Revista Mexicana de Ciencias Agrícolas

DOI: https://doi.org/10.29312/remexca.v17i4.4358

Growth and CO_2assimilation of *Agave potatorum* Zucc. supplied at different nutritional levels

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Abstract

In the state of Oaxaca, Mexico, *Agave potatorum* is collected from wild populations or propagated by seeds in small areas and used to make the distilled beverage mezcal. The species has been propagated in vitro, and the resulting plants are transplanted into a substrate for 90 days of acclimatization, then established in a greenhouse for 12 months to reach a larger size; likewise, fertilizing the plants has improved their growth. The objective was to evaluate the leaf area and CO_2assimilation rate of micropropagated-acclimatized plants fertigated with California (Cal) or Steiner (St) nutrient solutions. Plants fertigated with Cal-5% and Cal-100% had 20.8 and 27.7 leaves, leaf areas of 1 031.5 $cm^2$and 1 867.4 cm^2, rosette diameters of 37 and 52.3 cm, and heights of 19.5 and 29.5 cm, respectively. Stomatal opening and CO_2assimilation began at 16:00 h as photosynthetically active radiation decreased, reaching maximum assimilation values between 19:00 and 22:00 h. Plants fertigated with Cal-100% and St-100% showed CO_2assimilation values of 17 and 11 µmol $CO_2m^{-2}s^{-1}$, respectively.

Keywords:

leaf area, micropropagated plants, nutrient solution, photosynthesis.

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Introduction

Agaves have morphological and physiological characteristics, such as shallow and branched roots, thick cuticle, succulent tissues, sunken stomata and CAM photosynthesis, to fix CO_2during the night and accumulate it as malic acid, so they use water more efficiently than $C_3$and C_4plants (Carrillo *et al* ., 2014) and are adapted to arid and semi-arid environments and poor soils (Cen-Cen *et al* ., 2015).

In the state of Oaxaca, Mexico, *Agave potatorum* Zucc., called maguey Tobalá, is used to produce the distilled alcoholic beverage mezcal. Due to the intensive collection of adult specimens, their populations have declined, and since the 1990s, peasant groups have implemented seed propagation and established plantations (Enríquez-del Valle, 2008). The asexual micropropagation of *A. potatorum* has been carried out through the plant culture technique, and the plants obtained are acclimatized in greenhouses, where thickening of the stem and development of new leaves (large, rigid, and succulent) occur in preparation for their establishment in a greenhouse (Cruz-García *et al* ., 2017 ; Bautista-Castellanos *et al* ., 2020 ; Correa-Hernández *et al* ., 2022).

They are then established in the greenhouse for 12 months to achieve the greater size and hardiness needed in the field (Enríquez-del Valle, 2008). The plant's vigor is affected by its nutritional condition and requires energy and photosynthates produced in the photosynthetic organs (Jarquín-Rosales *et al* ., 2022).

The nutritional supply in micropropagated-acclimatized plants of *A. potatorum* was related to their growth in greenhouses and nurseries (Enríquez-del Valle *et al* ., 2016 ; Luna-Luna *et al* ., 2017 ; Bautista-Castellanos *et al* ., 2020 ; Ramírez-Mosqueda *et al* ., 2022). It is important to understand the photosynthetic activity in interaction with the nutritional supply; the objective was to evaluate the leaf area and the CO_2assimilation rate of micropropagated-acclimatized plants that were fertigated.

Materials and methods

Location and plant material

Micropropagated-acclimatized plants of *Agave potatorum* Zucc were used, following the methodology of Luna-Luna *et al* . (2017) . Acclimatization was carried out in the greenhouse of the Technological Institute of the Valley of Oaxaca, Mexico, and the plants were then taken to a greenhouse of the College of Postgraduates, Montecillo Campus, Texcoco, State of Mexico. After 220 days of ex vitro growth, 42 plants, each between 10 and 13 cm tall, were selected and established in 30 x 30 cm pots containing sand as the substrate.

