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EFFECT OF SUBSTRATES AND FERTIGATION ON GROWTH AND PHOTOSYNTHETIC EFFICIENCY OF MAGUEY PULQUERO PLANTS OF MEZQUITAL VALLEY LANDRACES

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ABSTRACT

Maguey pulquero (*Agave spp.*) seedling cultivation is an emerging alternative capable of supply the demand of its diverse products. This research aimed to evaluate the growth and maximum quantum yield of Photosystem II (Fv/Fm) of three landraces of maguey pulquero young plants (10 months-old) germinated from seeds, growing under greenhouse within interaction effect of four substrates and four concentration levels of nutrient solution. The hypothesis was that phenotypic variation of young maguey pulquero landraces growing under greenhouse conditions could help to identify genotypes ideal for commercial production and to elucidate its nutrient and substrate requirements. The variables evaluated were: Fv/Fm, number of leaves, length and width (cm) of biggest leaf, and plant dry biomass (g), the results were analyzed by a two-way ANOVA and means comparison by Tukey's test. The results demonstrated that Penca larga landrace (*Agave mapisaga* Trel.) had the highest values in all the growth variables evaluated compared to Manso and Xamini landraces (both *A. salmiana* Otto ex Salm-Dyck). Penca larga exhibited similar growth in the substrate agricultural soil and volcanic scoria mixture (SVM), and substrate agricultural soil alone (S) regardless of the nutrient solution concentration used, while both *A. salmiana* landraces exhibited total biomass reduction in the maximum nutrient concentration added in the S substrate (S+L4 treatment) compared to their respective effect on SVM substrate without nutrient addition (SVM+L1 treatment). All landraces exhibited growth inhibition in the commercial substrate mixture (CSM) and volcanic scoria alone (VS) without nutrient addition (CSM+L1 and VS+L1), while growth increase of all landraces in those substrates was relative to the increasing nutrient concentration. Photoinhibition was observed in all landraces in the treatment VS+L1. The growth variations observed across the landraces were helpful to identify potential genotypes ideal for commercial production and to set adequate substrates and nutrient requirements for agave cultivation.

Keywords: *Agave mapisaga*, *Agave salmiana*, andesite scoria, Cardonal, nutrient toxicity, photoinhibition.

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INTRODUCTION

The genus *Agave* possess the crassulacean acid metabolism (CAM) and other physiological modifications that increase its water use efficiency and adaptation to limiting abiotic conditions, these features can facilitate the productivity in marginal lands where traditional crops cannot prosper (Garcia-Moya *et al.,* 2011). The "maguey pulquero" term incorporates the species *Agave salmiana* Otto ex Salm-Dyck., *A. mapisaga* Trel., *A. americana* L., *A. atrovirens* Karw. ex Salm-Dyck. distributed in Central Mexico (Gentry, 1982; Mora-Lopez *et al.,* 2011); these plants are traditionally used for sap extraction to produce a low-alcohol fermented beverage called "pulque", and the leaves are highly demanded in the Mexican traditional cuisine (Reyes-Aguero *et al.,* 2019).

Maguey pulquero plantations and wild populations in Central Mexico have been declining due to overexploitation and urban expansion; asexual shoot cultivation is the traditional propagation method that has not meet the increasing demand of maguey pulquero products, which has encouraged to research on the cultivation requirements of maguey pulquero seedlings in order to comply the market needs (Cruz-Vasconcelos *et al.,* 2020). Another advantage of seedling propagation is genetic diversification and the opportunity to select ideal genotypes for specific purposes (Aspinwall *et al.,* 2015). Several maguey pulquero landraces are distributed in the convergence of the Mexican Central Plateau and the Trans-Mexican Neo Volcanic Belt, where the influence of abiotic elements and the humanization-domestication process have been shaping the maguey pulquero morphology and genotype (Mora-Lopez *et al.,* 2011; Alfaro *et al.,* 2007). Within that area exists ecoregions with contrasting microclimates and soils where maguey pulquero is traditionally cultivated, that ecological diversity represents a pool of genetic richness propitious for performing the assessment of phenotypic variation to identify and select maguey pulquero genotypes ideal for commercial production; for which plant biomass accumulation under abiotic limiting conditions is a phenotypic trait that could reveal tolerance mechanisms to stress (Jimenez-Torres *et al.,* 2021).

Fertilization requirements and fertilizer delivery for Agave plants may differ to traditional crops because CAM plants have slower growth rate relative to C3 and C4 plants; although, favorable growing conditions in the most cultivated Agave species, *A. tequilana* Weber*, A. salmiana, A. mapisaga*, can let yields comparable to some C3 or C4 crops (Nobel *et al.,* 1991). Studies of nutrient requirements for maguey pulquero plants since the early growing stages are limited (Arrazola-Cardenas *et al.,* 2020), but with the studies available it can be inferred that nutrient requirement is proportional to the age, influenced by substrate type and growing conditions. In early growth stages of agave plants (≤ one-year-old), fertilization can be unnecessary or minimum depending on substrate used (Diaz *et al.,* 2011; Arrazola-Cardenas *et al.,* 2020), this can respond due to the effect of agave endophytes that can provide nutrients to the plant with greater efficiency than mineral fertilization (Beltran-Garcia *et al.,* 2014); when agricultural soils are used for agave seedling growth evaluation, it can be present free-living nitrogen fixing bacteria that can promote plant growth (Bautista-Cruz and Martinez-Gallegos, 2020), in contrast to pure mineral substrates where microbial activity might be inferior that increases the dependence on fertilization (Arrazola-Cardenas *et al.,* 2020). Maguey pulquero and agave plants older than one year can respond adequately to fertilization schemes (Cruz-Vasconcelos *et al.,* 2020); however, it is still required to evaluate agave growth under standardized conditions to elucidate the actual element requirements and to differentiate the effect of the interaction of side treatments applied during nutrient evaluations (Martinez *et al.,* 2012; Garcia-Martinez *et al.,* 2020).

