

# Eco-physiological attributes of *Physalis philadelphica*, *Physalis angulata* and *Physalis pubescens* in the Valley of Mexico

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**Abstract:** The processes and mechanisms that determine the growth and yield of crops in different environments are necessary to increase agricultural production, since they guide us in the choice of the most appropriate management practices. The aim of the study was to evaluate, during the years 2018, 2019, 2020, the performance of *Physalis philadelphica*, *Physalis angulata* and *Physalis pubescens* as a function of leaf area index, light extinction coefficient and radiation use efficiency. Research was carried out at the Center of Research and Advanced Studies of the Autonomous University of the State of Mexico. Results revealed that the environmental conditions of 2018 positively influenced the expression of leaf area index and radiation use efficiency, increasing the average production of *Physalis* sp. (10.65 t/ha) compared to 2019 (9.67 t/ha) and 2020 (8.13 t/ha). *P. philadelphica* produced the greatest amount of fruit (16.69 t/ha), followed by *P. angulata* (10.46 t/ha) and *P. pubescens* (1.33 t/ha). Genotype × environment interaction in 2018 stimulated the expression of the eco-physiological attributes of *P. philadelphica*, achieving a yield of 18.83 t/ha.

**Keywords:** husk tomato; leaf area index; light extinction coefficient; intercepted radiation

*Physalis* is a genus that produces edible fruits known as green tomato, husk tomato, and mil-tomate. In America, some husk tomato species have economic and cultural importance for several ethnic groups (Kindscher et al. 2021). Their fruits have been used as food since pre-Hispanic times, and the flavour varies between species from acid to sweet, and acid fruits are a main ingredient in traditional Mesoamerican cuisine (Kindscher et al. 2021). It is one of the main vegetables in Mexico, and its production is destined for the national and export markets (Camposeco

et al. 2020). It prefers soils with a clay texture with a pH range of 5.0 to 6.8, a temperature of 18 to 25 °C, an altitude of 0 to 2 500 meters above sea level (m a.s.l.), and rainfall of 600 to 1 200 mm. Its fruits have bioactive compounds, phenols, and antioxidants, so their consumption may prevent diseases (Grigolo et al. 2021).

In 2017, 42 639 ha of *P. philadelphica* were planted in the Mexican Republic under rainfed conditions with an average yield of 16.4 t/ha. This yield is considered low since, under experimental conditions, up to 47 t/ha have been obtained

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(Peña et al. 2014). Research by Camposeco et al. (2020) showed that low yields are due to poor agronomic management, limited use of improved varieties and an unfavourable environment. Peña et al. (2014) revealed that the cultivar ‘Rendidora’ (*P. philadelphica*) is sensitive to climatic changes, so its yield potential is modified by environmental and edaphic factors. It is an early, high-yielding genotype and is mainly distributed in the highlands of Mexico.

*P. angulata* and *P. pubescens* species are cultivated incipiently in some areas of the country (Ordoñez et al. 2022). *P. angulata* has neither morphological nor physiological differences between wild and cultivated species since their fruits are very small (1–1.5 cm in diameter), with an enjoyable flavour and a good sales price (Goecke et al. 2020). In addition, the substances found in its extract are used as an inhibitor of cancer cells (Anh et al. 2021). *P. pubescens* is an annual plant with a stem and branches covered in trichomes. It is a shrub with an average height of 30 cm, which can reach up to 1.5 m, and is considered a weed (Cheng et al. 2022). It has aromatic fruits with a pleasant flavour and is collected in various locations across Mexico (Valdivia et al. 2016). Berries have vitamins A and C, phosphorus, iron, proteins, carotene, sugars, and organic acids, and are a source of nutraceutical compounds. Due to its functional qualities, its intake has spread throughout the country, mainly in western Mexico (Mirzaee et al. 2019).

According to the studies of Garcia et al. (2023), genotype, environment, and their interaction are determinants in husk tomato production since the fruit yield is influenced by the environmental factors of the region where it is grown. The light absorbed, radiation use efficiency, and crop cycle duration determine berry production (Chapepa et al. 2020). The interception of solar radiation by the canopy is linked to the leaf area index (LAI) and the arrangement of the leaves. LAI measures the leaf surface that controls photosynthesis and respiration, while the intercepted radiation (IR) is a function of the light extinction coefficient ( $k$ ), which indicates how light is extinguished within the canopy (De Oliveira et al. 2019).