Six groups of seven plants were formed to be fertigated with Steiner (1984) universal solution and California nutrient solution (Sánchez-del Castillo, 1989) at concentrations of 5%, 50% and 100%, with the pH adjusted to 5.8. The Steiner (1984) universal solution and the California solution contain the following in mg L^{-1}: $MgSO_4.7H_2O$, 49.768 and 52.0; $Ca(NO_3)_2.4H_2O$,107.415 and 72; $K(NO_3)$, 28.128 and 66; K_2SO_4, 25.153 and 0.0; KOH, 2.329 and 0.0; KH_2PO, 26.95 and 0.0; $MnSO_4$, 0.62 and 0.62; $ZnSO_4$, 0.11 and 0.11; H_3BO_3, 0.44 and 0.44; $CuSO_4.5H_2O$, 0.02 and 0.02; $Na_2MoO_4.2H_2O$, 0.048 and 0.048, respectively.

Fertigation was performed at the substrate level using 400 ml twice a week for 360 days. At 60 and 360 days, the following variables were recorded: plant height (PH), number of unfolded leaves (NL), rosette diameter (RD), and the distance of the distal ends of the largest opposite leaves. The experiment was established under a CRD with one plant as the experimental unit. Analysis of variance and comparison of means (Tukey, 0.05) were performed using SAS 9.4 (SAS Institute Inc., 2022).

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Leaf area

On each fully extended leaf, the mean length (L), excluding the terminal spine, and the mean width (W) were recorded. To determine the leaf area (LA), 30 leaves of different sizes were selected; their outline was traced on paper and cut out and the area was quantified using a LI-3100 optical leaf area integrator. A linear regression analysis was performed, with LA as a function of its length L and W, to obtain a conversion factor.

This factor was used to estimate the individual leaf area of each leaf and the total leaf area per plant. Analysis of variance and comparison of means using Tukey's test (α= 0.05) were performed with the SAS statistical package, version 9.4 (SAS Institute Inc. 2022).

CO_2assimilation

At six months of age, three plants per treatment (St-100%, St-5%, Cal-100% and Cal-5%) were established in 25.5 x 20 cm pots (9.4 dm^3) containing soil-moss peat substrate (1:2). Thirty days after transplanting, a fully developed leaf was selected from the middle part of the rosette of each plant, and the instantaneous CO_2assimilation rate was recorded using a LI 6400 portable IRGA and attachments to quantify CO_2.

The plants were subjected to two edaphic moisture conditions to determine the instantaneous CO_2assimilation rate: 1) irrigation once a week (without restriction); and 2) when they were not irrigated for 17 days and soil moisture was less than the permanent wilting point, PWP (soil drought). To determine the moisture content, field capacity (85%), and PWP (60%) of the substrate, a moisture retention curve was developed in the Soil Physics Laboratory of the College of Postgraduates, Montecillo Campus.

In each period, CO_2assimilation rate, stomatal conductance, transpiration, mesophyll CO_2(Ci) and photosynthetically active radiation (PAR) were determined, with eight measurements of each leaf at 3 h intervals for 24 h starting at 10:00 h. The experiment was established under a completely randomized design with a 2 x 2 x 2 x 9 factorial arrangement (two levels of soil moisture, two levels of NS, two levels of NS concentration, and nine levels of times in which measurements were taken), with a total of 72 treatments.

One plant was used as an experimental unit with three replications per treatment and a total of 216 experimental units. Analysis of variance and comparisons of means (Tukey, 0.05) were performed using the SAS 9.4 package (SAS Institute Inc., 2022).

Results and discussion

Plant development in the greenhouse

Leaf area, photosynthetic capacity, biomass accumulation, and crop yield are factors that depend on nutrient supply (Makino, 2011). Corn plants that received fertilization developed up to 4.6 times leaf area index, 1.06 times height, 1.38 times dry weight, 1.4 times grain yield, 1.11 times the weight of 1 000 grains and 66 days after planting, the photosynthetic rate was 1.27 times compared to unfertilized plants. In addition, there was a high correlation (r= 0.926) between photosynthetic rate and yield (Efthimiadou *et al* ., 2010).