Photoinhibition is the reduced functionality of the light-harvesting complexes situated in the chloroplast caused by light saturation, it can result momentarily as a natural response by high light exposure alone, or as a chronic condition because the combined effect with other stresses, it can be measured *in vivo* by the maximum quantum yield efficiency of Photosystem II with the ratio Fv/Fm (Morales *et al.,* 2008). Nutrient deficiency can reduce the biosynthesis of active photosynthetic organelles or substances related with photochemical processes, as the iron (Fe) deficiency can reduce the number and quality of photosynthetic membranes; nitrogen (N) deficiency can reduce considerably the leaf area and the photosynthetic productivity (Morales *et al.,* 2008).

Ecoregions where traditional crops have been reducing the expected productivity due to climatic and abiotic factors such as drought and soil quality loss, maguey pulquero plants can be an alternative crop thanks to its adaptability to poor soils, high water use efficiency and potential use for bioethanol production (Garcia-Moya *et al.,* 2011). The genetic richness of the maguey pulquero landraces can support breeding programs, while more studies on the cultivation requirements for maguey pulquero seedlings are required. Taking into consideration the need of supply the increasing demand of maguey pulquero products and its potential use as bioethanol feedstock in marginal lands, while is still required to determine the adequate growing parameters of maguey pulquero seedlings for commercial production.

Based on the above, the hypothesis of the study was that the evaluation of phenotypic variation of maguey pulquero landraces growing under greenhouse conditions could help to identify genotypes ideal for commercial production and to elucidate its nutrient and substrate requirements. Therefore, the objective was to evaluate the effect of four substrates combined with four concentrations of Douglas nutrient solution on the growth and maximum quantum yield from the Photosystem II, of three landraces of *Agave mapisaga* and *A. salmiana* under greenhouse conditions.

MATERIALS AND METHODS

Biological material and substrates

Seeds of *Agave mapisaga* (Penca larga landrace) and *A. salmiana* (Manso and Xamini landraces) were collected from inflorescences in the Cardonal, Hidalgo, Mexico (20° 37′ N and 99° 7′ W); located in the Mezquital Valley, where the predominant soils are Leptosols dominated by calcareous rocks as parent material (INEGI, 1992). Both species belongs to Salmianae group of the *Agave* subgenus (Gentry, 1982). Seeds were placed into petri dishes with watered paper and germinated in growth chamber at 28 °C and 16 h / 8 h light / dark period. After 5 days when the maximum accumulated germination was reached, the seedlings were transplanted to the substrates under greenhouse conditions with a 50 % shade during two months; thereafter, shade was removed. All the seedlings were watered daily with tap-water for one month; thereafter, nutrient solution treatments started.

Four substrates were used; first, commercial substrate mixture (CSM) peat moss: agrolite: vermiculite 2:1:1; second, agricultural soil: volcanic scoria mixture (SVM) 1:1; third, agricultural soil (S) alone; and fourth, volcanic scoria (VS) alone. The soil was collected from agricultural fields from Tlajomulco, Zempoala, Hidalgo which is located at 19° 54′ 14″ N and 98° 33′ 04″ W, in the Trans-Mexican Neovolcanic Belt region. The location has occurrence of cultivated maguey pulquero (*Agave salmiana*) plants and wild populations of *Agave* spp. The dominant soil's parent material was volcanic andesitic tephra with intrusive material of sedimentary calcareous rocks; the soil was classified as Andosol (IUSS 2015). The andesite volcanic scoria was collected from a quarry in Tlajomulco location as well, with average particle size of ≤ 5 mm. Containers used were 30 ´ 30 cm plastic bags with 5 L capacity. Physical and chemical characteristics of each substrate were evaluated per triplicate from sub-samples collected randomly.

Substrates physical characteristics

Apparent density (AD w/v) was evaluated with the test-tube method, dry substrate was put into the test-tube and hit softly until no volume reduction was observed (100 mL), then the substrate was weighted, and AD calculated according to the weight/volume g mL^{-1}. Porosity was evaluated with gravimetric method according to Landis *et al.* (1990) the substrates were placed into 130 mL plastic containers, and slowly saturated with water. The water added represented the total porosity (TP %): [water used (mL) / container volume (mL)] * 100. Thereafter, the container was freely drained, and the water collected represented the air porosity (AP %): [water drained (mL) / container volume (mL)] * 100. Finally, the water holding capacity (WH %): was calculated with total porosity (%) - air porosity (%).