In optimal environments, biomass is positively correlated with the amount of radiation absorbed by the plant cover (Chavez et al. 2022). Intercepted photosynthetically active radiation (iPAR) is transformed into fresh or dry matter, so the slope

of the linear relation between the two variables constitutes the radiation use efficiency (RUE) and is expressed in g/MJ (Sinclair, Muchow 1999). LAI,  $k$ , and RUE are eco-physiological attributes that determine crop production; iPAR is linked to LAI and  $k$ , so growth and production are related to the amount of leaf area needed to intercept solar radiation (SR) and convert it into fresh matter (Saleh et al. 2022). The aim of the research was to evaluate the fruit yield of *P. philadelphica*, *P. angulata*, and *P. pubescens* as a function of leaf area index, light extinction coefficient, and efficiency in the use of radiation during the years 2018, 2019, and 2020 in the central highlands of Mexico.

## MATERIAL AND METHODS

**Experimental site and period.** Research was carried out during the summers of 2018, 2019, and 2020 at the Center of Research and Advanced Studies in Plant Breeding of the Autonomous University of the State of Mexico. The site is located at 19°99'N and 99°59'W, at 2 600 m a.s.l. Temperature and rainfall data were recorded from the meteorological station in Cerrillo, Mexico.

**Plant material and genotypes.** Genotypes used were *P. philadelphica* ‘Rendidora’, which has a determined, precocious growth habit, with high production potential (20 t/ha) and adapts to different climatic and soil conditions in Mexico. *P. angulata* is an herbaceous, annual, erect, and branched native plant with angular stems and an average yield of 4 t/ha. *P. pubescens* is an herbaceous, shrubby, annual genotype; its leaves have toothed edges and trichomes, and it has not been subjected to domestication. It is produced in small areas, and its yield is 1.8 t/ha. Both native species are found naturally in the regions of Jalisco and Michoacán, Mexico (Table 1).

**Experimental management.** In each agricultural cycle, the following activities were carried out: husk tomato seed was sown in 200-cavity polystyrene trays filled with compost as a substrate. Soil preparation included fallow and harrowing. Seedlings were transplanted during the first week of May each year, when they had developed two fully expanded leaves. Fertilisation was applied at a rate of 120 : 80 : 120 (N : P : K) : 80 : 80 : 80 units at transplanting and 40 : 00 : 40 units at fruit set, using urea, triple superphosphate, and potassium chloride as nutrient sources. Weed control was

Table 1. Geographic location of *Physalis angulata* and *Physalis pubescens* accessions in Mexico

Species	Code	Location	Altitude (m a.s.l.)	North latitude	West longitude
<i>P. angulata</i>	AngC	Ocotic, Jalisco	1 854	20°59'	103°02'
	PM	Maravatío, Michoacán	2 036	19°51'	100°27'
<i>P. pubescens</i>	PC	Palos Altos, Jalisco	1 928	21°01'	103°08'
	PZ	Tepopote, Jalisco	1 610	20°43'	103°34'

carried out manually with a hoe, and no pests or diseases were observed.

**Treatments and study factors.** There were two study factors: climatic variability in the years 2018, 2019, and 2020, and growth and yield performance of genotypes *P. philadelphica* 'Rendidora', *P. angulata*, and *P. pubescens*, resulting in nine treatments (Table 2).

The experimental plot consisted of four rows, each 10 m in length, spaced 1 m apart. Plant spacing within rows was consistent across treatments. Each year, the experiment comprised three treatments with four replications.