At the beginning of the experiment, *A. potatorum* plants had 7.9 to 8.3 leaves, a rosette diameter of 16.6 to 17 cm and a height of 10.3 to 13 cm. From fertigation over 12 months, the number of leaves (Table 1 showed that nutrient solution treatments had significant (p# 0.05) different effects on rosette diameter and plant height at 60 days, and highly significant effects at 360 days (p# 0.01) for leaf number, plant height, and rosette diameter.

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Table 1. Summary of the analysis of variance of *A. potatorum* that received different nutrient supply levels with nutrient solution.

SV	DF	NL60	NL360	RD60	RD360	PH60	PH360
Treatment	5	7.23ns	59.75**	54.7*	308.89**	9.47*	105.71**
Error	36	2.92	7.03	10.56	33.18	1.98	14.16
Total	41						

SV= sources of variation; DF= degrees of freedom; NL= number of leaves; DR= rosette diameter; PH= plant height; 60= 60 days of establishment; 360= 360 days of establishment, *= significant F-value (p> 0.05); **= highly significant F-value (p≤ 0.01).

All plant groups that received nutrient solutions were larger at 60 days of age than at the start date, and plant size was positively related to the NS dose. The largest plants were those that received 100% NS, either Cal or St, whereas the smallest plants were those fertigated with 5% NS, either Cal or St.

Plants fertigated with Cal-100% and St-5% had, on average, 11.7 and 8.7 leaves, rosette diameters of 24.1 and 17.9 cm, and heights of 13.3 and 10.4 cm, respectively, which were significantly different (Tukey, 0.05) (Table 2).

Table 2. Morphological characteristics of micropropagated-acclimatized plants of *Agave potatorum* Zucc.

NS	NL60	NL360	RD60 (cm)	RD360 (cm)	PH60 (cm)	PH360 (cm)
S100	9.2 ±2.1ab	25.6 ±3a	22.6 ±3.7abc	45.4 ±6.6ab	12.1 ±1.6ab	25.9 ±4.9ab
S50	10.1 ±2ab	24.1 ±1.8ab	25 ±3.1a	45.1 ±4.9ab	13 ±1a	24.9 ±2.3abc
S5	8.7 ±0.8b	20.1 ±2.3b	17.9 ±1.7c	34 ±5.8c	10.4 ±0.8b	19.9 ±3.2bc
C100	11.7 ±1.4a	27.7 ±2.6a	24.1 ±0.9ab	52.3 ±4.8a	13.3 ±0.8a	29.5 ±4.4a
C50	9.9 ±2.3ab	25.2 ±2.6a	23.7 ±5.1ab	45.4 ±6.6ab	12 ±2.1ab	26 ±3.4a
C5	9.3 ±1.3ab	20.8 ±2.4b	19.7 ±3.1bc	37 ±5.6bc	10.7 ±1.7b	19.6 ±3.9c

S= Steiner; C= California; NS= nutrient solution; NL= number of leaves; RD= rosette diameter; PH= plant height; 60= 60 days of establishment; 360= 360 days of establishment. Different letters within columns indicate significant differences (p≤ 0.05); the mean is included ± the standard error.

After 360 days, the plants fertigated with NS Cal-100% and NS St-5% had 27.7 and 20.1 leaves, rosette diameters of 52.3 and 34 cm, heights of 29.5 and 19.9 cm, respectively; significantly different magnitudes (Tukey, 0.05); on the other hand, they had 3.4 and 2.4 times the number of leaves, 3.11 and 2.02 times the diameter of the rosette, 2.54 and 1.71 times the height compared with their size at the beginning of the experiment (Table 2). Morales *et al* . (2017) reported that *A. potatorum* plants fertigated with St-50% showed an increase of 13% in height but not in the number of leaves, compared to unfertilized plants.