Substrates chemical characteristics

Substrate pH was measured with pH meter (Hanna Instruments, HI991301 Romania) in a suspension soil: distilled water, ratio 1: 2. Organic matter (OM) content was evaluated based on the redox Walkley and Black method, substrates were sieved to size particle ≤ 0.3 mm, and weighted 0.1 g for commercial substrate CSM, and 0.5 g for the rest of the substrates, the procedure and OM calculations were performed according to Aguilar *et al.* (1987). Total nitrogen content (NC) of the substrates was determined with micro-Kjeldahl method, substrates were sieved to size particle ≤ 0.212 mm, then were weighted 0.1 g of CSM, 2.5 g of VS and 1 g of S and SVM. The NC was calculated according to Aguilar *et al.* (1987). The cation exchange capacity (CEC) (cmol kg^{-1}) of the substrates was determined with ammonium acetate 1 N method according to Aguilar *et al.* (1987), the substrates were sieved to size particle ≤ 2 mm, then weighted 2 g of CSM, 6 g of VS, 5 g of S and SVM.

Watering and fertilization

The modified Douglas (1976) base nutrient solution was formulated according to the required element concentration given by the following compounds: 500 ppm of N from $Ca(NO_3)_2\ 4H_2O$ and KNO_3, this latter provided 300 ppm of K, 100 ppm of P from $NaH_2PO_4\ H_2O$ and H_3PO_4, 300 ppm of Ca from $CaSO_4\ 2H_2O$ and calcium nitrate used for N, 150 ppm of Mg from $MgSO_4\ 7H_2O$, 6 ppm of Fe from $FeSO_4\ H_2O$, 0.1 ppm of Cu from $CuSO_4\ 5H_2O$, 1 ppm of B from H_3BO_3, 1 ppm of Mn from $MnSO_4\ H_2O$, 0.1 ppm of Zn from $ZnSO_4\ 7H_2O$, and 200 ppm of S given by all the compounds with it.

To prevent possible nutrient toxicity the base nutrient solution was diluted through four stages, in each stage respective dilutions of the base nutrient solution used were performed according to the nutrient solution treatments L1 = 0 %, L2 = 25 %, L3 = 50 % and L4 = 100 % applied. First stage, during first month the plants were watered with tap water daily no nutrient solution was used. Second stage, from 2nd to 3rd month the base nutrient solution was at 25 % of concentration. Third stage, from 4th to 8th month base nutrient solution was at 75 % concentration; during the above-mentioned stages the nutrient solution applied was 83 mL per plant once per week, and all plants were watered three times per week with tap water. Fourth stage, from 8th to 10th month base nutrient solution was at 100 % concentration, in this last stage nutrient solution was applied 125 mL per plant two times per week and watered three times per week with tap water.

Growth, biomass accumulation and fluorescence evaluation

After ten months of growth, the maximum quantum yield efficiency of Photosystem II of the biggest leaf was evaluated *in vivo* using a Handy PEA (Hansatech Instruments Ltd, Norfolk UK). Plants were incubated in darkness for 20 minutes subsequently irradiated with red light pulse (640 nm) at 600 W m^{-2} (Morales *et al.*, 2008); with the values obtained the variable considered was the Fv/Fm ratio measured per triplicate in different spots of the same leaf. Thereafter, plants were harvested, root rinsed with tap water, and the maximum leaf longitude and maximum leaf width were evaluated from the biggest leaf of the plant with a micrometer (Mitutoyo, Japan). It was counted all the unfolded leaves, excluding the apical meristem (central spike). Thereafter, the plant biomass was dried in electrical oven (70 °C) until constant weight, the root, shoot and total dry biomass accumulation was weighted on analytical balance (Sartorius, Germany).

Experimental design

The experiment was set in completely randomized design, one plant was the experimental unit of the respective three maguey pulquero landraces Penca Larga

(*A. mapisaga*), Manso and Xamini (both *A. salmiana*) under the interaction effect of substrates (four levels) and nutrient solution concentration (four levels) which in total composed 16 treatments, and five replications per treatment were used (n = 5). The results were assessed by a two-way ANOVA and by the interaction substrate´nutrient solution concentration (16 treatments), it was performed a means comparison by Tukey´s test ($p \leq 0.05$) using SAS v. 6.12. Where appropriate, a multivariate analysis of hierarchical dendrogram (complete linkage) with city block distance and standardized data was performed using the software Statgraphics 19.

RESULTS AND DISCUSSION

Leaf size and biomass allocation

According to the two-way ANOVA of the results, the landrace Penca larga (*A. mapisaga*) showed the highest values in all the growth variables evaluated, except for the fact that all landraces had similar average values of 5 leaves released from the apical meristem; while, both of the *A. salmiana* landraces, Manso and Xamini, exhibited similar intermediate results in all the variables evaluated (Table 1). The substrates evaluated exhibited an increase in all growth variables of the maguey

Table 1. Effect of substrates and nutrient solution concentrations on growth and photosynthetic efficiency of maguey pulquero plants propagated from Mezquital Valley landraces Penca larga (*Agave mapisaga*), and Manso and Xamini (both *A. salmiana*).

