

Limitations in the growth and development of chayote (*Sechium edule* (Jacq.) Sw., due to habitat change

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Abstract

Several soil minerals have not been considered in the expansion of chayote cultivation with and without biotic and abiotic stress, despite being an essential and necessary element in plant growth and development. The objective of this study was to describe the changes that occur in the growth of *Sechium edule* (Jacq.) Sw. under the influence of agroclimatic conditions different from those of its center of origin, such as temperature, light, and soil types. The study was carried out in three production localities in Veracruz, Mexico in one year equivalent to two productive seasons. Physiological variables were recorded under field and cultivated conditions in three different agroclimatic conditions in the Mesophilic Cloud Forest (MNF), Medium Sub-evergreen Forest (MBS) and Seasonal Dry Forest (SSE). It was found that the calcium (Ca²⁺) concentration and pH value of the soils of the three regions. X-ray analysis showed the formation of crystals in leaf, petiole and stem tissue, consisting mainly of phosphorus, calcium and silicon. Leaf area showed burns and leaf necrosis in soils with high Ca²⁺ content. Chlorophyll content and CO₂ assimilation rate were lower in plants grown under MSF and SDF conditions compared to CMF. Environmental temperature, altitude, precipitation, pH, chlorophylls, as well as Ca²⁺, Mg, organic matter, N, Fe, Zn and Mn, were variables that help to explain the limitations of *S. edule* development in the crop expansion sites. The results can be considered as a reference and avoid failures due to displacement of *S. edule* to limiting agroclimatic conditions.

Received: 12 Jul 2024. Received in revised form: 09 Sep 2024. Accepted: 24 Oct 2024. Published online: 05 Nov 2024.

From Volume 49, Issue 1, 2021, Notulae Botanicae Horti Agrobotanici Cluj-Napoca journal uses article numbers in place of the traditional method of continuous pagination through the volume. The journal will continue to appear quarterly, as before, with four annual numbers.

Keywords: calcium; crystals; environmental stress; growth

Introduction

The chayote (*Sechium edule* (Jacq.) Sw.) (Cucurbitaceae) is a neotropical specie, originally from cloud forest (Barrera-Guzmán *et al.*, 2021). Presents within its biological diversity the cultivar *S. edule* var. *virens levis* of high economic value as an export product from México, middle America and Caribbean countries for United States and Canada markets. Commercial success has displaced their cultivation to different agroclimatic regions (Cisneros-Solano, 2018) with important differences regarding their habitat of origin. Under these conditions, the yield and persistence of plants in the field decrease due to lower rainfall, increased temperature, and interaction with the presence of soils with different characteristics from the habitat of origin (Taneja and Upadhyay, 2021). The producing countries are Mexico, Costa Rica, and the Dominican Republic in the Caribbean. Recently some Mediterranean countries in Europe have become interested in its production, as well as Asian countries such as India, China, and Japan (Cadena-Iñiguez *et al.*, 2023; Shi *et al.*, 2023).

Historically, chayote cultivation had been established within the limits of cloud forests in altitudes between 1200 and 1400 m. However, its commercial success has displaced it to different agroclimatic regions, generating a series of physiological alterations that affect its growth and development (SIAP, 2022). Based on this, we considered the hypothesis that the soil and environmental conditions of three agroclimatic regions where chayote is grown induce physiological alterations that affect the production (Cisneros-Solano, 2018).

In this regard, calcium and other minerals content in soils has not been considered in the expansion of chayote cultivation, even though these nutrients are an essential and necessary element in the growth and development of plants under different conditions, with and without biotic and abiotic stress (Thor, 2019; Wang *et al.*, 2023); for example, calcium is found in the cytoplasm of cells in low concentrations (Hepler, 2005) and is part of various structures and functions (Taneja and Upadhyay, 2021), as in the cell wall where it regulates the rigidity and stabilization of cell membranes (González-Fontes *et al.*, 2017) and acts as a second messenger (Kleist and Wudick, 2022). Without calcium, the development of new tissues in roots and shoots is stopped (El Habbasha and Faten, 2015), while the excesses available in the soil and its effect on the pH and solubility of minerals can cause physiological alterations in the plants.

Calcium excess is expressed with external symptoms (He *et al.*, 2024) as the growth rate of the plant decreases (Wang *et al.*, 2023) and changes of green to yellow in the leaves due to an increase in calcium accumulation leading to the death of the plant (Zuñiga-Valenzuela *et al.*, 2018). In some soils it can induce ionic alterations to the detriment of other nutrients (Lopez-Arredondo *et al.*, 2013), in addition to the formation of crystals in plant tissues, including leaves (Zhang *et al.*, 2020). Based on this, we consider the hypothesis that the edaphic and environmental conditions of three agroclimatic regions where chayote is grown induce physiological alterations that affect growth and development. The objective was to describe changes that occur in the growth of *Sechium edule* (Jacq.) Sw., under agroclimatic conditions different from those of its center of origin, such as temperature, light, and minerals in the soil.

Materials and Methods

Experimental site, vegetation, and types of soils

The study was carried out in three representative locations of producing areas of Veracruz, Mexico. The first evaluation site was Tlaltengo (19.05 NL; 97.00 WL; 1480 m altitude) with cloud mountain forest (CMF) vegetation, 2250 mm precipitation, average annual temperature of 19 °C and relative humidity (RH) of 85% with vitric luvisol soil. The second evaluation site was in Escamela (18.51 NL; 97.04 WL; 1140 m altitude)

with medium subperennial forest (FMS), 1800 mm of precipitation, average annual temperature of 22 °C and 80 % RH, and Luvisol soils. The third site was in the Pedregal (19.31 NL; 96.30 WL; 298 m altitude) with seasonal dry forest (SDF), 241 mm of precipitation, average annual temperature of 31 °C and 60% RH and luvisol vertic soils (INEGI, 2017). The above parameters were obtained with a datalogger located in the center of each plot to record temperature and humidity (Onset HOBO UA-002-64 Pendant Temperature/Light Data Logger 64). Precipitation and location through local weather stations, while altitude and geoposition through the free program GPStatus and Toolbox (<https://play.google.com/store/apps/details?id=com.eclipsim.gpsstatus2&hl=es&gl=US&pli=1>). The average regional variables according to the climatic stations 30066, 30151, 3003 of Veracruz, Mexico, close to the study sites, temperature, precipitation and altitude are: 19.4, 22.8 and 25.1 °C for CMF, MSF and SDF respectively. In the same order for precipitation: 2011.7, 2213.7 and 870.5 mm annually. Finally with the average altitude of 1284, 781 and 250 m above sea level.