Leaf area and CO_2assimilation rate

Leaf area together with the periods in which *A. potatorum* plants were exposed to contrasting edaphic moisture conditions: 1) without moisture restriction; and 2) soil drought condition; the analyses of variance (Table 3) showed that the plants had significant differences (p≤ 0.01) in leaf area according to the measurement period, since during the first period, they had 1 053.5 cm^2, with an increase to 1 221.4 cm^2, significantly (Tukey 0.05) different.

Table 3. Summary of the analysis of variance for LA and CO_2assimilation rate of *A. potatorum* plants.

SV	DF	CO_2A (µmol $CO_2 m^{-2} s^{-1}$)	Trans	Cond	CO_2(Ci)	LA (cm^2)
Per	1	0.96ns	0.0000005ns	0.036ns	71465771.9ns	1532586.2**

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SV	DF	CO_2A (µmol $CO_2m^{-2}s^{-1}$)	Trans	Cond	CO_2(Ci)	LA (cm^2)
NS	1	4.52ns	0.0000002ns	0.003ns	61521904ns	2459140.23**
Conc	1	4.98ns	0.000022*	0.045**	90175268ns	15750132.9**
MeaT	8	1123.3**	0.00009**	0.051**	34789727.8ns	0ns
Int2	1	0.14ns	0.0000004ns	0.019**	15241053ns	209183.39ns
Int3	8	38.36**	0.000027**	0.025**	28593932.8ns	0
Int6	8	14.6ns	0.0000001	0.013**	27630158.1ns	0ns
Int9	8	4.98ns	0.00000002ns	0.002*	15078401.8ns	0ns
Int10	16	10.05ns	0.00000002ns	0.007**	29104032.3ns	0ns
Error	144	9.71	0.0000002	0.146	35821589	83123.06
Total	215	11187.4	0.0001	1.145	7133430170	32034330.94

SV= sources of variation; DF= degrees of freedom; Per= periods that contrasted in soil moisture; NS= nutrient solution; Conc= concentration of nutrients; MeaT= measurement time; Int= interaction; Int1= Per x NS; Int2= Per x Conc; Int3= Per x MeaT; Int4= NS x Conc; Int5= NS x MeaT; Int6= Conc x MeaT; Int7= Per x NS x Conc; Int8= Per x NS x MeaT; Int9= NS x Conc x MeaT; Int10= Per x NS x Conc x MeaT; CO_2A= CO_2assimilation; Trans= transpiration; Cond= stomatal conductance; CO_2(Ci)= mesophyll carbon dioxide; LA= leaf area; *= significant F-value (p> 0.05); **= highly significant F-value (p≤ 0.01). For space reasons, non-significant interactions were not included in the table.

Therefore, short periods of water supply in the soil did not affect the growth of agave plants (Tables 3 and 4). The natural habitat of this species is sloping, stony terrain, so it can be useful for productively taking advantage of areas where water is limited. In corn plants (Badr and Brüggemann, 2020) and wheat plants (Osipova *et al* ., 2019), limited soil water availability negatively affects growth, transpiration rate, stomatal conductance, leaf photosynthetic capacity and yield.

Table 4. CO_2assimilation rate, transpiration, and stomatal conductance of *Agave potatorum* plants of 12 months of fertigation.

Factors	CO_2A (µmol $CO_2m^{-2}s^{-1}$)	Trans	Cond (g) mmol $CO_2m^{-2}s^{-1}$	CO_2(Ci)	LA (cm^2)
Per					
withI	5.6a	0.0009a	0.036b	257.4a	1 053b
withoutI	5.47a	0.0008a	0.062a	1407.8a	1 221.4a
NS					
St	5.390a	0.0008a	0.04a	1366.3a	1 030.5b
Cal	5.680a	0.0009a	0.05a	298.9a	1 234.9a
Conc					
100	5.69a	0.0007b	0.03b	1860.5a	1 407.2a
5	5.39a	0.0009a	0.06a	1478.7a	867.2b
Time (h)					
10:00	-0.63e	0.0004de	0.01b	521a	1 137.2a
13:00	-1.22e	0.0001de	0.005b	516a	1 137.2a
14:00	-0.56e	0.0006bc	0.01b	187.2a	1 137.2a
19:00	12.72ab	0.002a	0.08a	157a	1 137.2a
22:00	15.29a	0.001bc	0.09a	130a	1 137.2a
01:00	12.72b	0.001bc	0.1	116a	1 137.2a
04:00	9.09c	0.001b	0.11a	294a	1 137.2a
07:00	4.58d	0.0009bc	0.011b	350a	1 137.2a
10:00	-1.5e	0.0002e	0.01b	368.1a	1 137.2a

