Colegio de Postgraduados

# Physiological diversity in native Mexican tomatoes (*Solanum lycopersicum* L.)

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**ABSTRACT**

**Objective**: This study aimed to evaluate the biodiversity in postharvest fruit quality and photosynthetic attributes of eight native tomato varieties compared to commercial hybrids.

**Design/Methodology/Approach**: A randomized complete block design with four replicates and four plants per plot was used to allocate treatments. Statistical analysis was conducted with SAS 9.4 using analysis of variance (ANOVA) and mean comparison of by Tukey ($p \leq 0.05$).

**Results**: Varietal diversity in transpiration rate (E) was detected, but not in net photosynthetic rate (A) nor in water use efficiency (WUE). Variety Oax-131 stood out for its high photosynthetic parameters, such as Amax and its saturation point, as well as by having a carboxylation efficiency similar to the El Cid® hybrid. In terms of fruit postharvest quality, five native varieties had weight losses below the conventional limit of 7%, while the Oax-131 varietey maintained similar fruit firmness to the hybrids during the first 6 days.

**Study Limitations/Implications**: The study was limited to eight native varieties and the diversity measured in gas exchange rates and photosynthetic parameters may not represent all native varieties.

**Findings/Conclusions**: The native Oax-131 variety excelled in photosynthetic traits and postharvest quality, demonstrating equal or superior performance compared to commercial hybrids.

**Keywords**: *Solanum lycopersicum*, native varieties, photosynthetic parameters, postharvest fruit quality.

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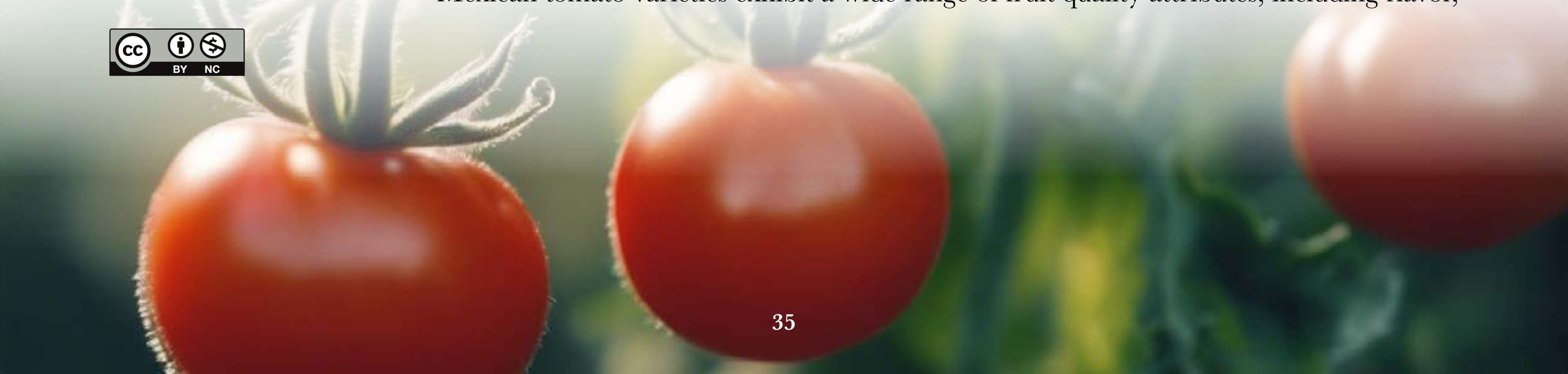
## INTRODUCTION

Tomato (*Solanum lycopersicum* L.) is one of the most important crops worldwide, due to its economic significance and nutritional properties, providing essential vitamins, minerals, and antioxidants (SADER, 2022). In Mexico, approximately 48 thousand hectares are cultivated, with an average yield of 69 t $ha^{-1}$, and a national consumption of 13.4 kg/year per person (SADER, 2020). The predominant tomato types sold in Mexico are saladette (87%) and bola (9%) (SIACON, 2021). However, native tomatoes are cultivated and consumed mainly in local and regional markets, where they are favored for their organoleptic qualities (Parisi *et al.*, 2005) and are integral to many traditional dishes. Native Mexican tomato varieties exhibit a wide range of fruit quality attributes, including flavor,



aroma, color, soluble solids, vitamin C, lycopene and $\beta$-carotene content, which contribute to their digestive, antiseptic, diuretic, and anti-inflammatory properties (Juárez-López *et al.*, 2009; Ceballos-Aguirre *et al.*, 2012; SADER, 2022; Vásquez-Ortiz *et al.*, 2010).