Factors	Biggest leaf			Dry biomass			PSII
Levels	L[†]	W[¶]	NL[§]	R[Þ]	S[¤]	T[††]	Fv/Fm[¶¶]
	(cm)			(g)			
Landrace							
Penca l.	4.35 a	1.46 a	5.02 a	1 a	3.11 a	4.12 a	0.79 a
Manso	3.72 c	1.33 b	5.04 a	0.72 b	2.17 b	2.9 b	0.76 b
Shamini	4.1 b	1.28 b	4.9 a	0.71 b	2.36 b	3.08 b	0.75 b
Substrate							
CSM[§§]	3.41 c	1.24 c	4.58 c	0.56 c	1.81 c	2.37 c	0.75 b
SVM[ÞÞ]	5.29 a	1.63 a	5.75 a	1.31 a	3.99 a	5.3 a	0.8 a
S[¤¤]	4.66 b	1.43 b	5.43 b	0.94 b	2.98 b	3.92 b	0.78 a
VS[†††]	2.87 d	1.13 d	4.18 d	0.45 c	1.43 c	1.89 c	0.73 b
Nut. sol.							
L1[¶¶¶]	3.38 c	1.16 c	4.11 c	0.7 ab	1.88 b	2.58 b	0.7 b
L2[§§§]	4.02 b	1.31 b	5.06 b	0.76 ab	2.3 b	3.07 b	0.78 a
L3[ÞÞÞ]	4.25 b	1.41 b	5.35 a	0.9 a	2.9 a	3.8 a	0.78 a
L4[¤¤¤]	4.57 a	1.56 a	5.42 a	0.88 ab	3.08 a	3.96 a	0.79 a

Response variables evaluated [†]L: length; [¶]W: width; [§]NL: number of leaves; [Þ]R: root; [¤]S: shoot; [††]T: total; [¶¶]Fv/Fm: maximum quantum yield of Photosystem II. Substrates used were [§§]CSM: commercial substrate mixture peat moss-based; [ÞÞ]SVM: agricultural soil and volcanic scoria mixture; [¤¤]S: agricultural soil alone; [†††]VS: volcanic scoria alone. Nutrient solution concentrations used were [¶¶¶]L1: 0 %; [§§§]L2: 25 %; [ÞÞÞ]L3: 50 %; and [¤¤¤]L4: 100 %. Mean values within the column per factor with different letters are statistically different according to Tukey's test ($p \leq 0.05$).

pulquero landraces proportional to the following order: agricultural soil and volcanic scoria mixture (SVM) > agricultural soil alone (S) > commercial substrate mixture (CSM) > volcanic scoria alone (VS) (Table 1). The highest concentration of the nutrient solution (L4 = 100 %) exhibited the greatest values of all growth variables, except for root biomass which no differences were observed (Table 1).

The interaction analysis of substrate´nutrient solution concentration (16 treatments) showed a growth trend in Penca larga for biomass allocation variables. In the substrates SVM and S Penca Larga exhibited similar elevated biomass values regardless of the nutrient solution concentration used from L1 to L4 (Table 2). In contrast, for Manso and Xamini (both *A. salimiana* landraces) the absence of nutrient solution in SVM substrate (SVM+L1) allowed greater total biomass accumulation in comparison to a total biomass reduction occurred in their respective S+L4 treatment (Table 2). These results suggested that the maximum concentration of the nutrient solution L4 (100 %) applied to agricultural soil alone (S) might cause nutrient toxicity to both *A. salmiana* landraces. On the other hand the effect of S+L4 on *A.mapisaga* doubled the shoot and total biomass accumulated respect to both landraces within *A. salmiana* (Table 2).

Manso and Xamini exhibited optimum biomass allocation across the interaction of SVM and all nutrient solution concentrations, in this substrate the content of agricultural soil was halved by the volcanic scoria added, which consequently halved the CEC and reduced the water holding capacity compared to S (Table 3). Therefore, less cation retention and greater water infiltration on SVM diminished nutrient accumulation and the risks of potential nutrient toxicity at L4 for both *A. salmiana* landraces.

Table 2. Effect of substrates and nutrient solution concentrations on dry root (R), shoot (S) and total (T) biomass accumulation (g) of maguey pulquero plants propagated from Mezquital Valley landraces Penca larga (*Agave mapisaga*), Manso and Xamini (both of *A. salmiana*).