Biological material

The study was carried out under field conditions in the period 2020-2021, which includes a production season. *S. edule* is perennial; however, under cultivated conditions only 14 to 16 months are considered, and subsequently a new plantation is carried out. Chayote plants of the *S. edule* var. *virens levis* (Figure 1A), were evaluated during the reproductive stage at six months of age after sowing. Sampling was carried out for three months once the plants began production. The cultivation is carried out on a horizontal support structure, where the stems (vine) grow horizontally (Figure 1 B-C).

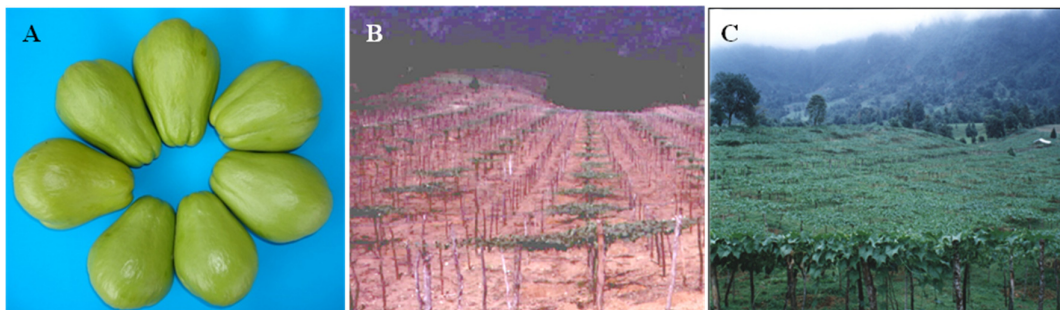


Figure 1. (A) Chayote fruits at horticultural maturity (18±2 days) var. *virens levis*; (B) Support structure for the growth of var. *virens levis*; (C) Plants in production

Soil and leaf analysis

For soil analysis, 25 field subsamples were taken at a depth of 0-30 cm per study location and with these a 2 kg sample was formed. For the foliar analysis, 200 fully expanded leaves were taken, that is, their growth has ceased. They were taken at the fifth node of the vine before the apical bud. They were dried in an oven at 60 °C (FELISA® TE-HV30D, Zapopan, Jalisco, Mexico) distributed evenly on aluminium trays, previously washed and brought to constant weight (AOAC, 2023). The electrical conductivity of the soil was obtained with a glass bridge Wheatstone conductivity meter with the saturated paste extract (soluble ions) (Panzardi *et al.*, 2020).

Micrographs, crystal morphology and crystal composition

Stem, leaf, and petiole samples were taken from fully expanded leaves, discarding the first six leaves as juveniles and the sample corresponded to 10 intermediate leaves to make observations in a scanning electron microscope (model JEOL SM 35 C), with the following process: fixing with glutaraldehyde (2.5%) for 180 min and later wash with phosphate buffer solution (pH 7.3; 0.16 M) by triplicate to remove the excess fixative. Dehydration with ethanol starting at 30% up to 80% for 5 min each, and in 90%, 96% and absolute for ten

minutes. The samples were dried with CO₂ until critical point and mounting was done with adherent carbon tape and vacuum packed with gold. A scanning electron microscope (model JEOL SM 35 C) was used, and the analysis of tissue precipitates with X-rays (EDX) by taking micrographs. The measurement was carried out with the Image Tool on the photomicrographs.

Gas exchange

The variables of stomatal conductance, transpiration and CO₂ assimilation rate were considered in 10 young leaves, completely expanded, from 10 vines of the plants selected in the experimental area. A closed portable system was used for gas analysis in the infra-red spectrum (IRGA) (model CIRAS-1 PPSYSTEMS, Amesbury, MA 01913 USA). The measurements per day were carried out from 7:00 to 19:00 h. To facilitate the recording of maximum leaf activity in each measurement hour, the IRGA clamp was always directed towards where it recorded the greatest amount of light on the leaf. The conditions of temperature, precipitation, altitude, and total evaporation of the three agroclimatic regions were recorded. Additionally, photosynthetically active radiation (PAR), conductance, leaf temperature and CO₂ assimilation rate were analysed separately from the IRGA records for each location, in order to identify their correlation.

Total chlorophyll

The chlorophyll concentration was determined in the third fully exposed leaf of the main stem of the plant, and four samples were taken from each plant (Inskeep and Bloom, 1985). Two discs from each leaf sampled were taken with a 2 cm diameter puncher. One disc was used for dry weight and the other was placed in a test tube with 5 mL of N, N- Dimethylformamide for chemical determination. They were kept in the dark at 4 °C for 24 h for pigment extraction. The reading was performed in 1 mL of extract to measure absorbance in a spectrophotometer (Spectronic 21D-Milton Roy, Industrial and Scientific, USA) using the N, N-Dimethylformamide as target. For chlorophyll a (Chl a) the maximum absorbance was 664.5 nm and for chlorophyll b (Chl b) 647 nm. With the absorbance data, the concentration of Chl a, Chl b, and total concentration was calculated with the following formula: Chl a= 12.7 (A664.5) - 2.79 (A647); Chl b= 20.7 (A647) - 4.62 (A664.5); total= 17.9 (A647) + 8.08 (A664.5); where 12.7, 2.79, 20.7, 4.62, 17.9 and 8.08 are constants and A647nm and A664.5 nm are the absorbance values obtained.

Statistical analysis

The database was processed by descriptive analysis and multiple correspondence analysis (MCA) using FactoMineR libraries (Kassambara and Mundt, 2020). For variables between locations of sampled crop regions and nutrients in plant leaf tissue were analyzed by principal component analysis (PCA) using RStudio software (R Core Team, 2023).

Results

Soil analysis

The elements Fe, Mn and Zn register greater solubility in soils of volcanic origin such as CMF, where they even form iron, manganese, or zinc phosphates, when the pH value is less than 5.0, limiting the availability of phosphorus. However, the results of the analysis (Table 1) indicate that also in the MSF and SDF soils, the values were high compared to the cloud forest. Boron (B) and copper (Cu) recorded values that can be referenced for future studies, since there are currently no extraction values from chayote plants that allow comparison. The physical-chemical analysis of the soil indicated significant differences between the sites of the producing regions in pH with Ca and organic matter (OM) with N ($P \leq 0.05$) (Figure 2). The OM decreased in MSF and SDF by more than 64.7% on average compared to CMF. P, Ca, and Mg increased significantly in MSF and SDF soils, suggesting high availability considering the pH value (6.03-7.71) (Table 1).