Despite these qualities, there is limited information on the physiological performance and resistance of these native tomatoes in adverse conditions (Martínez-Vázquez *et al.*, 2016). Photosynthesis, a critical physiological process, enables plants to capture inorganic carbon ($CO_2$) and sunlight to produce sugars (Lambers *et al.*, 2008) which feed not only plants but also animals and humans. Photosynthetic and gas exchange studies, including transpiration and water use efficiency (Medrano *et al.*, 2007), may help to identify varieties that are resilient to climate change.

The A/Ci photosynthetic curves relate net photosynthesis rate (A) to increasing concentrations of $CO_2$ within the leaf (Ci), allowing the estimation of essential photosynthetic parameters (Sharkey *et al.*, 2007; Blanco, 2013), such as compensation point (CP), saturation point (SP), the maximum rate of net $CO_2$ assimilation (Amax), and Rubisco enzyme carboxylation efficiency (RE). This type of physiological characterization is used to assess varieties by their photosynthetic capacity, which is the main driver of growth and fruit yield. In this case, the photosynthetic parameters are crucial for promoting the preservation of valuable native varieties.

This study's objective was to characterize eight native varieties in terms of their yield potential and postharvest fruit quality, compared with two commercial hybrids, and to quantify essential physiological characteristics in a subset of two native varieties and one hybrid. The hypothesis is that the characterization will define outstanding native tomato varieties that match or surpass commercial hybrids in postarvest quality and photosynthetic capacity.

## MATERIALS AND METHODS

The study was carried out during the summer-autumn period of 2022, in a plastic greenhouse located at the Colegio de Postgraduados (19° 28' 05" N, 98° 54' 09" W, at an altitude of 2,243 m). Eight native Mexican tomato varieties from five states were evaluated: two from Puebla state (Pue-105, Pue-55), two from Estado de Mexico (Mex-r92, Mex-12), one from Guerrero state (Gro-78), one from Yucatán state (Yuc-63), and two from Oaxaca state (Oax-131, Oax-130). The hybrids El Cid-F1® and Río Grande® were included as commercial controls.

### Experimental management

The seeds from each genotype were germinated in trays and subsequently transplanted into pots, following the protocol outlined by Sandoval (2018). The pots were arranged in double rows, with 25 cm spacing between pots and 50 cm between rows. From this stage onward, irrigation was applied eight times a day with a 100% Steiner nutrient solution at 1 h intervals. The initial daily dosage was 0.2 L per plant, then increasing it every 15 days to a maximum of 1.5 L per plant/day.

The plants were grown with a single stem through periodic prunings of the axillary sprouts and were topped after the seventh cluster. Clusters were thinned to seven or eight fruits. The plants were supported using raffia and hooks to keep them upright. For pest and disease management, the following chemicals were periodically sprayed: Engeo® (1.5 mL $L^{-1}$) to control whiteflies (*Bremisia tabaci*), Mancozeb® (3 g $L^{-1}$) to prevent for blight (*Alternaria* sp.), and Kasumin® (2 mL $L^{-1}$) for preventing bacterial spot.

**Experimental design**

The 10 genotypes were arranged in randomized complete block designs with four replications and four plants per experimental unit. Harvesting was done as the fruits reached the cutting stage (ripe green stage, physiological maturity). Fruit firmness (F) was measured using a manual texturometer (FORCE FIVE®, Model FDV-30LB × 0.01 LB) in newtons (N), and weight loss (WL) was assessed using a digital scale (Noval, TH- I-EK®, China). The fruits were weighed starting at the ripe green stage and monitored until they reached red ripeness, suitable for consumption.

The three photosynthetic variables —net photosynthesis rate (A), stomatal conductance (gs), and transpiration rate (E)— were measured simultaneously on three plants per variety with a portable photosynthesis device (LI-6400®, LICOR, USA). Measurements were taken on the mature leaf of a raceme with full fruit growth, at 92 days after transplating (dat). All measurements were done between 12:00 and 14:00 hours. Water use efficiency (WUE) was calculated by the A/E ratio.