**Evaluated variables.** Leaf area index was determined at the beginning of flowering using a Li-Cor area meter (LI-3100, Li-Cor Environmental, USA). It was calculated by multiplying the total leaf area by plant density and dividing by the sown area.

$$\text{Leaf area index} = \frac{\text{leaf area} \times \text{plant density}}{\text{sown area}} \quad (1)$$

The light extinction coefficient ( $k$ ) was calculated using the natural logarithm (nl), transmitted photosynthetically active radiation (tPAR), intercepted photosynthetically active radiation (iPAR), and leaf area index (LAI).

$$k = \frac{-\ln(\text{tPAR}/\text{iPAR})}{\text{LAI}} \quad (2)$$

Fruit yield (Y): Four harvests were carried out at 10-day intervals per treatment. Fruits were weighed, and yield was expressed in t/ha.

Radiation use efficiency (RUE) was calculated as the quotient between crop yield and photosynthetically active radiation intercepted (iPAR) and was expressed in g/MJ.

Incident radiation (IR) was measured at noon with an LP-80 Ceptometer (Producer, Country). Intercepted radiation (InR) was calculated from the difference between radiation at the top of the canopy (IRo) and at the lower stratum (IR).

$$\text{InR} = (\text{IRo} - \text{IR}) \times 100 \quad (3)$$

**Experimental design and statistical analysis.** Data was taken from each plot by randomly choosing five plants. A randomised complete block design was used across years. Analysis of variance was performed at two levels of significance ( $P < 0.05$  and  $P < 0.01$ ). When  $F$  values were significant, treatment means were compared using Tukey's honestly significant difference (HSD) test ( $P < 0.01$ ). Statistical analyses were performed with SAS software (version 8.02).

Table 2. Combination of three genotypes of husk tomato evaluated in three environments

Treatment	Combination	Year	Description
T1	a <sub>1</sub> b <sub>1</sub>	2018	<i>Physalis philadelphica</i> cv. 'Rendidora'
T2	a <sub>1</sub> b <sub>2</sub>		<i>P. angulata</i>
T3	a <sub>1</sub> b <sub>3</sub>		<i>P. pubescens</i>
T4	a <sub>2</sub> b <sub>1</sub>	2019	<i>P. philadelphica</i> cv. 'Rendidora'
T5	a <sub>2</sub> b <sub>2</sub>		<i>P. angulata</i>
T6	a <sub>2</sub> b <sub>3</sub>		<i>P. pubescens</i>
T7	a <sub>3</sub> b <sub>1</sub>	2020	<i>P. philadelphica</i> cv. 'Rendidora'
T8	a <sub>3</sub> b <sub>2</sub>		<i>P. angulata</i>
T9	a <sub>3</sub> b <sub>3</sub>		<i>P. pubescens</i>

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## RESULTS AND DISCUSSION

**Climatic variability among study years.** Average temperatures in 2018, 2019, and 2020 were 17.1 °C, 16.2 °C, and 16.4 °C, respectively. September in 2018 and 2020 was the month with the least heat, while in 2019 it was August (Figure 1). The temperature in the three growing seasons was maintained within the range where the husk tomato thrives since the interval for its growth and development is from 13 °C to 25 °C. Rainfall in 2018 was 640.9 mm (198 mm at the vegetative stage and 442.9 mm at the reproductive period); in 2019, it was 552.1 mm (153.7 mm at vegetative growth and the rest at flowering). In 2020, it was 523.7 mm (202.7) in the vegetative phase and 321 mm in the reproductive period. The rainfall in 2018 exceeded that in 2019 and 2020 by 13.9% and 18.3%, respectively (Figure 1). The rainfall was decisive for the fruit yield in 2018 to be higher in the two subsequent growing seasons. Ordoñez et al. (2022) reported that eco-physiological attributes are enhanced when rainfall is adequately distributed during crop growth. In this sense, native species of husk tomato thrive at elevations between 2 000 and 2 650 m a.s.l. Furthermore, as *P. angulata* is a synanthropic plant, it adapted to the cool temperatures of the region and became habituated to the environmental conditions of each growing season (Lopez-Sandioval et al. 2015). The *pubescens* species grew and developed well in the cold climate of the central highlands of Mexico (Valdivia et al. 2016).