Treatment	Penca larga			Manso			Xamini		
	R[†]	S[¶]	T[§]	R[†]	S[¶]	T[§]	R[†]	S[¶]	T[§]
CSM[Þ]+L1[§§]	0.16 ef	0.45 f	0.6 e	0.21 b	0.39 ef	0.6 fg	0.13 c	0.38 e	0.51 e
CSM+L2[ÞÞ]	0.44 def	1.12 ef	1.56 de	0.66 b	1.69 cdef	2.34 cdefg	0.55 abc	1.66 cde	2.21 cde
CSM+L3[¤¤]	0.64 cdef	2.18 cdef	2.82 bcde	0.81 b	2.64 abcd	3.46 abcd	0.76 abc	2.55 bcd	3.35 abcde
CSM+L4[†††]	0.84 bcdef	3.59 abcde	4.43 abcd	0.49 b	2.05 bcdef	2.54 bcdefg	0.98 ab	2.92 abcd	3.9 abcd
SVM[¤]+L1	1.89 a	4.54 abc	6.43 a	2.17 a	3.75 ab	5.91 a	1.37 a	4.65 a	6.18 a
SVM+L2	1.61 abc	4.98 ab	6.59 a	1.02 b	3.4 abc	4.41 abc	1.05 ab	3.32 abc	4.37 abc
SVM+L3	1.7 ab	6.04 a	7.75 a	0.7 b	2.18 abcde	2.89 bcdefg	1.35 a	4.11 ab	5.46 ab
SVM+L4	1.46 abcd	4.24 abc	5.7 ab	0.97 b	4.06 a	5.03 ab	0.81 abc	3.27 abc	4.83 abcd
S[††]+L1	1.16 abcde	3.98 abcd	5.14 abc	0.96 b	2.98 abc	3.94 abcd	0.63 abc	2.28 bcde	2.92 bcde
S+L2	1.11 abcde	3.34 bcde	4.45 abcd	0.81 b	2.92 abc	3.73 abcd	0.85 abc	2.35 bcde	3.2 bcde
S+L3	1.47 abcd	4.27 abc	5.74 ab	0.73 b	2.46 abcd	3.19 bcdef	1.04 ab	3.49 abc	4.53 abc
S+L4	1.55 abc	3.98 abcd	5.53 ab	0.59 b	1.96 bcdef	2.55 bcdefg	0.42 bc	1.86 cde	2.28 cde
VS[¶¶]+L1	0.05 f	0.24 f	0.29 e	0.06 b	0.16 f	0.22 g	0.13 c	0.39 e	0.52 e
VS+L2	0.46 def	1.35 def	1.81 cde	0.33 b	0.73 def	1.05 efg	0.38 bc	0.97 de	1.34 de
VS+L3	0.75 bcdef	2.1 cdef	2.85 bcde	0.36 b	0.94 def	1.3 defg	0.48 bc	1.46 cde	1.94 cde
VS+L4	1.13 abcde	4.26 abc	5.39 ab	0.83 b	2.45 abcd	3.28 abcd	0.6 abc	2.44 bcde	3.44 bcde

Table 3. Evaluation of substrates physical characteristics: apparent density (g cm^{-3}), total, air porosity (%) and water holding capacity (WHC) (%); and substrates chemical characteristics: total organic matter (%), total nitrogen (%), cation exchange capacity (CEC) (cmol kg^{-1}) and pH.

Physical	CSM[†]	SVM[¶]	S[§]	VS[Þ]
App. Density	0.187 ± 0.013	1.07 ± 0.23	0.91 ± 0.244	1.15 ± 0.18
Total Porosity	76.92 ± 1.28	50.19 ± 1.37	54.87 ± 2.64	51.15 ± 0.88
Air Porosity	14.61 ± 1.34	9.23 ± 0.85	7.69 ± 2.57	17.34 ± 0.57
WHC	62.31 ± 0.63	40.96 ± 1.86	47.18 ± 0.92	33.8 ± 0.85
Chemical	CSM	SVM	S	VS
Organic Matter	20.1 ± 1.77	3.75 ± 1.11	5.5 ± 1.11	0.59 ± 0.14
Total Nitrogen	2.7 ± 0.71	0.27 ± 0.07	0.32 ± 0.19	0.02 ± 0.01
CEC	73.2 ± 4.16	26.1 ± 2.99	49.1 ± 5.75	8.7 ± 2.9
pH	6.5 ± 0.52	8.1 ± 0.37	7.9 ± 0.4	8.05 ± 0.36

[†]CSM: commercial substrate mixture; [¶]SVM: agricultural soil and volcanic scoria mixture; [§]S: agricultural soil alone; [Þ]VS: volcanic scoria alone. Mean values (n = 3) ± standard deviation.

The growth of all landraces in CSM and VS was proportional to the increasing concentration of the nutrient solution applied, which absence of nutrient solution (L1) in both substrates restricted plant growth (Table 2). Even though CSM possessed better chemical characteristics than the other substrates, such as greater organic matter content, total nitrogen content and high CEC (Table 3), ion imbalance might occur in CSM substrate that reduced the total biomass mean values of all the landraces relative to the respective effect on S and SVM substrates (Table 1).

Substrates based on peat moss tend to accumulate NH_4^+ due to elevated raw organic matter (OM), which its decomposition tend to acidify the media, these conditions are suitable for fungi proliferation while ongoing acidification and microorganisms antagonism can reduce the occurrence of nitrifying bacteria; additionally, acidic conditions might promote the reduction of oxidized forms (NO_3^-) added by nutrient solution to a reduced form (NH^+) (Landis *et al.,* 1990). N reduced forms can be phytotoxic under certain conditions; however, peat moss characteristics are tolerated and adequate for temperate forest species (Landis *et al.,* 1990). In this work, the CSM was composed of 50% peat moss and the rest was innocuous mineral material, according to the effect caused by the CSM on the plants of all landraces, as biomass reduction (Table 1) in function of nutrient solution absence (Table 2), indicated that CSM hindered the growth of the plants evaluated. The CSM had the highest CEC across the substrates evaluated (Table 3), which inferred greater cation retention, including NH_4^+; although, peat moss use for Agave commercial production seems unsuitable due to its high costs and incompatibility with Agave's growth requirements and dependence on nutrient solution addition, the evaluation of CSM was helpful to elucidate the potential sensitivity of the evaluated landraces from the Cardonal region to the potential ion imbalance caused by this substrate.