Per= periods contrasting in soil moisture; withI= with irrigation; withoutI= without irrigation; NS= nutrient solution; St= Steiner; Cal= California; Conc= concentration; CO_2A= CO_2assimilation; Trans= transpiration; Cond= stomatal conductance; CO_2(Ci)= mesophyll carbon dioxide; LA= leaf area. Different letters within columns indicate significant differences (p≤ 0.05).

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Plants fertigated with Cal-100% or St-100% had a leaf area of 1 407.2 cm^2, 1.62 times, significantly higher (Tukey, 0.05) than the 867.2 $cm^2$of LA of plants fertilized with Cal-5% or St-5%. NS dilutions had different significant (p≤ 0.05) and highly significant (p# 0.01) effects on leaf area and stomatal conductance.

During the times in a 24-h cycle when photosynthetically active radiation variation occurs, there were highly significant, different values (p≤ 0.01) in CO_2assimilation, transpiration, and stomatal conductance. The irrigation period and recording time showed highly significant effects (p# 0.01) on transpiration intensity, photosynthesis, and stomatal conductance.

CO_2assimilation rate

During a 24-h cycle in the first and second periods in which CO_2assimilation rate was evaluated, photosynthetically active radiation (PAR) presented a characteristic diurnal pattern, reaching its maximum value at 13:00 h with approximately 900 µmol photon $m^{-2}s^{-1}$, and decreased to zero at 19:00 h, and increased again from 07:00 h the next day.

CO_2assimilation occurred during the night period and began from 16:00 h, with the onset of stomatal opening, when PAR was around 300 µmol photon $m^{-2}s^{-1}$, which favored the progressive increase in CO_2fixation (Figure 1), with the highest values between 19:00 h and 01:00 h, and the maximum fixation occurred at 22:00 h, with a rate of 15.29 µmol $m^{-2}s^{-1}$.