Table 1. Values of the physicochemical analysis of the soil of the three evaluation places

	pH	OM	N	P	K	Ca	Mg	Fe	Mn	Zn	B	Cu	Na	CE
Site		%	%	mg kg ⁻¹										dS/m
CMF	5.71	11.47	0.61	1.08	0.53	3.55	1.25	2.33	23.9	2.5	3.8	2.38	0	0.79
MSF	6.03	4.52	0.25	74.6	0.20	14.5	2.70	46.7	40.9	15.2	2.4	1.68	0.26	2.71
SDF	7.71	3.53	0.17	6.70	1.26	53.9	6.00	1.7	6.6	11.2	0.01	0.56	0.43	2.69

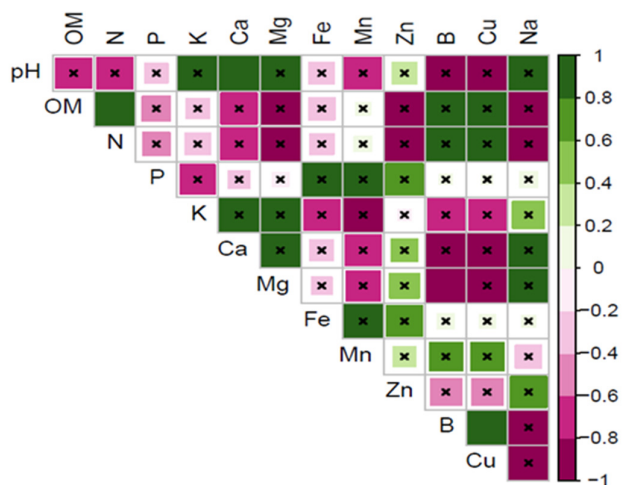


Figure 2. Soil physicochemical analysis between the sites of the production regions sampled. Those correlations with “x” are not significant ($P \geq 0.05$)

Soil nutrient content

Principal component analysis revealed that each experimental site has distinctive soil characteristics. Showing in Figure 3A that there is a relationship between physiological variables (chlorophylls), soil minerals and environmental variables. For example, the “MSF” site has components rich in Zn, P, Fe, Mn, in addition, rainfall is an important variable in its aggregation. The “CMF” site is rich in minerals such as B, Cu, N and Organic Matter (Figure 3B). Additionally, the content of chlorophyll a, b and total, as well as the altitude (Alt) are explanatory since the values were 1480, 1140 and 241 meters above sea level, for CMF, MSF and SDF respectively. As a result of the PCA, the dependent variables were divided into two components. The contribution of component 1 was 74.1%, while component 2 was 25.9%. Macronutrient concentrations showed high K, Mg, Ca, Na values in the SDF that influence the pH value (Figure 3B). Regarding the Ca²⁺ content, the values showed increases in SDF, while P and N were higher in MSF. The foliar analysis showed that Ca²⁺ registered an increasing percentage trend for the plants grown in the CMF, MSF and SDF sites respectively (Appendix Table 1). The above coincides with the trend observed in the soil analysis (Table 1).

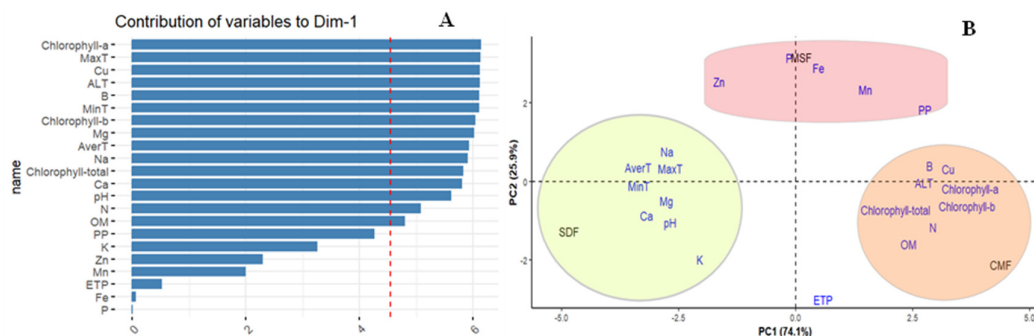


Figure 3. (A) Principal component analysis of soil nutrient content, chlorophyll, and climatic variables of the three evaluated regions. The most important variables of CPI are Chlorophyll-a, Maximum Temperature (MaxT), Cu, Altitude (Alt); B, Minimum temperature (MinT), chlorophyll b, Mg, Average temperature (AverT), total chlorophyll, Ca²⁺, pH. These variables explain about 75% of the total variance. (B) distribution of the variables by their statistical weight and agroecological site. CMF: cloud mountain forest; MSF: medium subperennial forest; SDF: seasonal dry forest

Crystal morphology and crystal composition

The formation of crystals in the leaf, petiole, and stem tissue of *S. edule* plants growing in three contrasting environments is presented in Figures 4, 5 and 6. The sections in Figure 4A, B, C correspond to plants grown in CMF soils with no apparent formation of crystals, attributable to soil acidity conditions and low Ca²⁺ content.

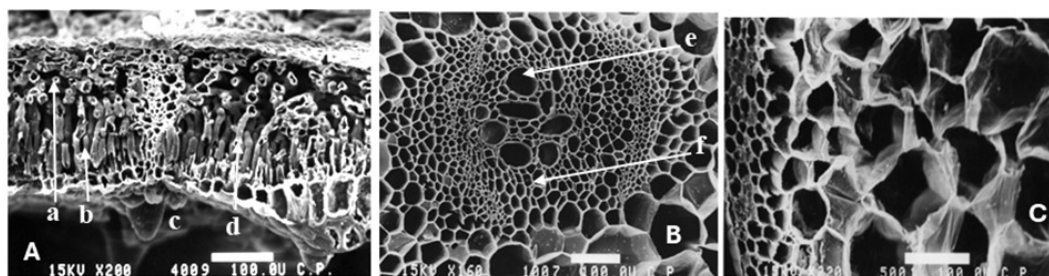


Figure 4. (A) Section of leaf tissue; (B) Vascular bundles of stem (vine); (C) Section of leaf petiole tissue from *S. edule* plants developed in the cloud mountain forest (CMF) region; (a) Spongy parenchyma; (b) Palisade parenchyma; (c) Cystolytic trichome of the leaf; (d) Mesophyll; (e) Xylem; (f) Phloem. Micrographs obtained with scanning electron microscope at 200×, 160× 220× respectively

The Figure 5 A, B, C corresponds to plants grown in MSF with less acidic soil pH (6.03) and a notable increase to 14.5 and 74.6 mg kg⁻¹ of Ca²⁺ and phosphorus respectively, while in Figure 6 A, B, C, refers to plants developed in SDF environment with alkaline soil and 53.9 mg kg⁻¹ of Ca²⁺. Figure 5A shows the increase in leaf thickness for MSF (303.7 μm) and Figure 6A, recorded 315.38 μm thickness increase for SDF plant leaves. The above is relevant when compared to CMF site sheets with sheet thickness of 229.62 μm (see Figure 4A), emphasizing that in the MSF and SDF sites there was formation of crystals in stem and petiole (Figure 5C, 5C) of styloid, druse and spherical type, while in CMF (Figure 4C) no crystals were recorded in petiole tissues.