The growth trend observed in all the landraces across the VS substrate treatments demonstrated that VS restricted plant growth as consequence of poor physical and chemical characteristics that let inferior water holding capacity and reduced nutrient retention due to low CEC (Table 3). The mixture of agricultural soil and volcanic scoria (SVM) improved the chemical and physical characteristics, compared to the individual effects of each substrate. The use of agricultural soil for maguey pulquero nursery using containers can be adverse as might promote soil extraction which would reduce arable land, eventually. On the other hand, the use of volcanic scoria in Mexico as substrate for hydroponic production is widely extended due to its high availability and low costs, to this date (Gutierrez-Castorena *et al.*, 2011); therefore, volcanic scoria can support and reduce the costs of maguey pulquero nursery production.

The results of this research suggested that the nutrient delivery form used in the experiment was inadequate for VS, as high-water infiltration and poor nutrient retention restricted plant growth; it is possible that slow-release fertilizers would be a better option for that substrate. Also, the physical and chemical characteristics of volcanic scoria can be improved using amendments, such as agroindustrial residues or other organic materials (Gutierrez-Castorena *et al.*, 2011). Despite the limiting conditions of VS for the growth of maguey pulquero plants evaluated in this study, Penca larga exhibited greater total biomass allocation across the nutrient solution concentrations from L2 to L4 relative to Manso and Xamini (Table 2).

According to their morphological traits the *A. mapisaga* landraces have been described as highly homogeneous due to intense artificial selection, in comparison to those highly variable of *A. salmiana* (Mora-Lopez *et al.*, 2011). DNA analyses have shown potential genetic flow among some populations of *A. salmiana* and *A. mapisaga* landraces, which infers that human influence might let hybridization between both species, while specific abiotic elements of a region/microhabitat and high plasticity that is characteristic of agave plants can shape the morphological divergences/similarities (Alfaro *et al.*, 2007; Trejo *et al.*, 2020). The underlying genetic richness of *A. mapisaga* able to overcome stress can be underestimated by its homogeneous morphological traits that could suppose low genetic variation; in this regard, studies performed on five month-old maguey pulquero plants (*A. mapisaga* and *A. salmiana*) propagated from seeds collected in same provenance Metepec, Hidalgo, located in the maguey pulquero region, demonstrated that *A. mapisaga* accumulated greater total dry biomass in comparison to *A. salmiana*, both were subjected for 30 days to a temperature treatment of 45 °C applied from 11 am to 3 pm within a temperature regime of 25/15 °C for 12/12 h (Jimenez-Torres *et al.*, 2021). Taking into consideration the humanization process of *A. mapisaga* that has favoured the selection of bigger plants (Mora-Lopez *et al.*, 2011) and its physiological adaptation to stressing temperatures (Jimenez-Torres *et al.*, 2021), those traits might influence on the responses observed in this work, as *A. mapisaga* exhibited optimum growth across the treatments relative to the *A. salmiana* landraces (Table 1).

The growth differences of the *A. salmiana* landraces observed in this work can be associated to the humanization process as well. Manso is one of the most used landraces of *A. salmiana* and widely distributed in the maguey pulquero region in Central Mexico (Mora-Lopez *et al.*, 2011), it is characterized by big sized plants with small teeth and smooth leaf margin, these traits are appreciated by maguey pulquero producers, who tend to introduce cultivated and/or wild plants from an ecoregion to another in order to fulfil their plantation requirements; therefore, plant commerce and introduction of Manso plants from different ecoregions might enhance morphological and genetic variability of Manso landrace (Alfaro *et al.*, 2007; Mora-Lopez *et al.*, 2011; Trejo *et al.*, 2020); while sexual reproduction boost the genetic pool and morphological diversity (Cruz-Vasconcelos *et al.*, 2020). In this work, a multivariate hierarchical dendrogram analysis was performed using the variables width and length of the biggest leaf of all the plants under S+L1 treatment, the Manso individuals were randomly scattered within different groups (Figure 1), which inferred less aggrupation of Manso individuals, meaning greater leaf morphological diversity growing under the S+L1 treatment.

In the other hand, Xamini individuals exhibited a clear aggrupation within the dendrogram under the S+L1 treatment (Figure 1) and S+L4 (Figure 2), which inferred less morphological variation of Xamini plants comparing to Penca Larga and Manso, regardless of the nutrient solution dosing differences. That can be explained as the Xamini landrace has been mostly cultivated in the Mezquital Valley, it is a smaller plant with lower sap production and leaves with bigger teeth, and those are undesirable traits for most maguey pulquero producers. Therefore, the interest to introduce Xamini to other locations beyond the Mezquital Valley appears to be limited. This landrace, then, has been adapted to Mezquital Valley through several generations, Xamini has been traditionally used by Otomi communities in the Cardonal location (Reyes-Aguero *et al.*, 2019), which has arid climate, dominated by Leptosols soils originated from sedimentary calcareous rocks (INEGI, 1992).