The curves of the photosynthetic rate (A) performance relative to the intercellular concentration of $CO_2$ (Ci), known as A/Ci kinetics, were measured one week later (99 dat) using the apparatus LI-6400® (LICOR, USA). It was equipped with a $CO_2$ dispenser (Model LI-COR P/N 9964-037) and with a mini assimilation chamber designed to measure gas exchange in small leaves —1 $cm^2$ of leaf area— (Model LI-6400XT QUANTUM), suitable for the small tomato leaflets. The system was programmed to record data when the coefficient of variation remained at or below 2% for a few seconds, as the leaf was exposed to the following external $CO_2$ concentrations: 400, 200, 100, 0, 200, 400, 800, 1200, and 1600 ppm, in this order. Since the 1 $cm^2$ mini-chamber lacks the sensors of the standard 6 $cm^2$ chamber, each external $CO_2$ value was adjusted under the assumption that $Ci=0.5\ CO_2$. These kinetics were measured on a young mature leaf from each of three plants in two native varieties (Pue-105 and Oax-131) and in the control hybrid (El Cid®). Each curve lasted 40 to 60 min.

Statistical analyses were performed using the GLM procedure of the Statistical Analysis System software (SAS Institute Inc., version 9.4), for the analysis of variance (ANOVA) for each variable, and for the mean comparisons of varieties with the Tukey test ($p \leq 0.05$).

**RESULTS AND DISCUSSION**

The extensive morphological diversity observed in fruit shapes and sizes among the eight native varieties, is shown in Figure 1.

**Physiological diversity in gas exchange**

A significant diversity ($p \leq 0.05$) was recorded among the studied varieties in transpiration rates (E), with averages ranging from 6.9 to 15.5 mmol $H_2O\ m^{-2}\ s^{-1}$, where