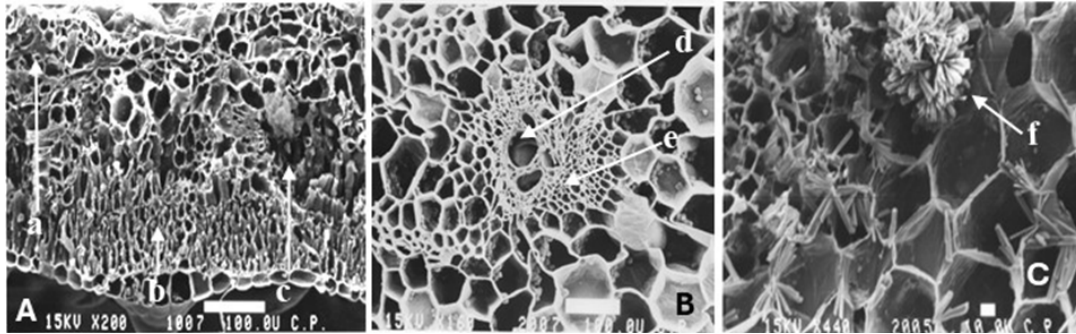


Figure 5. (A) Section of leaf tissue; (B) Vascular bundles of stem (vine); (C) Section of leaf petiole tissue from *S. edule* plants developed in the medium subperennial forest (MSF) region; (a) Spongy parenchyma; (b) Palisade parenchyma; (c) Mesophyll; (d) Xylem; (e) Phloem; (f) Drusen crystals. Micrographs obtained with scanning electron microscope at 200×, 160× and 440× respectively

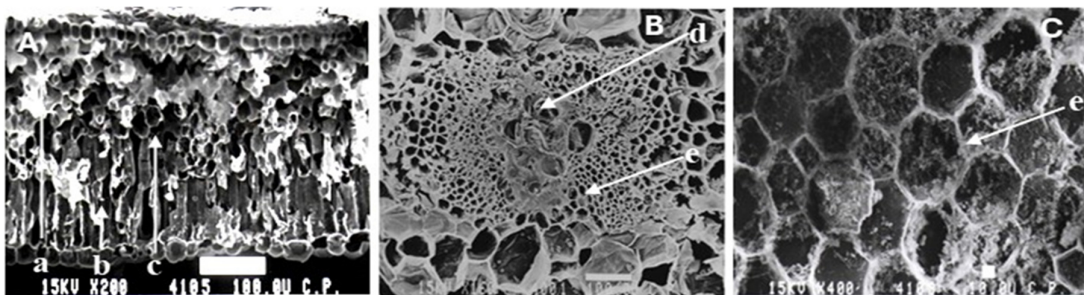


Figure 6. (A) Section of leaf tissue; (B) Vascular bundles of stem (vine); (C) Section of leaf petiole tissue from *S. edule* plants developed in the seasonal dry forest (SDF) region; (a) Spongy parenchyma; (b) Palisade parenchyma; (c) Mesophyll; (d) Xylem and (e) Phloem. Micrographs obtained with scanning electron microscope at 200×, 160× and 400× respectively.

The formation of styloid-like crystals that break the epidermal cells of the adaxial surface of the leaf are shown in Figure 7A, B, and just as the excess of crystals breaks a cystolytic trichome (Figure 7C). Table S1 indicates the values of the foliar analysis showing that at least calcium is the majority component, followed by N, K and P. It is possible that the gradual absorption of these minerals could accumulate and form crystals if the higher content of the soil is considered.

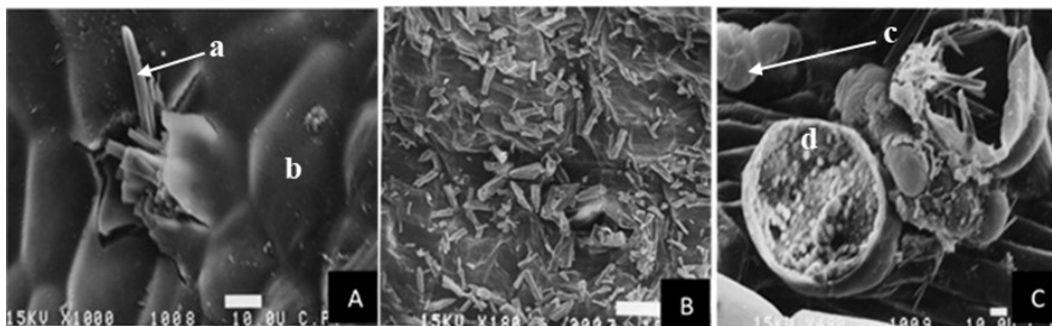


Figure 7. Crystals formed in tissues of *S. edule* plants developed under medium subperennial forest (MSF) region (A-B), and in seasonal dry forest (SDF) region (C). (a) Crystals in styloid breaking the surface of the leaf; (b) Subepidermal cell of the leaf surface; (c) Globose trichome on the leaf surface; (d) Cystolytic trichome on the leaf surface. Micrographs obtained with scanning electron microscope at 100×, 180×, 480×, respectively

Micrographs in S. edule

The X-ray analysis showed differences between the mineral composition of the crystals present in plants that grew under MSF and SDF conditions (Appendix Table 2). The mineral composition of the crystals observed in the MSF and SDF environments showed high concentrations of P and Ca²⁺, and in the case of the SDF locality a significant increase in Si and Na. Figure 8A indicates the sequence of color loss and death of the leaves with the highest concentration of calcium (SDF), and this effect was also present in the vines (Figure 8A, B). In relation to the quality of the fruits, the loss of color from green to yellow was observed in the two years of evaluation, a situation that is reversed when the yellow fruits are moved to their original habitat (they are used as “seed” by be endocarpic and recalcitrant), generating normal fruits. However, when they change color, they lose their commercial value and commercial orchards are abandoned (Figure 8C, D).

