Leaf Size ^y
High altitude (1401–2555 masl)							
0216-243.NAR	0.00e ^x	0.00h	48.39jkl	31.59m	0.59abcd	3	5
0816-610.BOY	0.00e	0.00h	91.95defgh	44.43hijklm	0.59abcde	3	5
0316-286.STR	0.00e	0.00h	45.41jkl	107.46a	0.05k	3	5
0816-587A.BOY	0.00e	0.00h	75.73efghij	39.13klm	0.62ab	3	5
0816-600.BOY	5.33bc	889.00c	53.49ijkl	56.82efghij	0.21ij	5	5
0516-491.CLD	0.00e	0.00h	66.22fghijkl	40.41ijklm	0.51cdefg	3	3
0516-515.CLD	0.00e	0.00h	64.20ghijkl	42.91ijklm	0.44fgh	3	3
0316-299.STR	10.33a	1326.00b	121.40bcd	51.46ghijkl	0.58abcde	7	5
0516-503.CLD	0.00e	0.00h	94.36defgh	53.86fghijkl	0.41gh	3	3
0816-595.BOY	0.00e	0.00h	102.10cdef	48.53ghijklm	0.55abcde	3	5
0816-596.BOY	0.00e	0.00h	133.26bc	52.50ghijkl	0.61abc	3	5
0816-582.BOY	0.00e	0.00h	102.99cdef	49.20ghijklm	0.54abcde	3	3
0816-581.BOY	0.00e	0.00h	77.88efghij	43.39ijklm	0.52bcdef	3	3
0316-263.STR	0.00e	0.00h	58.18hijkl	37.83lm	0.51cdef	3	3
0316-251.STR	1.33de	211.00fg	118.32bcd	54.96efghijkl	0.49efgh	5	5
0316-261.STR	0.00e	0.00h	57.60hijkl	42.11ijklm	0.41h	3	3
0316-283A.STR	6.33b	670.00d	97.68cdefg	47.50ghijklm	0.54abcde	5	5
0816-615.STR	0.00e	0.00h	92.99defgh	64.29defg	0.28i	3	5
0316-257.STR	0.00e	0.00h	32.90kl	87.59bc	0.05k	3	5
Group mean	1.22	162.9	80.79	52.41	0.44		
Intermediate altitude (924–1298 masl)							
0516-357.QND	0.00e	0.00h	28.81l	88.72b	0.05k	3	5
0715-096.NS	0.00e	0.00h	85.88defghi	70.79cdef	0.22ij	5	5
0715-099.NS	0.00e	0.00h	72.46efghij	76.28bcd	0.16j	5	5
0816-618.STR	1.33de	56.00gh	69.03fghijk	41.51ijklm	0.50defgh	3	5
0715-086.CES	0.00e	0.00h	92.65defgh	45.79hijklm	0.53bcdef	3	3
0316-300.STR	5.67bc	415.33e	73.28efghij	39.36ijklm	0.59abcd	3	5
0113-660.VAL	0.00e	0.00h	152.99b	57.63efghi	0.58abcde	7	5
0113-668.VAL	4.67c	160.00fgh	191.66a	61.41defgh	0.64a	5	5
0316-256.STR	2.33d	430.67e	146.61b	54.99efghijkl	0.60abc	7	7
Group mean	1.55	118	101.49	59.60	0.43		

Table 6. Cont.

Genotypes	Number of Storage Roots per Plant	Storage Roots Weight per Plant	Leaf Area	Leaf Perimeter	Circularity	Soil Cover ^z	Mature Leaf Size ^y
Low altitude (18–599 masl)							
0715-076.CES	2.67d	322.00ef	94.05defgh	45.12hijklm	0.58abcde	5	5
0516-352-HUI	2.67d	162.00fgh	53.49ijkl	49.97ghijkl	0.27i	5	5
0816-620.STR	0.00e	0.00h	58.54hijkl	56.39efghijk	0.23ij	3	3
0715-105.CES	0.00e	0.00h	99.21cdefg	72.47bcde	0.24ij	3	5
Ambarina	2.33d	1226.67b	113.07bcde	52.75fghijkl	0.50defgh	3	7
Aurora	6.67b	1874.33a	67.81fghijkl	36.24lm	0.65a	7	7
Group mean	2.39	597.5	81.03	52.15	0.41		

^z Soil cover, 3: low < 50%, 5: medium 50–74%, 7: high > 75%; ^y Mature leaf size, 3: small < 3 cm, 5: medium 8–15 cm, 7: large 16–25 cm. Different letters represent significant differences between genotypes at $p \leq 0.05$ (Tukey's test for genotypes and LSD's test for altitude groups).