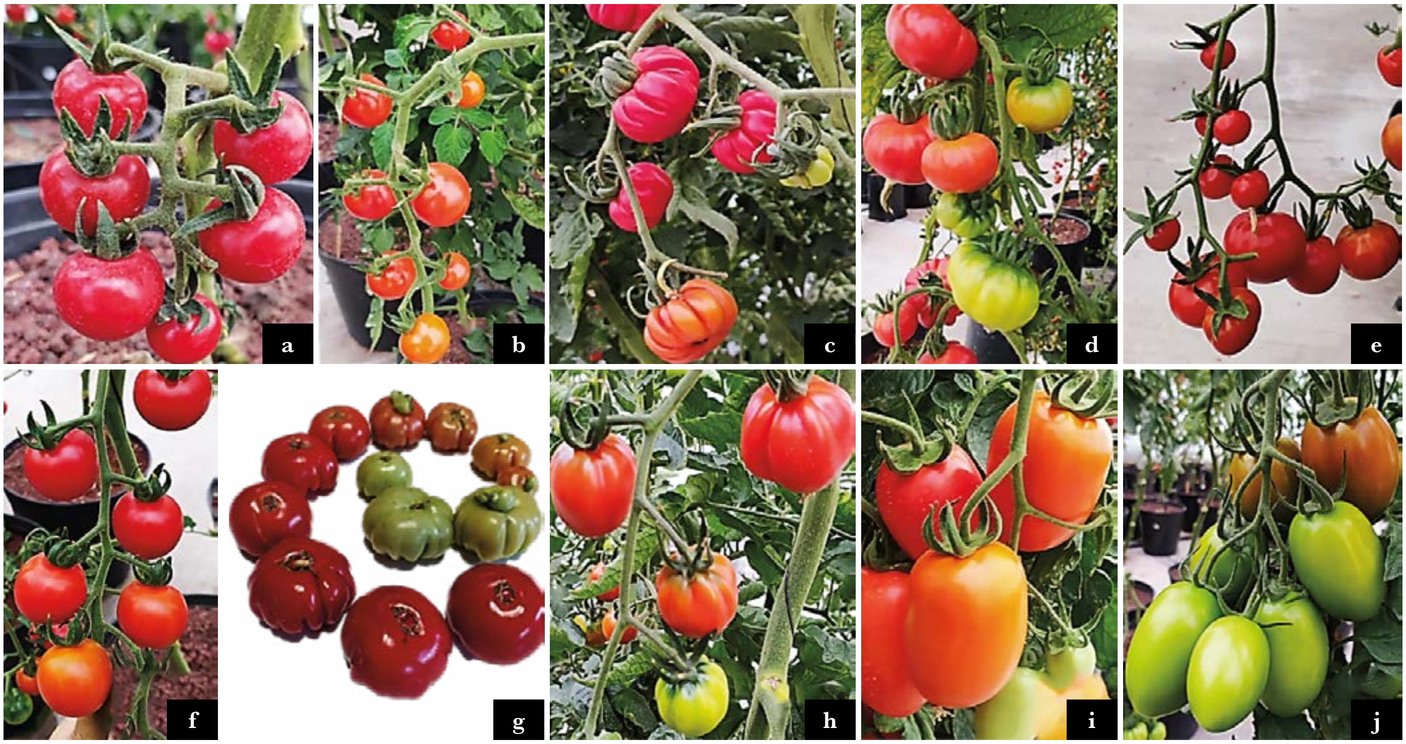



**Figure 1**. Morphological diversity in eight native varieties of tomato (a-h), and two commercial hybrids (i and j). a) Pue-105 (cherry), b) Pue-55 (cherry), c) Oax-130, d) Oax-131 (pumpkin shape), e) Yuc-63 (cherry), f) Mex-12 (cherry), g) Mex-r92 (pumpkin shape), h) Gro-78 (pepper shape), i) Río Grande® (saladette), j) El Cid® (saladette).

the hybrid El Cid® attained the top E rate, but it was was statistically equaled by two native varieties, Oax-130 and Oax-131 (Table 1). A wide varietal diversity was also recorded in the instantaneous net photosynthesis rates (A), ranging from 23.2 to 41.8 $\mu$mol $CO_2$ $m^{-2}$ $s^{-1}$. However, no significant differences were found between varieties probably due to the large heterogeneity observed among the individual plants of the same variety (standard deviations ranged from 6.4 to 18.0% relative to their respective means). The overall average for A was 31.7 $\mu$m $CO_2$ $m^{-2}$ $s^{-1}$, a value comparable to the 34.9 $\mu$mol $CO_2$ $m^{-2}$ $s^{-1}$ reported by Aguiñaga-Bravo *et al.* (2020) in native tomatoes treated with organic fertilizers. Water use efficiency (WUE=A/E) ranged among varieties from 2.8 to 6.0 $\mu$mol $CO_2$ $m^{-2}$ $s^{-1}$/mmol $H_2O$ $mm^{-2}$ $s^{-1}$, with no statistical differences among genotypes. Liang *et al.* (2020) reported lower gas exchange rates in a commercial tomato variety in China, with averages of 6.6 for A, 2 for E, and 3.6 for WUE. In Brazil, Gorni *et al.* (2022) also recorded lower values than ours, with 14 and 2.5 units for A and WUE, respectively.

Although transpiration represents the main water use for plants (Taiz *et al.*, 2023), it also plays a crucial role in cooling the leaves and preventing them from overheating, especially during sunny and warm days (Nobel, 1999). Additionally, stomatal transpiration drives the rise of xylem sap from roots to leaves, thus providing water and minerals to the leaves and stem (Taiz *et al.*, 2023). Therefore, stomata exert primary control over water consumption (Medrano *et al.*, 2007), as reflected in the significant correlation (r=0.52***) between E and WUE, which is twice as strong as the correlation between A and WUE (r=0.23*).

**Table 1**. Mean values of net photosynthetic rate (A), stomatal conductance (gs), transpiration rate (E), and water use efficiency (WUE) in a young mature leaf of each tomato variety.

| Tomato variety | Net photosynthesis rate, A ($\mu$mol $CO_2$ $m^{-2}$ $s^{-1}$) | Stomatal conductance, gs (mol $H_2O$ $m^{-2}$ $s^{-1}$) | Transpiration rate, E (mmol $H_2O$ $m^{-2}$ $s^{-1}$) | Water use efficiency, WUE ($\mu$mol $CO_2$ $m^{-2}$ $s^{-1}$/ mmol $H_2O$ $m^{-2}$ $s^{-1}$) |
|---|---|---|---|---|
| Pue-105 | 25.2±2.1 a | 0.6±0.3 a | 6.9±5.0 c | 6.0±3.0 a |
| Pue-55 | 23.2±2.8 a | 0.7±0.2 a | 9.2±5.0 bc | 2.8±1.5 a |
| Oax-130 | 33.6±3.1 a | 1.0±0.2 a | 14.0±4.9 ab | 2.9±1.2 a |
| Oax-131 | 33.4±3.1 a | 0.8±0.3 a | 12.5±4.7 ab | 3.1±1.5 a |
| Yuc-63 | 28.6±4.8 a | 0.5±0.1 a | 9.4±4.5 bc | 3.4±1.3 a |
| Mex-12 | 34.9±3.9 a | 0.6±0.1 a | 10.5±6.0 abc | 5.6±3.9 a |
| Mex-r92 | 34.4±2.2 a | 0.8±0.2 a | 12.6±5.4 ab | 3.8±1.9 a |
| Gro-78 | 26.6±4.8 a | 0.5±0.2 a | 9.2±4.8 bc | 3.3±1.2 a |
| El Cid® | 41.8±3.2 a | 1.0±0.1 a | 15.5±4.5 a | 2.9±2. a |
| Río Grande® | 35.6±4.9 a | 0.6±0.2 a | 11.5±3.6 abc | 3.4±3.0 a |
| Mean | 31.77 | 0.73 | 11.17 | 3.76 |