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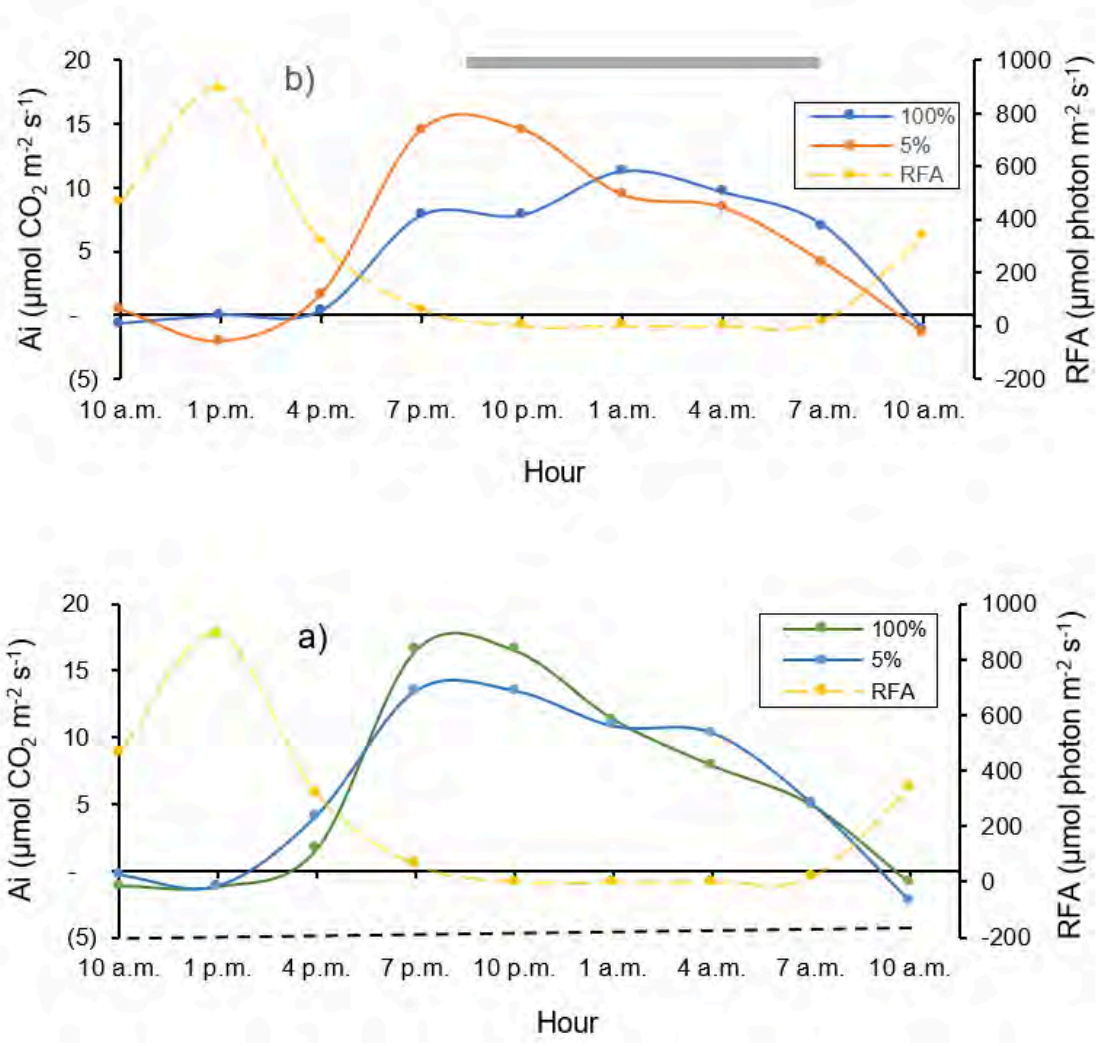
Figure 1. Photosynthetic rate of instantaneous net CO_2assimilation (Ai) of micropropagated-acclimatized *Agave potatorum* plants at different (a) California or (b) Steiner nutrient solutions. The gray horizontal bar represents the night period from sunset (20:13 h) to sunrise (7:11 h) in daylight saving time.



The plants maintained CO_2assimilation during the early hours of the morning, which ceased at approximately 09:00 h, when PAR reached values near 200 µmol photon $m^{-2}s^{-1}$. Nobel (1976) documented that plants of *A. deserti* Engelm, in the field, showed maximum CO_2assimilation (5.5 µmol $m^{-2}s^{-1}$) around 22:00 h, and this process remained active even after sunrise.

A. potatorum plants that had water availability showed nocturnal CO_2assimilation (CAM mechanism) for almost 18 h. Plants fertigated with Cal-100% and with St-100% showed CO_2assimilation of 17 µmol $CO_2m^{-2}s^{-1}$and 11 µmol $CO_2m^{-2}s^{-1}$, respectively (Figure 1).

Similar trends were observed in plants subjected to edaphic drought conditions, when the substrate was below the PWP (Figure 2); that is, *A. potatorum* plants continued to assimilate CO_2, probably because they had water stored in their tissues, as they exhibit crassulaceous acid metabolism (CAM).