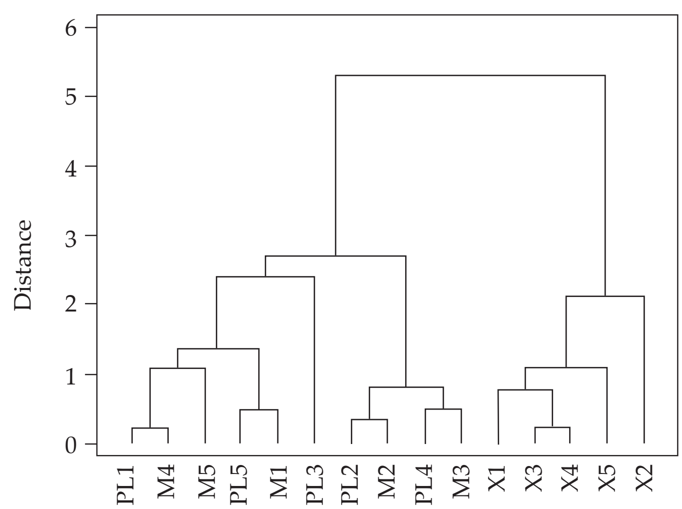

Figure 1. Dendrogram constructed with the variables length and width of biggest leaf from landraces Penca larga (PL) *Agave mapisaga*, Manso (M) and Xamini (X), both *A. salmiana*, under treatment agricultural soil alone without nutrient solution (S+L1). Numbers next to each landrace acronym correspond to the respective replicate.

The adaptation of Xamini parent plants to the abiotic elements of the Cardonal, can help to explain the growth variation observed in this work. The substrates SVM and S were composed by an agricultural soil, where in SVM+L1 (halved soil without nutrient solution) exhibited better growing conditions for Xamini than in S+L1 (100 % agricultural soil) where reduced its shoot and total biomass (Table 2). It was used an Andosol type agricultural soil as S substrate, with dominant parent material of volcanic andesitic tephra. Andosols possess abundant aluminium and iron oxy-hydroxides minerals, that confer high anion retention capacity and soil organic matter stabilization (IUSS, 2015); also, the agricultural management might enhance microstructure loss, due to continuous tillage which leads to compaction (Naderi-Boldaji and Keller, 2016). In contrast, Leptosols from arid regions are shallow gravel-rich with low-forming soil processes (IUSS, 2015), characteristics that confer low water holding capacity, inferior nutrient retention capacity and loose structure. In this work, the chemical and physical characteristics of S in combination with a higher fertigation regime, might constrain Xamini shoot and total biomass accumulation, which were attenuated in SVM substrate.

In this regard, the maximum nutrient solution concentration (L4) addition in S (S+L4) let a clear aggrupation of the individuals within its respective landrace (Figure 2). The maximum nutrient solution concentration (L4) in S substrate significantly reduced the length of the biggest leaf in both *A. salmiana* landraces in comparison to their respective treatment without nutrient solution (S+L1); similarly, shoot and total biomass reduction was observed on Xamini under S+L4 (Table 2). These results suggested that the potential stress exerted by the highest nutrient concentration in S could trigger

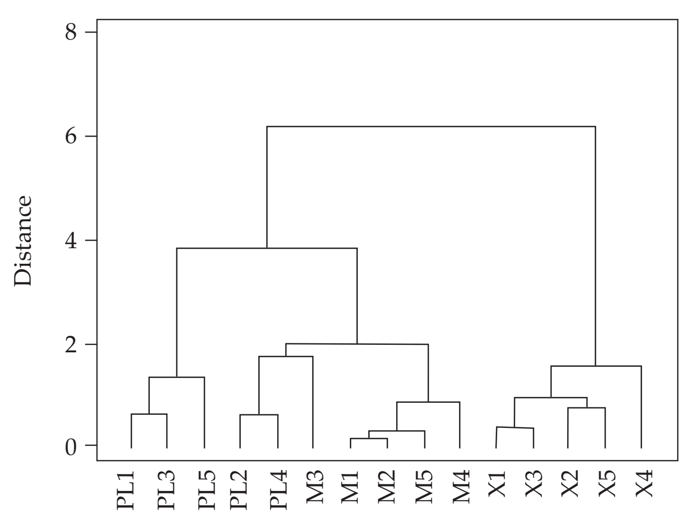

Figure 2. Dendrogram constructed with the variables length and width of biggest leaf from landraces Penca larga (PL) *Agave mapisaga*, Manso (M) and Xamini (X), both *A. salmiana*, under treatment agricultural soil alone with 100 % nutrient solution concentration (S+L4). Numbers next to each landrace acronym correspond to the respective replicate.

physiological responses specific to each landrace letting similar phenotypic variation as leaf size reduction (Jimenez-Torres *et al.,* 2021)

Results in this study can help to elucidate the nutrient requirements of maguey pulquero seedlings according to substrate used and the age of the plants. Fertilization schemes on substrates S and SVM was unnecessary, as the agricultural soil would provide the nutrients required for optimum growth in all the landraces evaluated; the slower growth of CAM plants than C3 or C4 might reduce the nutrient requirements of maguey pulquero young plants in early growth stages (Nobel *et al.,* 1991).

Taking into consideration the physical and chemical characteristics of the agricultural soil used in this work (Table 3); also, the potential presence of beneficial soil microorganisms and *Agave* endophytes that promote plant growth (Beltran-Garcia *et al.,* 2014; Bautista-Cruz and Martinez-Gallegos, 2020), those characteristics provided the optimum conditions for the growth of 10-month-old plants of all landraces.

In this regard, a nitrogen fertilization study performed in bulbils of *Agave cocui* under greenhouse conditions using soil as substrate, the *A. cocui* bulbils did not show statistical differences in fresh biomass accumulation and leaf longitude between control treatment 0 and 0.5 g of ammonium nitrate fertilization, which demonstrated adequate growth in soil regardless of nitrogen addition (Diaz *et al.,* 2011). On the other hand, nitrogen excess can affect plant development at that early growth stage; in that same study the application of 1 g ammonium nitrate showed toxicity and plant growth inhibition (Diaz *et al.,* 2011).