Note: The literals in each column represent groupings based in mean separation using the Tukey test ($p \leq 0.05$) conducted for each variable.

### Diversity in $CO_2$ assimilation parameters

The curves of A in response to the intercellular concentration of $CO_2$ (Ci), as illustrated in Figure 2, allow for the estimation of essential parameters of the photosynthetic process, such as the maximum potential rate of $CO_2$ assimilation (Amax); the efficiency of the Rubisco enzyme (RE) in fixing $CO_2$; the compensation point (CP), which represents the minimum concentration of this gaseous input required to get a net photosynthesis rate above zero; and the saturation point (SP) which is the Ci at which Amax is reached.

The photosynthetic kinetics (curves) obtained in three tomato varieties (Figure 2) indicate that these tomatoes reached their maximum A rates (Amax, SP) when the intercellular carbon concentration (Ci) was 800 $\mu$mol/mol (Figure 2 A, C, and D, at a saturation point (SP) of 800, equivalent to 1600 $\mu$mol/mol of $CO_2$ in the outer air, Co). The results suggest that the two native tomato varieties and the control hybrid have the capacity to assimilate the excess of $CO_2$ present in the air. Similarly, Kozai (2016) found that SP fluctuated between 1000 and 1500 ppm in mature tomato leaves. Therefore, it would be possible that other native Mexican tomatoes could achieve even higher Amax and SP values.

The native variety Oax-131 is particularly noteworthy, with an Amax of 70 $\mu$mol $m^{-2}$ $s^{-1}$ (Figure 2 C) which surpasses the commercial hybrid El Cid® by 21% in $CO_2$ assimilation rate under high concentrations of this gas. Variety Oax-131 also exhibits a compensation point (CP) of 128 $\mu$mol/mol (ppm) (Figure 2 D), nearly as low as the control hybrid, whose CP is 118 ppm (Figure 2 F). The CP represents the minimum concentration of $CO_2$ required for tomato leaves to achieve a net carbon gain.

These finding also show that the CP of tomato is higher than in other C3 plants, in which the reported CP values range from 50 to 100 ppm (Taiz *et al.*, 2023). Regarding the efficiency of the Rubisco enzyme (RE in Figure 2) that catalyzes $CO_2$ assimilation, the Oax-131 variety (Figure 2D) nearly matched the efficiency of the El Cid® hybrid (Figure 2