The group that had the ability to produce storage roots presented higher Pn, WUE and CEI, compared to the group that did not have the ability to produce storage roots (Table 7). This observation was consistent with reports in which the positive relationship between photosynthesis and root production is indicated [4,9]; this condition is also attributed to other C3 species such as cassava [28], guarantying a major amount of photo-assimilates that can be translocated to reserve organs, in this case the roots [30]. This group had a higher WUE and CEI compared to the group without storage roots, indicating that these genotypes made efficient use of the water resource [66], an aspect also corroborated by the low E found in this group. This group also presented the lowest VPD, which could be related to its adequate Pn behavior, since it has been reported that high VPD values indicate negative effects on Pn, due to high stomatal closure [41].

Table 7. Means comparison between groups of genotypes with storage roots and without storage roots according to ecophysiological, morphometric and agronomic parameters.

Traits	Units	Genotypes with Storage Roots	Genotypes without Storage Roots
Ecophysiological parameters			
Pn ^z	$\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$	29.55a ^y	26.78b
Gs	$\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$	1.41a	1.38a
ICO ₂	$\mu\text{mol CO}_2 \text{ mol}^{-1}$	292.54a	297.93a
E	$\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$	11.66b	12.46a
VPD	kPa	1.24b	1.39a
LT	°C	33.59a	33.08a
WUE	$\mu\text{mol CO}_2/\text{mmol H}_2\text{O}$	2.58a	2.19b
CEI	–	0.102a	0.09b
Morphometric parameters			
Leaf area	cm ²	102.03a	78.54b
Leaf perimeter	cm	49.56b	57.12a
Circularity	–	0.51a	0.39b
Round	–	0.89a	0.83b
Solidity	–	0.84a	0.73b
Number of storage roots per plant	Storage roots/plant	4.31	0
Storage roots weight per plant	g/planta	645.25	0

^z Pn: Net photosynthesis rate; Gs: Stomatal conductance; ICO₂: Internal CO₂; E: Transpiration; VPD: vapor pressure deficit; LT: Leaf internal temperature; WUE: Water use efficiency; CEI: Carboxylation efficiency index. ^y Each value represents the mean. Different letters represent significant differences between genotypes at $p \leq 0.05$ (LSD's test).

Regarding the morphometric characteristics of the leaves, the group that tuberized presented a larger leaf area, circularity, leaf roundness and leaf solidity, and lower perimeter, indicating the presence of lobed or more complex leaves [27], compared to the group without storage roots. These results indicated that in the group with capacity to produce storage roots, most of the genotypes had leaves with a major leaf area available for the capture of sunlight, an aspect that could favor the assimilation of CO₂

by having a larger reception area for photosynthetically active radiation (PAR). Furthermore, the best photosynthetic efficiency favors the production of carbohydrates and, consequently, the production of storage roots [4,8,9].

In the qualitative parameters, dependence analysis showed association of tuberization capacity with soil cover efficiency, mature leaf size and latex production in the stems (Table 8). The genotypes that produced storage roots had a higher soil cover and mature leaf size, and lower latex production, compared to the group without storage roots. These results were consistently confirmed by quantitative variables in which it was shown that the genotypes with capacity to store starches in the roots presented a major leaf area and complete leaf lamina (less lobed). Although, the physiological and agronomic response of the genotypes was not totally related to their altitudinal origin, most of the genotypes that tuberized originated from altitudes between 18 and 1160 m above sea level, with the exception of four genotypes, whose origin was between 1481 and 1901 masl (Figure 4). In general, tolerance to low altitude conditions, considered as the ability to survive and produce storage roots, involved a high Pn in certain genotypes that together with the controls, Aurora and Ambarina, had the ability produce storage roots. These results showed the phenotypic plasticity of the genotypes, since even some genotypes from high altitudes were able to produce storage roots in conditions contrasting to those of their origin, and others that, despite having been evaluated in comparable conditions, showed a low productive performance. The genotypes from high altitude that showed low Pn values had small leaves with major complexity (more lobed) and did not have the ability to produce storage roots.