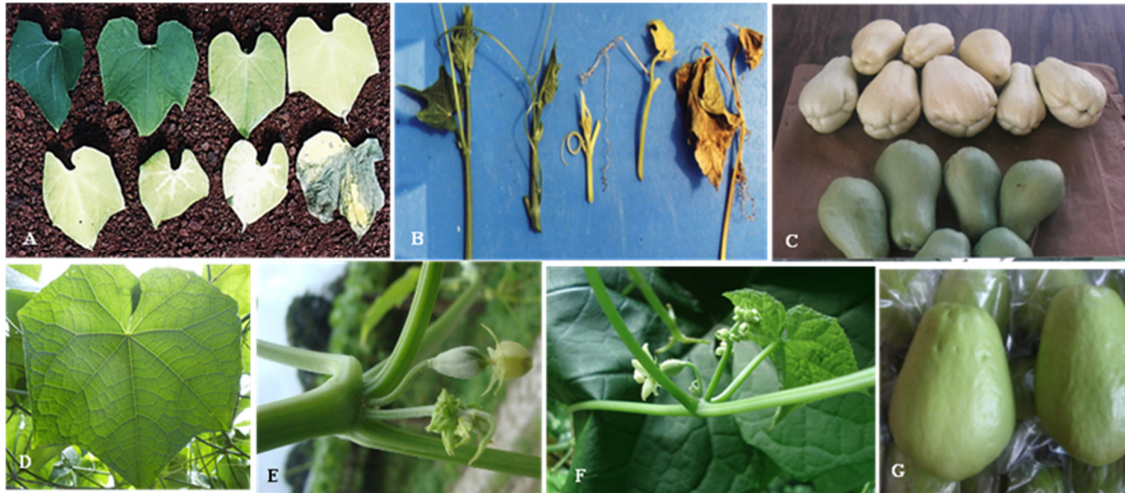


Figure 8. (A-B) Gradual loss of color, necrosis and death of leaves and apical bud of the vine; (C) Loss of fruit color, turning from green to yellow of plants developed in seasonal dry forest (SDF) conditions; (D- G) Leaf, vines and fruits of plants grown in CMF without apparent physiological alterations

Gas exchange

Regarding the rate of CO₂ assimilation and transpiration values showed stable behavior at the CMF site (Figure 9A), that means that the activity starts at 7:00 h and continues to increase until 13:30 h, to decline between 15:30 and 16:00 h, with average values of 4 μmol m⁻² s⁻¹ and 7.5 μmol m⁻² s⁻¹. At MSF and SDF sites, CO₂ assimilation recorded a daylight pattern with values below CMF (Figure 9B, C).

S. edule does not record total stomatic closure during the day, and it has been correlated with the environmental temperature of the site, and therefore it is attributable that the transpiration and assimilation values of CO₂ are lower with ups and downs, recording those initial values for MSF and SDF sites ranged as maximum from 2 to 0.5 μmol m⁻² s⁻¹, up to 3 and 2 m⁻² s⁻¹ m respectively. Figure 9D indicates that the leaf area of the leaves of plants developed in CMF is much higher than that of plants developed in MSF and SDF, which is also limiting for the efficiency of gas exchange.

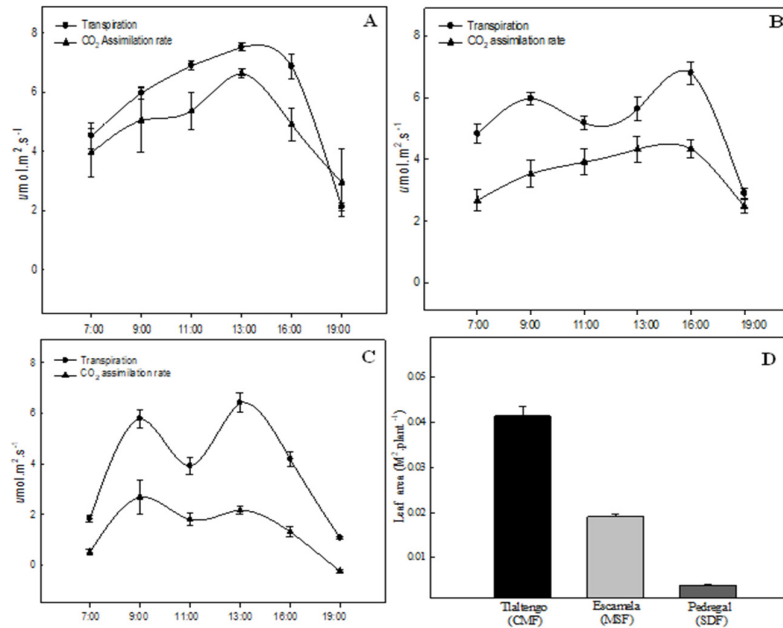


Figure 9. Description day pattern of gas exchange (transpiration and CO₂ assimilation rate) of *S. edule* plants under field conditions for the period 2020-2021. (A) Cloud mountain forest (CMF); (B) Medium superperennial forest (MSF); (C) Seasonal dry forest (SDF); (D) Leaf area of plants. The values are the product of ten leaves of ten vines measurements \pm standard error

Chlorophyll content

Chlorophyll content in *S. edule* leaves decreased at MSF and SDF locations compared to CMF (Figure 10 A, B). In the case of chlorophyll content in leaves, had a decreasing tendency as the agroclimatic cultivation conditions were different than those found in the original habitat. Also, an excessive concentration of salts was observed in the tissue and vascular shafts of the petiole, as well as a gradual loss of color and necrosis of apical vines and foliar sheets in plants grown under SDF conditions (Figure 8 A, B); in addition to recording with the values of the physicochemical analyzes a relationship between the Ca²⁺ content and the rising pH value, which influences the availability of minerals that contribute to chlorophyll, such as Fe, Mn and nitrogen (Figure 10C).