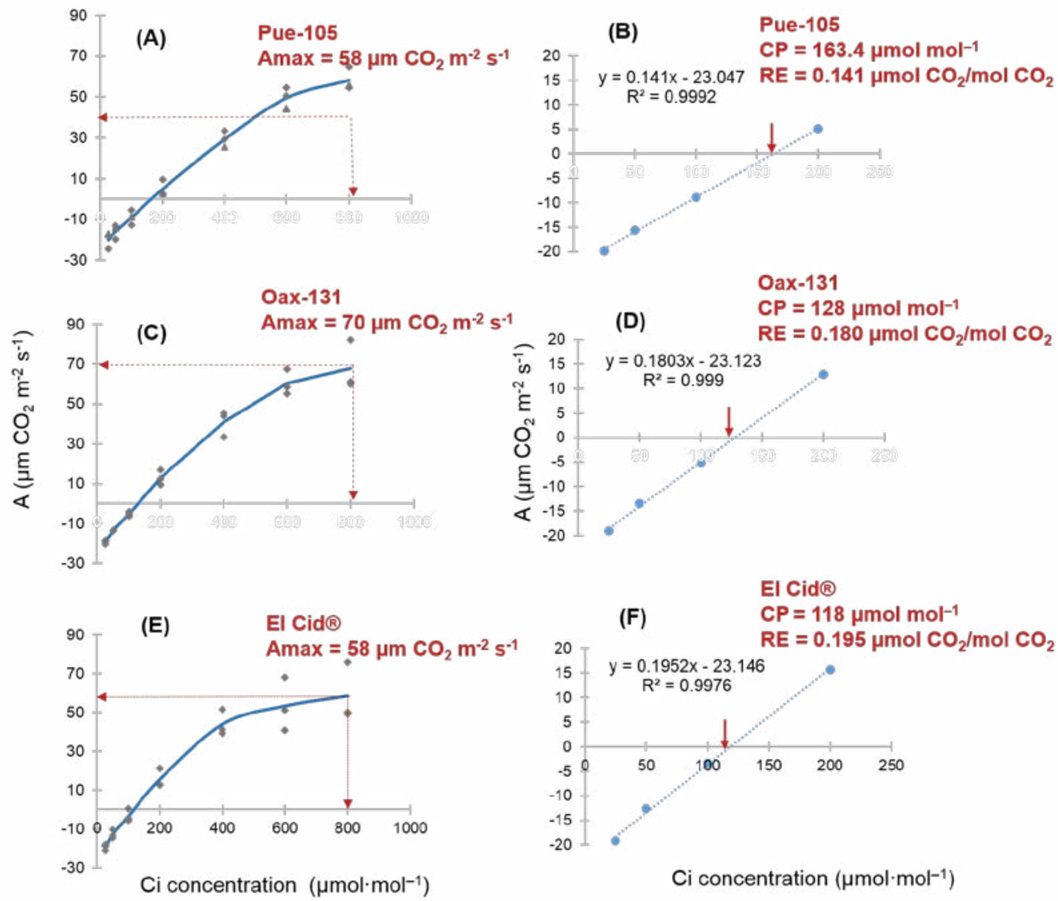



**Figure 2**. Curves of net photosynthetic rates (A) of tomato leaves in response to intercellular $CO_2$ concentration (Ci, in $\mu$mol mol$^{-1}$) of two native varieties (Pue-105, A and B; Oax-131, C and D), compared to the commercial hybrid El Cid® (E and F). Measurements were done at 99 days after transplant, during fruit growth. The arrows in (A), (C), and (E) indicate the values of Amax (maximum A, in $\mu$mol $CO_2$ m$^{-2}$ s$^{-1}$), and their corresponding saturation points for $CO_2$ concentration (Ci, in $\mu$mol mol$^{-1}$). Arrows in (B), (D), and (F) mark the compensation points (CP, in $\mu$mol mol$^{-1}$ of Ci), and their Rubisco efficiencies (RE, in mmol mol$^{-1}$ of Ci).

F), with values of 180 *vs.* 195 $\mu$mol CO2 m$^{-2}$ s$^{-1}$ respectively. In the current atmospheric air (420 ppm of $CO_2$, Co, equivalent to about 210 ppm Ci), both this hybrid and Oax-131 achieved an instantaneous photosynthesis rate (A) of 20 $\mu$mol $CO_2$ m$^{-2}$ s$^{-1}$, which is similar to the averaged rate for C3 plants.

## Diversity in postharvest quality of the fruit

Among the most important quality traits of harvested fruits are shelf-life length, fruit firmness (FF) maintenance, and minimal weight losses (WL). In all the varieties studied here, the firmness (F) monitored from physiological maturity (harvest) to consumption maturity (12 days later), decreased faster during the first 6 to 8 days of ripening (Figure 3). However, there were notorious differences among varieties on initial firmness and on the rate of firmness loss. The two hybrids evaluated here outperformed all the native varieties in F. But among the native varieties, Oax-130 and Oax-131, with kidney-shaped and pumpkin-type fruits, stood out for having the highest initial firmness (7.95 and 9.03 N