Illumination fluctuated from year to year due to changes in the intensity of incident radiation (IR). IR and iPAR in each growing season are presented in Figure 2. The mean IR in 2018 was 18.6 and 17.8 MJ/m<sup>2</sup> in 2019, and 17.6 MJ/m<sup>2</sup> in 2020, while the mean iPAR was 8.4 MJ/m<sup>2</sup> in 2018, 8.16 MJ/m<sup>2</sup> in 2019, and 7.94 MJ/m<sup>2</sup> in 2020. During 2018, accumulated IR and iPAR values were 93 and 42 MJ/m<sup>2</sup>, respectively; in 2019, they were 89 and 40.8 MJ/m<sup>2</sup>, and in 2020, the values were 88 and 39.7 MJ/m<sup>2</sup>. Ordoñez et al. (2022) confirmed that fruit production depends on the intercepted radiation, the plant cover, and the use of radiation. This efficiency is influenced by solar radiation, LAI, plant architecture, respiration, and the nutrition of the plant. This is summarised in internal growth factors related to the genotype and external factors related to the environment and the management practices used during the growing process (Xu et al. 2021). In 2018, the lighting and iPAR conditions led to the highest yield of husk tomato fruit.

**Growth and yield performance of genotypes.** Leaf area index of *P. philadelphica* was 2.1; this parameter is used to evaluate the performance of genotypes in contrasting environments (Campos et al. 2016). Table 3 shows that the value of this indicator influenced the fruit yield of *P. philadelphica* since it obtained 10% more compared to the one reported by Ordoñez et al. (2022). LAI and fruit yield values of *angulata* species were 1.34 and 10.46 t/ha, respectively; these data were 43.3% and 44.9% higher than those reported by Morales

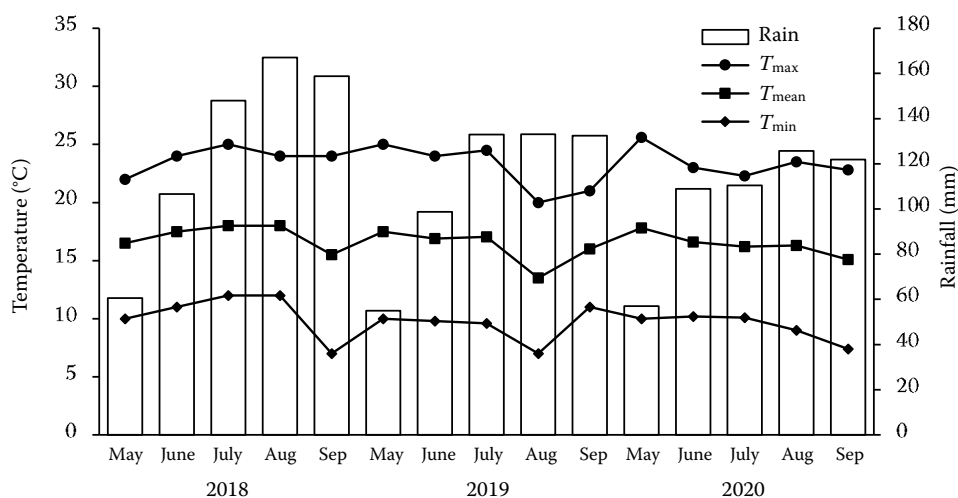


Figure 1. Maximum, medium, minimum temperature, and rainfall in the growth seasons during 2018, 2019, 2020