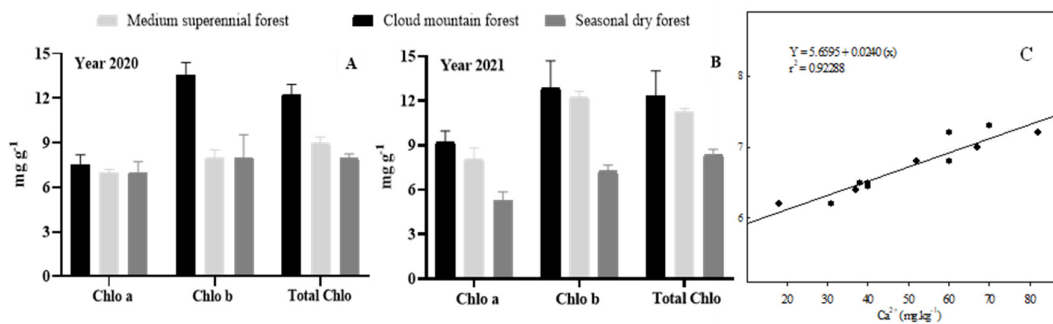


Figure 10. (A-B) Description of chlorophyll a, b, and total content of fully expanded leaves of *S. edule* plants developed in three agroclimatic regions of Veracruz, Mexico. Values are the product of quarterly measurements \pm standard error for the period 2020-2021; (C) Linear regression between calcium content and pH value from physicochemical determinations of the soil

The Figure 11 A, B, C shows that CO₂ content, ambient temperature, leaf temperature, and photosynthetically active radiation (PAR-CAM) mainly explain 38.9% of the photosynthetic activity of *S.*

edule plants in the three regions evaluated. Figure 11D shows blue circles that indicate that there is a group of positive correlations between the CO₂ assimilation rate (ASIMIL of CO₂), Photosynthetically active radiation (PAR-CAM), external temperature (TEMP), the leaf (LEAF-TEMP), internal water vapor (H₂O-VAP-IN) and transpiration (TRANSP); However, variables with negative correlation are also noted in red circles. The above suggests that the environmental characteristics of the evaluated sites determine that ambient temperature, leaf temperature, PAR and conductance mainly condition photosynthetic efficiency, explaining why the highest CO₂ assimilation rate was recorded in the CMF, followed by MSF and finally SDF.

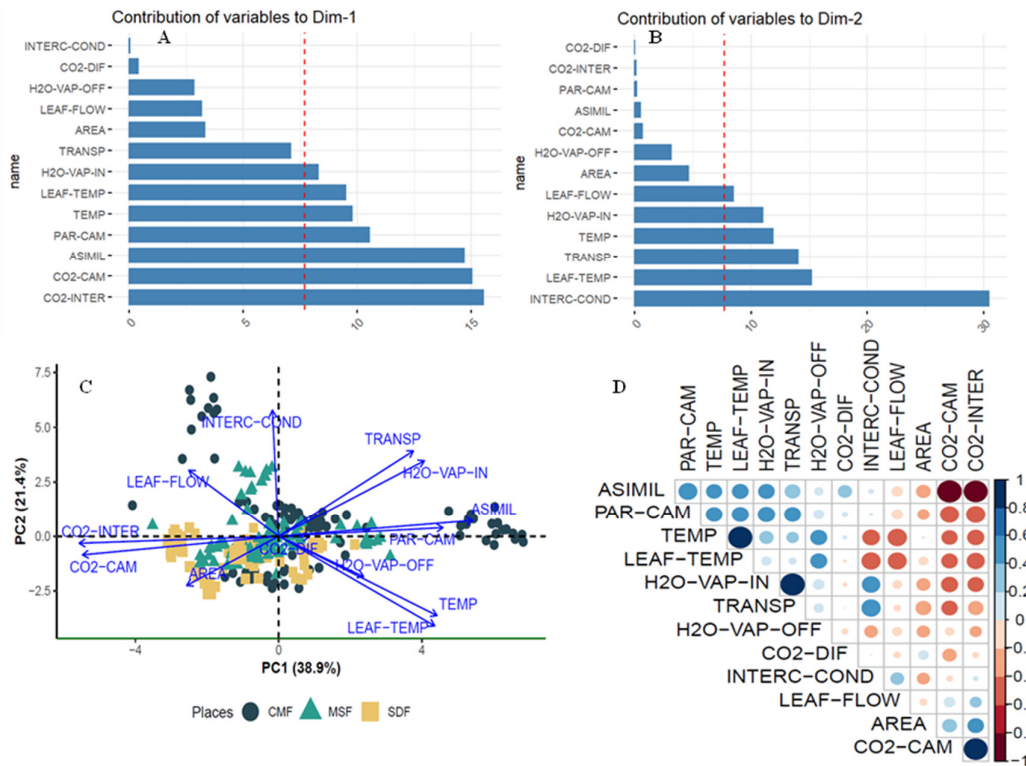


Figure 11. Analysis of principal components (PCA) for the variables that influence photosynthesis (CO₂ assimilation). ASIMIL = Assimilation, PAR-CAM = Photosynthetically active radiation, TEMP = Leaf temperature, H₂O-VAP-IN = internal leaf water vapor, TRANSP = Transpiration, H₂O-VAP-OFF = Output water vapor, CO₂-DIF = differential CO₂, INTER-COND = conductance, LEAF-FLOW = leaf flow, AREA = area, CO₂-CAM = chamber CO₂. (A-B) Contribution of the variables in the main components 1,2; (C) Dispersion of the variables according to the agroclimatic sites evaluated; (D) Positive (blue circle) and negative (red circles) correlations between the variables. CMF: cloud mountain forest, MSF: medium subperennial forest. SDF: seasonal dry forest

A relevant fact is that the leaf temperature recorded by the IRGA was different for the three sites; For example, in CMF if the ambient temperature was 26-28 °C, the leaf was 24-26 °C, always in that trend. Regarding MSF, the range was 28-32 °C and 34-36 °C in SDF, always with the trend of at least two degrees. One of the results of plant physiology is yields, which in this case are commercial fruits. In this regard, Appendix Table 3 shows that the biannual average is higher in plants grown in CMF followed by MSF and SDF with 140.18, 111.84 and 45.84 t ha⁻¹ respectively. The differences can be interpreted as reflecting the advantages and limitations of the cultivation sites.

Discussion

Changes in soil nutrient content

pH is an indicator of the availability and distribution of macro and some micronutrients, for example, Fe, Mn, and Zn in volcanic soils (CMF). Furthermore, there is a relationship between the content of organic matter, electrical conductivity, and the concentration of soluble salts, such as sodium chloride (Strekalovskaya *et al.*, 2024). Even though values greater than 2.5% of organic matter are not expected for non-volcanic soils with pH of 7.0 to 7.9, such as MSF and SDF, Table 1 reflected values of 4.52 and 3.53% respectively, which is unusual. The above is attributable to the addition of fresh manure amendments that producers make annually. The amendments are applied at the planting site of each plant, and in the following year the planting area is displaced between 2.5 and 5 m clockwise, in such a way that the plot is gradually enriched over a period of close to five years. The OM values are high in soils from all three regions; however, available N is relatively low. The above can be attributed to slow decomposition rates of organic matter sources, as well as high plant extraction, if it is considered that production per hectare is up to 140 t ha⁻¹ per year (Appendix Table 3). The soils of the study regions are slightly acidic (CMF, MSF) and slightly alkaline (SDF) and the number of salts in the soluble extract indicated low to intermediate values of electrical conductivity without the latter being saline soil, rather it could be classified as calcareous (Brooker *et al.*, 2021).