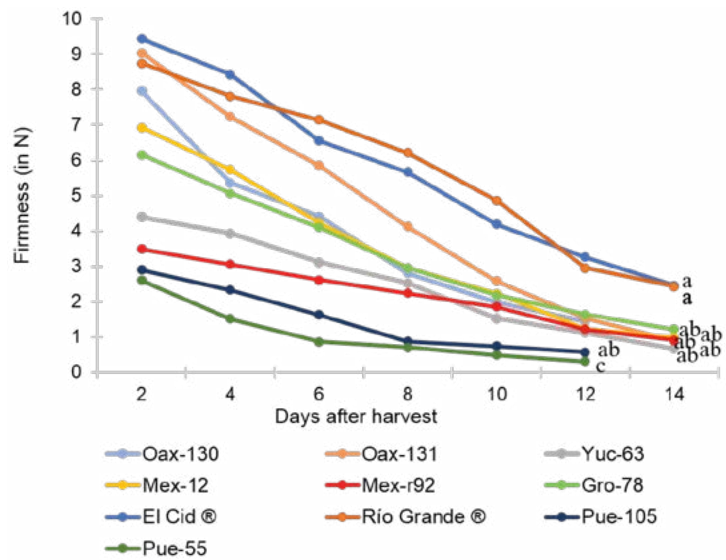



**Figure 3**. Loss of fruit firmness (in N) monitored after harvest in eight native tomatoes varieties and two commercial hybrids, from two days after the harvest day (at physiological maturity, green fruits) to the day when fruits reached consumption maturity (full red color). Varieties marked with the same letter are not statistically different (Tukey, 0.05; LSD=0.9).

respectively), which was close to the control hybrids (8.74 and 9.43 N). For native tomatoes from Spain, Pérez-Díaz *et al.* (2020) reported lower F values, ranging from 0.58 to 3.77 N on day 0, which further decreased to 0.34 and 0.93 N by day 14.

Fruit weight losses (WL) are attributed to water losses through the peduncle (Bouzo and Gariglio, 2016). On this regard, the WL of native varieties for 14 days, ranged from 5.2 to 10.4% of the initial weight (Figure 4), except for variety Gro-78 whose WL (3.5%) was statistically similar ($p \leq 0.05$) to that of the two commercial hybrids (3.3 and 3.9%). In contrast, other native varieties with cherry-type fruits showed higher WL (Yuc-63, Pue-

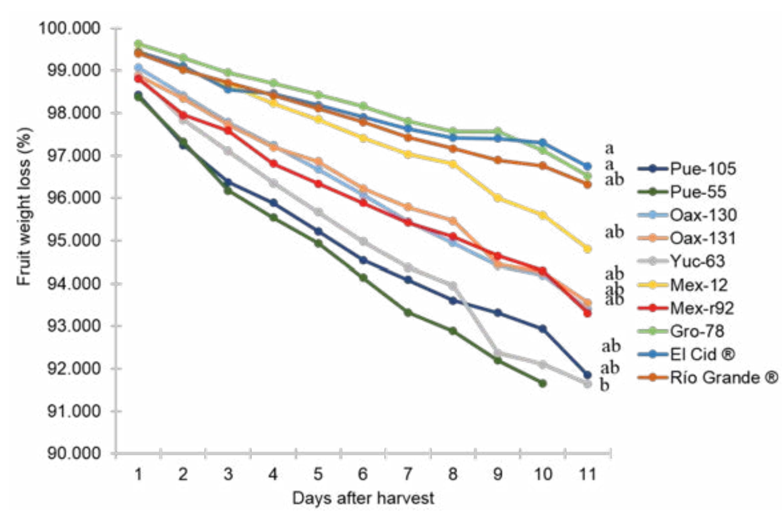



**Figure 4**. Weight loss (%) of fruit in eight native varieties and two commercial hybrids, measured from the harvest day (physiological maturity, green fruits) until reaching consumer maturity (full red color), in days after harvest. Varieties marked with the same letter are not statistically different (Tukey, 0.05; LSD = 0.9).

105, and Pue-55, with WL of 10.4, 8.2, and 7.9 %, respectively). According to Bouzo and Gariglio (2016), small fruits tend to lose more weight because they have a larger ratio of fruit area/volume, possibly due to a thinner and more permeable epidermis. Ballesteros (1995) noted that a WL of 7% significantly lowers the quality and nutritional value of the tomato fruits, giving them a withered appearance.

## CONCLUSIONS

Among the eight native Mexican tomatoes varieties evaluated here, Oax-131 stood out for its exceptional physiological traits, including its photosynthetic metabolism with enhanced $CO_2$ capture capacity and high carboxylation efficiency (*i.e.*, Rubisco efficiency), compared to the best hybrid control. Additionally, this native variety has a rather low fruit weight loss during postharvest as well as a high water use efficiency, achieving levels comparable to those of the top-performing control.

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