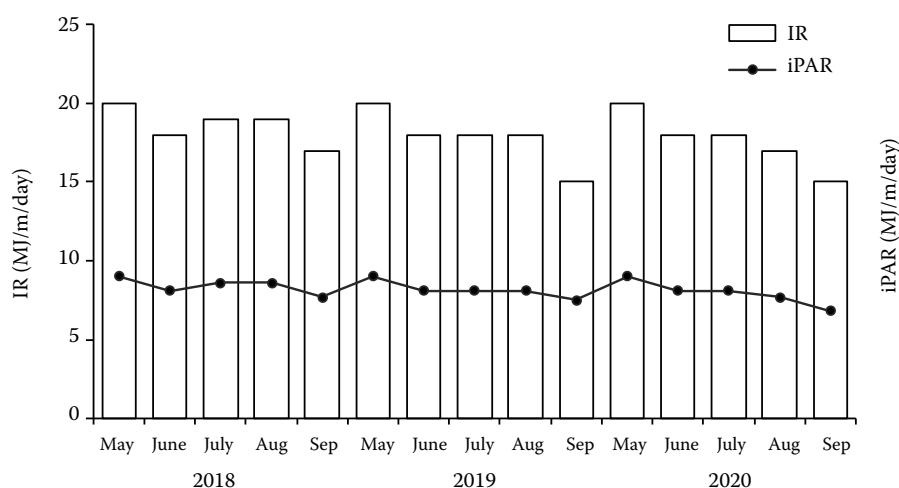


Figure 2. Incident radiation and photosynthetically active radiation intercepted during the 2018, 2019, and 2020 growing seasons

IR – incident radiation; iPAR – intercepted photosynthetically active radiation

Rosales et al. (2022). In *P. pubescens*, LAI was 1.06, which is a relevant result since currently no values for this variable are reported in the literature. The light extinction coefficient of *P. philadelphica* was 0.41, meaning that 41% of the solar radiation remained in the first stratum of the plant, and 59% was “extinct” in the middle and lower layers of the plant, being properly distributed. A similar light extinction coefficient was observed in winter wheat (0.36), maize (0.46), and soybean (0.48)

(Oconnell et al. 2004). On the contrary, *k* values of *P. angulata* (0.63) and *P. pubescens* (0.66) were higher than cultivars of *Solanum tuberosum* ‘Kufri Surya’ (0.59), ‘Kufri Chandramukhi’ (0.59), and ‘Kufri Jyoti’ (0.57). Therefore, the percentage of light extinction inside the crop was lower, reducing photosynthetic activity in the lower strata of both species (Samanta et al. 2020). The *k* values of native genotypes are due to the lack of domestication and null breeding (Morales et al. 2019). In this

Table 3. Effect of genotype and environment on *Physalis* spp. eco-physiological attributes

Factor	LAI	<i>k</i>	RUE (g/MJ)	Y (t/ha)
<b>Environment (E)</b>				
2018	1.61 <sup>A</sup>	0.56 <sup>A</sup>	1.4 <sup>A</sup>	10.65 <sup>A</sup>
2019	1.46 <sup>B</sup>	0.56 <sup>A</sup>	1.3 <sup>A</sup>	9.67 <sup>B</sup>
2020	1.35 <sup>C</sup>	0.57 <sup>A</sup>	1.1 <sup>B</sup>	8.13 <sup>C</sup>
HSD <sub>01</sub>	**	ns	**	**
<b>Genotype (G)</b>				
<i>P. philadelphica</i> cv ‘Rendidora’	2.01 <sup>A</sup>	0.41 <sup>A</sup>	2.21 <sup>A</sup>	16.69 <sup>A</sup>
<i>P. angulate</i>	1.34 <sup>B</sup>	0.63 <sup>B</sup>	1.41 <sup>B</sup>	10.46 <sup>B</sup>
<i>P. pubescens</i>	1.06 <sup>C</sup>	0.66 <sup>C</sup>	0.17 <sup>C</sup>	1.33 <sup>C</sup>
HSD <sub>01</sub>	**	**	**	**
<b>Interaction (G × E)</b>				
HSD <sub>01</sub>	**	**	**	**

LAI – leaf area index; *k* – light extinction coefficient; RUE – radiation use efficiency; Y – yield; data are the average of six plants and four repetitions; different letters within each column for each study factor indicate significant differences according to honestly significant difference (HSD<sub>01</sub>); statistical differences at \*\*, \**P* ≤ 0.01, 0.05; ns; no statistical difference