Electrical conductivity (EC) is related to the pH and the number of salts of the soluble extract in the medium, and can influence the nutrient exchange capacity (K, Ca, Mg) (Havlin, 2020). The EC can reflect the presence of Na in the soil, and in this regard, in the MSF and SDF soils the soluble sodium concentration was 0.26 and 0.46 mg kg⁻¹ respectively, and even though they are not high values they can be toxic depending on the plant species, limiting its growth, and as in the present study, burns of the leaf tissue and apical buds (Chhabra, 2021).

*Crystal composition in *S. edule**

Table S2 shows that in the composition of *S. edule* leaf crystals, Na is a component with values of 0.67 and 2.65 for the MSF and SDF soils, respectively. Similarly, Appendix Table 1 shows values of the concentration of higher nutrients in leaf tissue of plants grown in CMF, MSF, and SDF, highlighting calcium, with values of 4.08, 5.42 and 7.41% respectively. It is likely that minerals with greater availability and concentration in the soil promote gradual accumulation and generate toxicity and damage to plant leaf and guide tissues (Bravo *et al.*, 2017). Regarding zinc, in the soils of the three regions, the value of Zn was much higher than the limiting value of 0.67 mg kg⁻¹ (NOM-021, 2022) and its high solubility in the soils of the study regions (2.5, 15.2 and 11.2 mg kg⁻¹) is related to pH values of 7.0 to 7.8. Boron (B) and copper (Cu) are not minerals with high representation in the study soils, and their concentration is attributed to a greater extent to the applications each week/month/year to control the deficiency (foliar route 100 mL ha⁻¹) and fungal control (1.5 kg ha⁻¹); However, there are data that indicate that Cu is chemically fixed in soils with alkaline pH (NOM-021, 2022) and that the greater the amount of OM and acidic and slightly acidic pH, the greater the availability (Duplay *et al.*, 2014).

The high calcium content generates plant physiological disorders in MSF and SDF soils compared to the amounts present in CMF soils. Soil pH is a determining factor in the availability of nutrients for plants. In the case of *S. edule*, the pH values of 7.3 are the product of high calcium concentrations in MSF and SDF and are not suitable for growth. Soils in their original habitat (CMF) are acidic to slightly acidic (4.5-6.5) (Lira *et al.*, 2023). In other hand, the absence of crystals in leaf, stem, and petiole of *S. edule* in the CMF site is attributed to soil acidity and low Ca²⁺ content that could be within a suitable range for the species (Cadena-Iñiguez *et al.*, 2005). When calcium levels exceed plant tolerable limits, and, in order to avoid toxic effects, calcium binds to malate, carbonate or oxalate for the formation of easily identifiable crystals inside the vacuole, and the ascorbic acid molecule has been considered as a precursor of oxalate (He *et al.*, 2024). In the case of *S. edule* under CMF

conditions, Rivera-Ponce (2024) reports 16 mg 100 g⁻¹ of ascorbic acid in leaf dry matter, being the highest amount after the root whose maximum value reported was up to 19 mg 100 g⁻¹. This suggests that the presence of ascorbic acid and excessive Ca²⁺ absorption could facilitate the formation of crystals. Cadena-Iñiguez *et al.* (2011) mention for *S. edule* var. *virens levis* 6.76 ± 0.16 mg 100 g⁻¹.

Phosphorus and calcium were the minerals with the highest content in the composition of crystals attributable to the high solubility identified in the physicochemical analysis of soils. The presence of these elements as higher components of crystals could be due to the mobility of phosphorus in soils with neutral pH and above 7.2 (Jones, 2021), as the pH at the SDF site is presented. Crystals produced by plants are the final products of cellular metabolic processes, which usually are deposited in vacuoles and cytoplasm. The most common inorganic crystals are constituted by calcium salts, like calcium oxalate and calcium carbonate and a large part of the calcium in most plants is in the leaves due to the formation of calcium pectate in the middle lamina of the cells (El habbasha and Farten, 2015). For example, styloids have the particularity of being long, appearing alone or in groups, and their growth is not limited. This condition can deform the cell that contains them causing its breakage (Figure 7 A, B). Other crystals are form as druses (Paiva, 2019) (Figure 5C) up to 10.55 µm in diameter, which, according to Horner and Wagner (2020) are found one per cell and can reach 5 to 10 µm in diameter. Development of crystals implies a thickening of the cell wall that contacts crystals and start their development as recorded in this case (Figure 5A and 6A) (He *et al.*, 2024).

Differences between the mineral composition

The X-ray analysis showed differences between the mineral composition of crystals present in plants grown under MSF and SDF conditions. The results suggest that the limits for the cultivation of *S. edule* var. *virens levis* are strongly delimited by the chemical conditions of the soil, in addition to the levels of irradiance and ambient temperature. The temperature between the evaluation sites (19, 22 and 31 °C) in addition to precipitation, especially for SDF (241 mm), are factors of high environmental contrast that limit the growth of *S. edule* plants. The altitude of each region was shown to be an important variable (Figure 3) since the altitude in CMF is 1480 m, followed by 1140 in MSF and 298 m in SDF. This last site differs strongly from the conditions of the original habitat of *S. edule*, which is why its expansion can be counterproductive, especially if the physicochemical characteristics of the soil are added, which are also very contrasting and can influence the proper development of the plants.

According to Prasad and Shivay (2020) the effects of mineral accumulation can be observed with dead parts in leaf area, mottled spots and blotches, small brown spots, and stunting. In our case, calcium, and phosphorus content in leaves of plants grown in CMF was the lowest, while leaves of MSF and SDF plants recorded gradual increase as soil pH increased (Appendix Table 1 and 2). There are three main biominerals that appear in plants, calcium oxalate, calcium carbonate, and calcium phosphate (Cuéllar-Cruz *et al.*, 2020).

Authors such as Ding *et al.* (2018) establish that in plants grown with high calcium levels, the lamellar structure of chloroplasts can be altered and consequently the photosynthetic rate. In this regard, Jones (2021) mention that the phenomenon of mineral uptake is rarely qualitative, being able to increase the uptake in higher amounts of the mineral with greater availability in the soil. Quantitative absorption of one element can generate chemical antagonism with another, and the effect can be observed as plant growth and development progress, although unfortunately these are late and irreversible, as happened with the decrease in leaf area and loss of color (Figure 8 and 9D). Leaf damage and necrosis of nerves, suggest the onset of intoxication by a specific ion and are expressed differently among species and varieties (Gent *et al.*, 2015).