In this work, the total biomass accumulation of all landraces on VS was improved with mineral fertilization, reaching higher biomass in the 100% nutrient solution concentration (Table 2); although, physical and chemical characteristics of VS that let high water infiltration and restricted nutrient retention (Table 3) might overestimate the nutrient requirements at the age evaluated. Studies performed on seedlings of Xamini (*A. salmiana*) landrace from Cardonal growing on perlite, demonstrated that after 168 days, the total biomass accumulation and leaf growth were similar in the lowest nutrient concentration treatment of Steiner solution at 25 %, compared to 100 % concentration (both treatments were applied once every 3 days), which suggested that 25 % concentration was adequate for Xamini growth (Arrazola-Cardenas *et al.,* 2020).

Photosystem II fluorescence (Fv/Fm)

The two-way ANOVA showed that Penca larga (*A. mapisaga*) landrace exhibited the highest maximum quantum yield efficiency of Photosystem II (Fv/Fm); similarly, the substrates composed by agricultural soil, SVM and S, let greater Fv/Fm values compared to CSM and VS. In contrast, the absence of the nutrient solution (L1) showed the least Fv/Fm results, while the maximum nutrient solution concentration (L4) had the highest Fv/Fm values (Table 1). The interaction among substrate´nutrient solution concentration in VS+L1 treatment caused the least Fv/Fm values of all the landraces evaluated (Table 4). Those inferior Fv/Fm results in all the landraces were indicative of photoinhibition, as a consequence of nutrient deficiency caused by VS-L1 treatment (Table 4), since volcanic scoria and tap water did not provide enough nutrients for

Table 4. Effect of substrates and nutrient solution concentrations on maximum quantum yield of Photosystem II (Fv/Fm) of biggest leaf of young maguey pulquero plants from landraces: Penca larga (*Agave mapisaga*), Manso and Xamini (both of *Agave salmiana*).

Treatment Substrate* Nut.Sol.	Penca larga Fv/Fm	Manso Fv/Fm	Xamini Fv/Fm
CSM[†]+L1[¤]	0.73 b	0.74 ab	0.62 bc
CSM+L2[††]	0.8 ab	0.79 ab	0.74 ab
CSM+L3[¶¶]	0.78 ab	0.79 ab	0.76 ab
CSM+L4[§§]	0.78 ab	0.79 ab	0.76 ab
SVM[¶]+L1	0.81 a	0.79 a	0.82 a
SVM+L2	0.81 a	0.79 ab	0.79 a
SVM+L3	0.83 a	0.78 ab	0.8 a
SVM+L4	0.84 a	0.79 ab	0.79 a
S[§]+L1	0.81 a	0.79 ab	0.73 abc
S+L2	0.81 a	0.77 ab	0.78 a
S+L3	0.84 a	0.8 a	0.75 ab
S+L4	0.83 a	0.78 ab	0.75 ab
VS[Þ] +L1	0.6 c	0.54 c	0.59 c
VS+L2	0.8 ab	0.79 ab	0.79 a
VS+L3	0.8 ab	0.7 b	0.83 a
VS+L4	0.84 a	0.79 a	0.81 a

Substrates used were [†]CSM: commercial substrate mixture; [¶]SVM: agricultural soil and volcanic scoria mixture; [§]S: agricultural soil alone; and [Þ]VS: volcanic scoria alone. Nutrient solution concentrations used were [¤]L1: 0 %; [††]L2: 25 %; [¶¶]L3: 50 %; and [§§]L4: 100 %. Mean values within the column with different letters are statistically different according to Tukey's test ($p \leq 0.05$).

plant development. Nutrient deficiency can affect the leaf elongation and biosynthesis of photosynthetic organelles directly related to photosynthetic productivity (Morales *et al.,* 2008).

In this study, Penca larga and Xamini exhibited reduced Fv/Fm values on CSM+L1 as consequence of potential ion imbalance and nutrient deficiency. However, those results were statistically similar to rest of their respective treatments on CSM (Table 4), which indicated the functionality of the electron harvest complex regardless of the nutrients deficiency on CSM. In this regard, the *Agave* plants exhibit acclimatation of the photochemical system to stress, young *A. salmiana* plants (one-year-old) exposed to severe drought over 115 days of water withholding, after rehydration maintained the photon light harvest functionality, which demonstrated resilience to this stress by photo-protective mechanisms (Campos *et al.,* 2014).

CONCLUSIONS

The Penca larga landrace (*Agave mapisaga*) exhibited superior growth relative to Manso and Xamini (landraces of *A. salmiana*), under most of the treatments applied, except the absence of nutrient solution in commercial substrate mixture (CSM) and volcanic scoria (VS) which restricted plant growth in all the landraces. The physical and chemical characteristics of the substrate agricultural soil alone (S) in combination with maximum nutrient concentration 100 % (L4), affected shoot and total biomass accumulation of both Manso and Xamini landraces.

Volcanic scoria used for maguey pulquero commercial production may be suitable due to high availability and low costs in the maguey pulquero region of Central Mexico within the Trans Mexican Volcanic Belt. Nevertheless, it is suggested to improve the chemical and physical characteristics of the volcanic scoria by adding an organic amendment.

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