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sense, genetic improvement should focus on the leaf angle of insertion into the stem. The radiation use efficiency of *P. philadelphica* (2.2 g/MJ) was higher than that of *P. angulata* (1.41 g/MJ) and *P. pubescens* (0.17 g/MJ). The photosynthetic efficiency of *P. philadelphica* allowed it to assimilate more carbon and increase its fruit yield (Bonelli, Andrade 2020). According to Lacasa et al. (2021), fruit production depends on the capacity of the canopy to capture incident radiation, leaf area index, transmissivity of light, and radiation use efficiency. Rustic species of *Physalis*, due to their adaptation to diverse ecological conditions and their simple agricultural management, have the potential to be exploited as horticultural crops (Morales Rosales et al. 2022). Agronomic management of *P. angulata* in the highlands of Mexico is possible since berry production was 10.46 t/ha (Table 3), a similar amount to the cultivars ‘Konditer’ (11.3 t/ha) and ‘Konditer 2’ (11.0 t/ha) in Ukraine (Golubkina et al. 2018). Lopez et al. (2015) carried out two experiments on *P. angulata* in the Mexican localities of Texcoco (2 250 m a.s.l.) and Tlalquiltenango (911 m a.s.l.), finding that the average production was 6.1 t/ha, a quantity 47% lower than the obtained in this investigation. They concluded that the lower yield of the *angulata* species was due to the higher environmental temperature of Tlalquiltenango (30 °C).

Fruit production of *P. pubescens* was 1.33 t/ha, the same as cv. ‘Zolotaya’ (Golubkina et al. 2018), which suggests that *P. pubescens* through genetic improvement, is a promising species to establish as a crop in high valleys since it has agronomic potential and a good sale price due to its content of chemical compounds that are used in the

medical area (Valdivia et al. 2016). In summary, *P. angulata* and *P. pubescens* are an alternative for small producers in the Valley of Mexico since their agronomic management is similar to that of *P. philadelphica* (Ordoñez et al. 2022).

**Genotype × climate interaction.** Márquez et al. (2020) reported that the genotype × environment interaction highlights the importance of the environmental effect on adaptation and varietal behaviour. Gadise et al. (2019) indicated that the interaction involves agro-ecological conditions with the physiological and genetic factors that determine the growth and development of plants. When changing the environment from one year to the next, the eco-physiological variables had a different response depending on the genotypes (Alcala et al. 2021). Genotype × environment interaction was significant in LAI (Figure 3) and light extinction coefficient (Figure 4). During the 2018 agricultural cycle, *P. philadelphica*, *P. angulata*, and *P. pubescens* recorded outstanding LAI values compared to 2019 and 2020. LAI of *P. philadelphica* (2.2) in 2018 coincided with the results obtained by Morales Rosales et al. (2022). When evaluating different species of husk tomato, *P. philadelphica* had a LAI of 2.1, so it captured more solar radiation, increasing its photosynthetic activity and yield. In this sense, LAI imposes control on photosynthesis and respiration, increasing fruit production (Prabhugouda et al. 2018).

Light extinction coefficient ( $k$ ) describes the efficiency of radiation use and is inversely related to the light that reaches the lower layers of the canopy (Rahemi et al. 2021). Vegetative covers allow greater light transmission at a specific LAI and consequently a different value of  $k$ , which

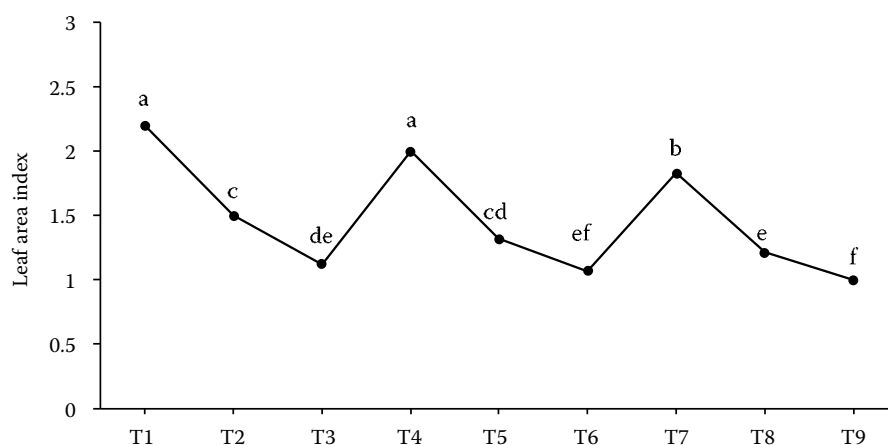


Figure 3. Genotype × environment interaction on leaf area index

T – treatment; line with the same letter do not differ statistically from each other ( $P \leq 0.05$ )