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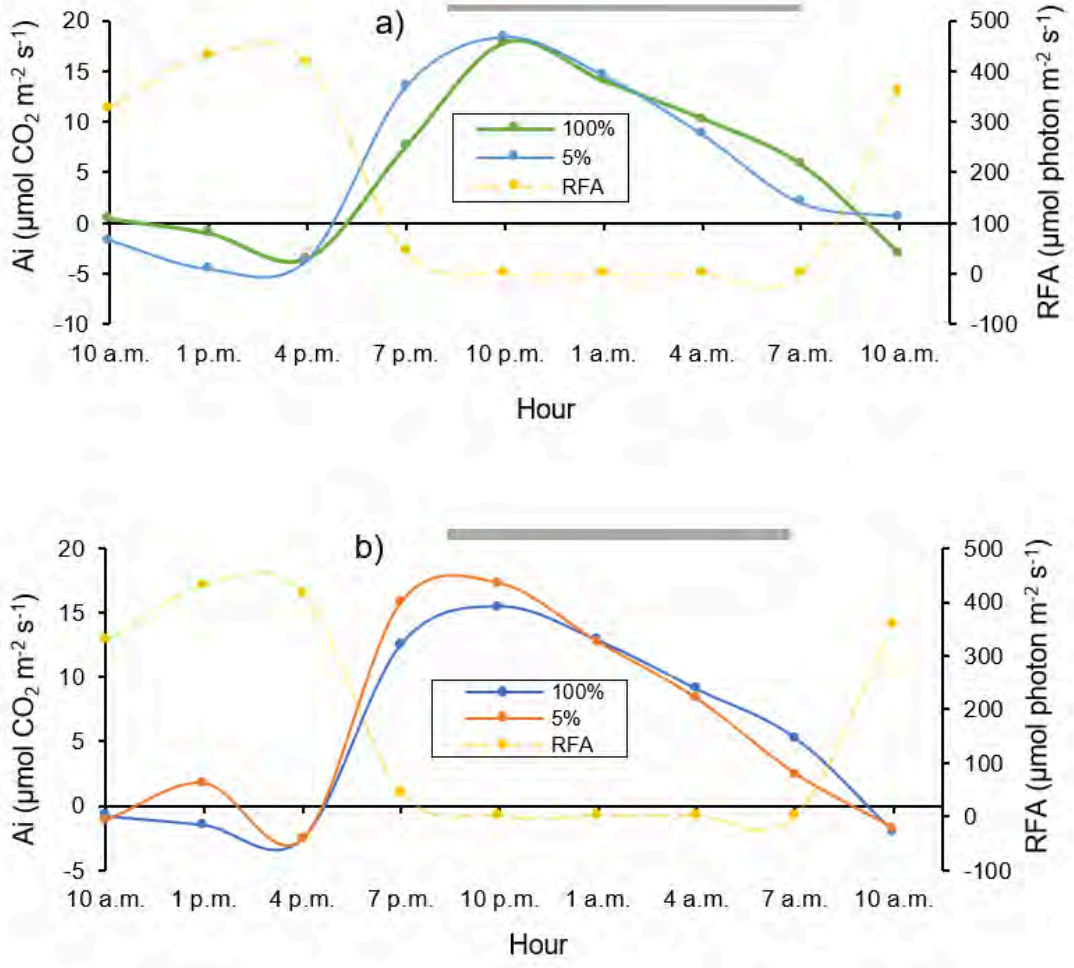
Figure 2. Photosynthetic rate of instantaneous net CO_2assimilation (Ai) of micropropagated-acclimatized plants of *Agave potatorum* , fertigated with different a) California and b) Steiner nutrient solutions. The gray horizontal bar represents the night period from sunset (20:13 h) to sunrise (7:11 h) in daylight saving time.



The plants fertigated at 100% and 5% showed no differences in CO_2assimilation per unit area. Plants supplied with 100% NS, either St or Cal, had a leaf area of 1 407.2 cm^2, which was 1.62 times the LA of plants supplied with 5% NS. The plants supplied with Cal-100% and Cal-5% had leaf areas of 1 867.37 and 1 031.16 cm^2, respectively.

In contrast, the plants supplied with St-100% and St-5% solution had leaf areas of 1 504.55 and 1 005.6 cm^2, respectively. Therefore, LA is a factor explaining the accumulation of biomass between plants with high-dose and low-dose fertilization.