Table 8. Comparison between qualitative characteristics using Chi² square test between groups of genotypes with storage roots and without storage roots.

Parameter	Scale	Genotypes without Storage Roots (%)	Genotypes with Storage Roots (%)	Total	dfb ^z	Chi ²
Soil cover	Low (<50%)	52.94	11.76	64.71	2	10.61 *** ^y
	Medium (50–74%)	5.88	17.65	23.53		
	High (75–90%)	2.94	8.82	11.76		
	Total	61.76	38.24	100		
Mature leaf size	Small (<8 cm)	23.53	2.94	26.47	2	7.71 *
	Medium (8–15 cm)	38.24	26.47	64.71		
	Large (16–25 cm)	0	8.82	8.82		
	Total	61.76	38.24	100		
Latex production	None	52.94	2.94	55.88	2	20.21 ***
	Little	8.82	29.41	38.24		
	Abundant	0	5.88	5.88		
	Total	61.76	38.24	100		

^z df: degree freedom. ^y Significance *** $p < 0.0001$, * $p < 0.05$.

These results suggested a wide variability in phenotypic and ecophysiological response in the sweet potato genotypes. Leaf size (large) and complexity (less lobed), together with soil cover efficiency, can influence the microclimate conditions and ensure major photosynthetic efficiency that favors the production and accumulation of carbohydrates [4,8,9]. In the evaluated sweet potato genotypes, these parameters played a key role in guaranteeing their tolerance to low altitude conditions. Additionally, factorial analysis showed that some ecophysiological parameters, morphological traits and the tuberization capacity were related to the altitudinal origin of the genotypes. Consistently, discrimination of genotypes according to tuberization capacity was found through parameters grouped in the synthetic variables SV2 (WUE, E and leaf area), SV4 (Pn, CEI and Mature leaf color) and SV1 (plant type, pubescence, tuberous roots formation, ground cover, leaf size and leaf roundness, among others), suggesting the key role of these traits for tolerance to low altitude condition.

Figure 4. Relationship between genotypes with storage roots and without storage roots according to Pn and altitude. Pn: Net photosynthetic rate; masl: meters above sea level.

4. Conclusions

Characteristics of high Pn, CEI and low VPD were decisive in the tolerance of ecotypes to low altitude conditions. Genotypes from lower altitudes showed a better physiological response, and only some genotypes from higher altitudes showed such tolerance.

The response of the Pn, WUE and CEI in evaluated genotypes was largely determined by Gs, ICO₂ and E. Changes in Gs directly affected the diffusion of CO₂, which led to modifications of the flux of CO₂ into the leaf, causing changes in E and Pn, which was translated as changes of water use efficiency.

Genotypes that exhibited leaves with larger size and less complexity (less lobed), together with more soil cover efficiency, showed major photosynthetic efficiency that favored the production and accumulation of carbohydrates in storage roots, and were key to guaranteeing tolerance to low altitude conditions.

Tuberization capacity was related to parameters such as WUE, E Pn, CEI, leaf area, mature leaf color, plant type, pubescence, ground cover, leaf size and leaf roundness, among others, suggesting the key role of these traits for tolerance to low altitude conditions

Supplementary Materials: The following are available online at <http://www.mdpi.com/2311-7524/6/4/99/s1>, Table S1: Matrix of principal component analysis for physiological parameters, Table S2: Synthetic variables created with Hierarchical clustering of physiological and morpho-agronomic variables (qualitative and quantitative), Table S3: Pearson and Spearman correlation among ecophysiological parameters and quantitative and qualitative traits of morpho-agronomic description.

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Abbreviations

Pn	Net photosynthetic rate
Gs	Stomatal conductance
ICO ₂	Internal CO ₂
E	Transpiration
VPD	Vapor pressure deficit
LT	Leaf internal temperature
WUE	Water use efficiency
CEI	Carboxylation efficiency index
DAP	Days after planting
SV	Synthetic variable

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