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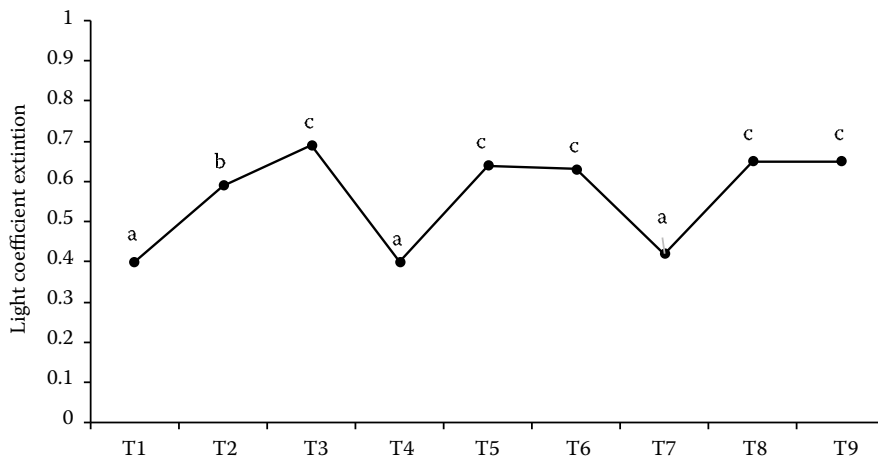


Figure 4. Genotype × environment interaction on light extinction coefficient

T – treatment; line with the same letter do not differ statistically from each other ( $P < 0.05$ )

implies that the relative rates of LAI and iPAR indices influence the value of  $k$  (Kukal, Irmak 2020).

The values of  $k$  in the *philadelphica* species were 0.40 (T1), 0.40 (T4), and 0.42 (T7), so the light distribution inside the crop was equal. In contrast, the mean  $k$  values of *P. angulata* and *P. pubescens* were (0.63) and (0.66), respectively, so that the *philadelphica* species captured a higher percentage of light in the upper stratum of the canopy, attenuating less in the middle and lower strata of the plants. (Figure 4); this being negative, since according to Chapepa et al. (2020), when the availability of light within the upper stratum of the plant cover is higher with respect to the middle and lower parts of the crop, the global photosynthetic rate and biomass accumulation decrease. On the contrary, the low  $k$  values in the upper stratum of *P. philadelphica* allowed a better distribution of light, since being a genotype subjected to genetic improvement, its architecture facilitated

the diffusion of light into the interior of the plant. Meanwhile, the planophilous arrangement of the leaves on the stem of wild plants is not adequate, and the greatest amount of solar radiation was captured by the upper stratum of the crop (Chapepa et al. 2020).

RUE in *P. philadelphica* ranged from 2.5 g/MJ (T1) to 1.8 g/MJ (T7); in *P. angulata*, it fluctuated between 1.4 g/MJ (T5) and 1.2 g/MJ (T8); and in *P. pubescens*, it was in a range from 0.29 g/MJ (T3) to 0.17 g/MJ (T6) (Figure 5). In the three years, *P. philadelphica* had a higher RUE than *P. angulata* and *P. pubescens*, which is attributed to the difference in the canopy morphology of the species. Chapepa et al. 2020 point out that in cotton (*Gossypium hirsutum* L.), there are two types of canopies, one open and the other closed, which are related to the shape and structure of the leaves. These differences in canopy affect the interception of light, RUE, and fibre production. Caval-