CO_2fixation gradually decreased from 4:00 am to 09:00 am (stomatal closure), after which negative values were recorded (Figures 1 and 2). In *A. tequilana* , higher values of nocturnal CO_2assimilation occurred (7.5 and 16.2 µmol $CO_2 m^{-2} s^{-1}$), and in the period from 10 am to 4 pm, negative assimilation rates were recorded (Pimienta-Barrios *et al* ., 2006).

For plants under conditions of available soil water, CO_2assimilation occurred between 16:00 h and 09:00 h the next day (Figure 1), and plants where irrigation was suspended for 17 days and the soil was below the PWP, assimilated CO_2in the interval from 17:00 h to 09:00 h the next day (Figure 2). Water-restricted plants kept their stomata open for a shorter time compared to plants without water limitations.

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The stomatal opening began at 16:00 h, and the maximum CO_2fixation occurred at 22 h, with values of 17.81 and 18.41 µmol $CO_2m^{-2}s^{-1}$in the plants that were fertigated with NS Cal-100 and Cal-5%, respectively. In each period, plants fertigated with NS Cal-100 and Cal-5% had higher CO_2assimilation than plants fertilized with NS St-100 and St-5%.

The evidence from the present work is consistent with Pimienta-Barrios *et al* . (2005) in that CAM plants subjected to lower soil water availability reduce their photosynthetic activity and increase respiration, but positive CO_2assimilation values remain. Patishtán *et al* . (2010) reported that *Aloe vera* plants subjected to water stress reduced stomatal conductance. Authors such as Pimienta-Barrios *et al* . (2006) report that *A. tequilana* , under conditions of extreme drought, decreased its CO_2assimilation but did not cease it.

When soil moisture was below the PWP, plants had stomatal conductance of 0.036 and 0.062 g (Table 4) and PAR of 223.3 and 176 µmol photon $m^{-2}s^{-1}$(Figure 1). The application of 100% and 5% nutrient solutions to plants showed transpiration rates of 0.0007 and 0.0009 mm, stomatal conductances of 0.03 and 0.06 mmol $CO_2m^{-2}s^{-1}$, and leaf areas of 1 407.2 and 867.2 cm^2, significantly different magnitudes (Tukey, 0.05).

Conclusions

Agave potatorum plants fertigated for 360 days with 100% California nutrient solution presented 27 leaves on average, a rosette diameter of 52.3 cm, and a height of 29.5 cm, which was a larger size than fertigated plants with 100% Steiner solution.

Plants given more nutrients developed greater leaf area. Plants show nocturnal CO_2assimilation when PAR decreases; the stomatal opening began at 16:00 h and reached maximum values of net CO_2assimilation of 15.29 µmol $m^{-2}s^{-1}$at 22:00 h.

Plants fertigated with Cal-100% showed higher CO_2assimilation than the rest of the plants. Plants that were in soil with moisture below the permanent wilting point for 17 days continued to assimilate CO_2.

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Revista Mexicana de Ciencias Agrícolas

DOI: https://doi.org/10.29312/remexca.v17i4.4358

Growth and CO_2 assimilation of *Agave potatorum* Zucc. supplied at different nutritional levels

Journal Information
Journal ID (publisher-id): remexca
Title: Revista mexicana de ciencias agrícolas
Abbreviated Title: Rev. Mex. Cienc. Agríc
ISSN (print): 2007-0934
Publisher: Instituto Nacional de Investigaciones Forestales, Agrícolas y Pecuarias

Article/Issue Information
Date received: 01 March 2026
Date accepted: 01 June 2026
Publication date: 01 July 2026
Publication date: 2026
Volume: 17
Issue: 4
Electronic Location Identifier: e4358
DOI: 10.29312/remexca.v17i4.4358

Categories

Subject: Artículo

Keywords:

Keywords:

leaf area
micropropagated plants
nutrient solution
photosynthesis

Counts

Figures: 2
Tables: 4
Equations: 0
References: 22