The growing conditions in MSF and SDF were different from those found in the original habitat. In addition, excessive mineral concentration was present in the tissue and vascular axes of the petiole (Figure 5C, 6C), as well as gradual loss of color and necrosis of the apical vines and leaf blades in plants grown under SDF conditions (Figure 8B). The color change from green to yellow in leaves and fruits of *S. edule* (Figure 8A, C, D) is a response cited in other crops, such as *Ficus* sp. (Zuñiga-Valenzuela *et al.*, 2018) or browning due to excess

calcium. In a general way, plant growth is stopped, and it is due to a decrease in calcium transport. It is known that calcium moves through xylem, and it is practically in phloem where it is relatively less mobile (Zuñiga-Valenzuela *et al.*, 2018; Prasad and Shivay, 2020).

Gas exchange and chlorophyll content

At the MSF and SDF sites, decreased transpiration and CO₂ assimilation were observed at midday. This could be related to physiological stress levels caused by an increase in irradiance intensity and temperature, since conductance responds to a need for leaf lamina cooling. The values were almost 50% of those recorded in the cloud forest, although it should also be remembered that stomatal closure in *S. edule* is not total (Cadena-Iñiguez *et al.*, 2007), and this facilitates the rapid response observed in the transpiration and CO₂ fixation curve during the diurnal pattern.

The decrease in the photosynthetic capacity of plants in the MSF and SDF sites could be related to the increase in intracellular and leaf temperature as a consequence of the increase in irradiance (Cadena-Iñiguez *et al.*, 2007). The light is the most important environmental signal that regulates calcium uptake related to the growth of plants and, in some way, their form. The role of all these light receptors for both blue and red light induce changes in the membrane properties, gene expressions and over-expression of proteins and polysaccharides related to calcium salts and formation of biominerals as hybrid materials (Cuellar-Cruz *et al.*, 2020).

Regarding chlorophyll content, Latsague *et al.* (2014) and Seneweera *et al.* (2011) point out its relationship with nitrogen, confirming that the amount of N stored in chloroplasts is directly related to the amount of chlorophyll. Table 1 and Table S1 show that the nitrogen recorded in the plants grown in CMF was higher (0.61 mg kg⁻¹ and 4.06%), while the plants from the MSF and SDF sites recorded 0.25, 0.17 mg kg⁻¹ in soil, and 3.82 and 1.09% in leaves respectively. In the same sense, Ca²⁺ showed an increasing trend according to the agroecological site, observing that the content was 3.55, 14.5 and 53.9 mg kg⁻¹ in soil, and 4.08, 5.42, 7.41% in leaves for the CMF sites, MSF and SDF respectively.

Conclusions

S. edule var. *virens levis* develops crystals in various amounts and forms in the MSF and SDF regions with alkaline soils, where increased phosphorus and calcium predominate. The presence of crystals increases as the amount of the mineral in the soil solution increases. It shows low tolerance to soils with high Ca²⁺ concentrations and its displacement to agricultural soils with alkaline pH values affects plant growth. In sites with high calcium concentration, leaf area decreases, and chlorosis is presented, burns and death of leaves and shoots occur. Excessive calcium absorption generates chemical antagonism with other minerals that decrease chlorophyll biosynthesis and probably induce the decrease in the photosynthetic capacity of plants in the MSF and SDF sites. It is likely that *S. edule* var. *virens levis* is a species that is not very tolerant to habitat changes where low altitude, higher ambient temperature and soils with high amounts of calcium in solution predominate. The results of research under field conditions can be considered as references and help avoid economic failures due to the displacement of *S. edule* towards limiting agroclimatic conditions.

Authors' Contributions

Conceptualization JCI, LDMRP, JFAM, Data curation; MLAG, Formal analysis, JFAM; Investigation; DACZ, Methodology; JCI, LDMRP, Resources; JCI, Software; JDCZ, L.A.B.G, Supervision; JFAM,

Validation; JCI, DACZ, Visualization; JCI, JDCZ, Writing - original draft; JCI, JFAM, Writing - review and editing; JCI, DACZ. All authors read and approved the final manuscript.

Ethical approval (for researches involving animals or humans)

Not applicable.

Acknowledgements

This research received no specific grant from any funding agency in the public, commercial, or not-for-profit sectors. We thank the Interdisciplinary Research Group at *Sechium edule* in Mexico (Non-governmental organization) for the genetic material.

Conflict of Interests

The authors declare that there are no conflicts of interest related to this article.

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Appendix

Table 1. Concentrations of macronutrients in fully expanded leaf of *Sechium edule* plants grown under three different crop management strategies and environmental systems for the period 2020-2021

Sites	N	P	K [%]	Ca	Mg
CMF	4.06 ±0.021	0.63 ±0.042	2.71 ±0.01	4.08 ±0.027	0.75 ± 0.084
MSF	3.82 ±0.032	1.28 ±0.031	1.83 ± 0.06	5.42 ±0.064	0.51 ±0.057
SDF	1.09 ±0.012	0.19 ±0.021	1.08 ±0.032	7.41 ±0.023	0.50 ±0.014

Table 2. Mineral composition of crystals formed in fully expanded leaf tissues of *Sechium edule* plants grown in MSF: medium subperennial forest; SDF: seasonal dry forest

Element	Mineral composition	
	MSF	SDF
P	24.04 ± 20.98	22.25 ± 15.79
Ca	14.27 ± 13.58	18.64 ± 11.87
Si	1.46 ± 0.12	3.77 ± 0.02
Na	0.67 ± 0.57	2.65 ± 2.06
Mg	0.16 ± 0.10	0.486 ± 0.34

Table 3. Average yield of commercial fruits for the period 2020-2021 in kg ha⁻¹ per evaluated agroclimatic site. Values obtained from weekly harvests according to the horticultural maturity index NOM-FF-47-1982 for chayote. CMF: cloud mountain forest, MSF: medium subperennial forest. SDF: seasonal dry forest

Month	2020-2021 (t ha ⁻¹)		
	CMF	MSF	SDF
May	4.92	2.49	1.62
June	63.94	42.57	13.84
July	138.65	102.84	52.32
August	185.46	130.19	61.26
September	214.50	172.18	73.16
October	195.16	161.37	55.56
November	207.88	187.56	55.64
December	110.90	95.52	53.31
Mean	140.18	111.84	45.84