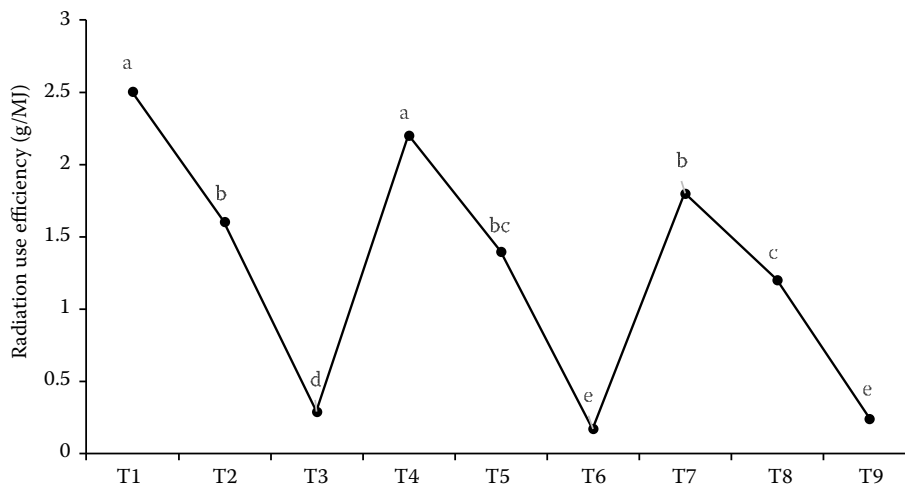


Figure 5. Genotype × environment interaction on radiation use efficiency

T – treatment; line with the same letter do not differ statistically from each other ( $P < 0.05$ )

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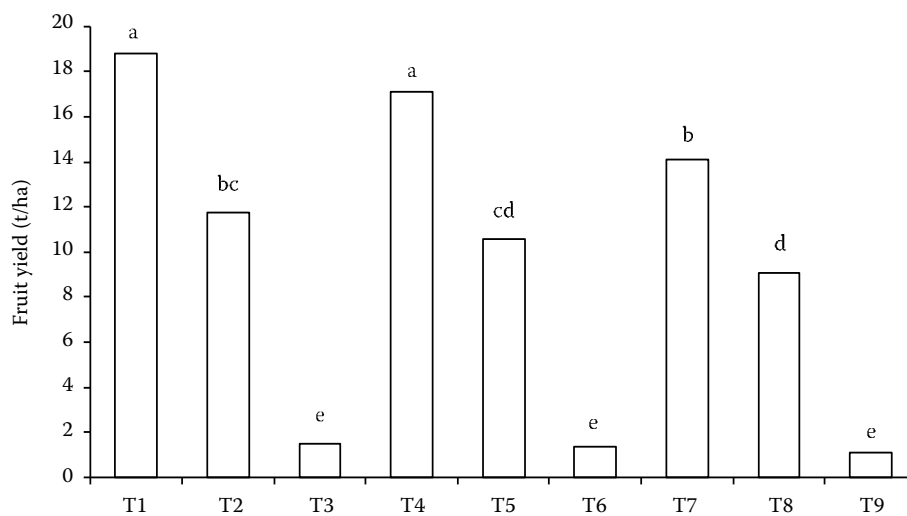


Figure 6. Genotype × environment interaction in fruit yield T – treatment; bars with the same letter do not differ statistically from each other ( $P < 0.05$ )

cante et al. (2019) confirmed that RUE is positively correlated with the yield of okra (*Abelmoschus esculentus*) ‘Valencia’ and that plant growth and productivity under field conditions depend mainly on the potential of the canopy to intercept incoming incident radiation and on the efficiency of genotypes in using radiation to convert it into biomass (Prabhugouda et al. 2018).

*P. angulata*, T8 (9.1 t/ha) had lower production compared to T5 (10.56 t/ha) and T2 (11.73 t/ha), which coincides with Naumova et al. (2019), who confirm that the environment is a limiting factor in the development of husk tomatoes. *P. pubescens* (T3, T6, and T9) maintained consistent values in the three years, which implies that environmental conditions do not affect this species (Figure 6). Genotype × environment interaction confirmed that PAR is a function of location, year, sowing date, and crop phenology, while the fraction of iPAR is related to LAI. Sadras et al. (2017) concluded that crop yield can be expressed as the amount of radiation intercepted by the LAI,  $k$ , and the RUE.

## CONCLUSION

Leaf area index, light extinction coefficient, and radiation use efficiency increased the fruit yield of the *Physalis* species. The greater production of the *P. philadelphica* was due to the better expression of its eco-physiological attributes. The native genotypes *P. angulata* and *P. pubescens* responded well to the conditions of the Toluca Valley, and their production was good. Under the agro-climatic conditions in 2018, *Physalis philadelphica* had its greatest fruit yield.

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