

# Review on the ecophysiology of important Andean fruits: *Passiflora* L.

Revisión sobre la ecofisiología de frutos andinos importantes: *Passiflora* L.

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## ABSTRACT

### Keywords:

Altitude  
Banana passion fruit  
Purple passion fruit  
Solar radiation  
Sweet granadilla  
Temperature  
Yellow passion fruit

The development of Andean fruit crops is viewed as an important and healthy contribution to global food consumption but ecophysiological studies on these fruit trees are scarce. 96% of approximately 520 *Passiflora* L. species are distributed in the Americas, especially in Colombia and Brazil. Many of these species originated on the edges of humid forests in tropical valleys. The four species: yellow passion fruit (*Passiflora edulis* f. *flavicarpa* Degener), sweet granadilla (*Passiflora ligularis* Juss.), purple passion fruit (*Passiflora edulis* f. *edulis* Sims) and banana passion fruit (*Passiflora tripartita* var. *mollissima* (Kunth) Holm-Nielsen & P.M. Jørg) are widely cultivated in Colombia, and their ecophysiological findings are described in this review. The demands, in terms of temperature (°C) and altitude (masl) are, for yellow passion fruits: 15-28 °C and 0-1,300 masl; sweet granadillas: 15-23 °C and 1,800-2,600 masl; purple passion fruits: 15-22/12-14 °C (day/night) and 1,600-2,300 masl; and banana passion fruit: 13-16 °C and 1,800-3,200 masl; all of them have high requirements for solar radiation, a minimum of 7 h of sunshine per day, to encourage flowering and fruit quality. Cloudy days decrease growth, flower bud induction and flower opening. Temperature and photosynthetic active radiation are the climatic factors that have the greatest effect on plant development. Relative humidity between 60 and 80% supports effective pollination and fecundation. *Passiflora* L. crops do not support long periods of waterlogging, with a maximum of 4 days for yellow passion fruit. Climatic events such as prolonged rain, intense droughts, strong winds and hail are harmful for these plants.

## RESUMEN

### Palabras clave:

Altitud  
Curuba  
Gulupa  
Radiación solar  
Granadilla  
Temperatura  
Maracuyá

El desarrollo de los cultivos frutales andinos se proyecta como una contribución importante y saludable para el consumo global de alimentos, pero los estudios ecofisiológicos de estos frutales son escasos. El 96% de aproximadamente 520 especies de *Passiflora* L. están distribuidas en las Américas, especialmente en los países Colombia y Brasil. Muchas de estas especies se originaron en los bordes de los bosques húmedos en los valles tropicales. Las cuatro especies: maracuyá (*Passiflora edulis* f. *flavicarpa*) granadilla (*P. ligularis*), gulupa (*P. edulis* f. *edulis*) y curuba (*P. tripartita* var. *mollissima*) son las más cultivadas en Colombia y de las cuales se describen hallazgos ecofisiológicos en esta revisión. Sus exigencias en temperatura (°C) y altitud (msnm) son para maracuyá: 15-28 °C y 0-1.300 msnm; granadilla: 15-23 °C y 1.800-2.600 msnm; gulupa: 15-22/12-14 °C (día/noche) y 1.600-2.300 msnm; curuba: 13-16 °C y 1.800-3.200 msnm, todas tienen altos requerimientos de radiación solar, necesitando mínimo 7 h de brillo solar por día lo que fomenta especialmente la floración y la calidad del fruto. Los días nublados disminuyen el crecimiento, la inducción de botones y apertura floral. La temperatura y la radiación fotosintéticamente activa son los factores climáticos que ejercen el efecto más grande sobre el desarrollo de las plantas. La humedad relativa entre 60 y 80% favorece una polinización y fecundación efectiva. Estos cultivos (*Passiflora* L.) no soportan periodos alargados de anegamiento, máximo por 4 días en maracuyá. Eventos climáticos como lluvia prolongada, sequías intensas, vientos fuertes y granizo son perjudiciales para estas plantas.

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## INTRODUCTION

Fruits of the tropics, with their production and supply throughout the year, open up a world of possibilities to expand crops and increase exports (Blancke, 2016). Nevertheless, much is lacking for proper cultivation and understanding their agroclimatic requirements (Fischer *et al.*, 2016). Thus, the development of Andean fruit crops is seen as an essential and healthy contribution to global food consumption (Viera *et al.*, 2019).

Many of these “exotic” fruits are classified as important functional foods (Moreno *et al.*, 2014; Campos *et al.*, 2018), not only in their countries of origin but also for populations in higher latitude regions (Ramadan, 2011), resulting in an excellent export opportunity for many Andean countries, which has been increasing in volume since the beginning of this century (Moreno-Miranda *et al.*, 2019).

The Andean region, geographically, is a mountain range, with a length of about 8,500 km, from Chile to Venezuela, passing through countries as Argentina, Peru, Bolivia, Ecuador, and Colombia, with altitudes between 3,000 and 4,000 masl, surrounding the coastal zone of the Pacific Ocean (Guerrero *et al.*, 2011). Its width ranges from 250 to 750 km and occupies an area of about 2'870,000 km<sup>2</sup> (Orme, 2007). The tropical Andes represent 15% of total global plant richness, standing out as a region with very high biodiversity (Peyre *et al.*, 2019; Campos *et al.*, 2018), and many fruit species originate in these South American areas (Ligarreto, 2012). Izquierdo and Roca (1998) characterized this “ecoregion” as one of the most fragile and misunderstood, where more than 60 million people live, half of them working in fields and many of them have very low income.

Ecophysiology studies examine environmental effects on plant physiology (Fischer *et al.*, 2016), describing physiological mechanisms that interact with physical and biotic environmental factors during plant growth and development (Lambers *et al.*, 2008). This information is of the utmost importance to achieve maximum production and quality on farms, which is only possible when environmental conditions are close to optimal for a species in order to benefit its genetic potential (Pérez and Melgarejo, 2015). Studies on environmental physiology have been widely used to improve species management or to recognize differences between different varieties (Restrepo-Díaz *et al.*, 2010).

Factors such as temperature, solar radiation, altitude, rain, wind, and air pressure are the principal factors that influence these Andean crops (Fischer and Melgarejo, 2020; Restrepo-Díaz and Sánchez-Reinoso, 2020). On the other hand, the tropics do not have the marked temperature seasons seen in temperate zones; thus, the wet and dry seasons define the seasons to which plants react physiologically (Fischer and Parra-Coronado, 2020).

In nature, ecophysiological factors act holistically (Mittler, 2006), meaning studies under controlled environments with only one or two factors are questionable, and the concept of multidimensional ecophysiology makes it difficult to compare results obtained in different areas and countries (Fischer and Orduz-Rodríguez, 2012). As such, as Restrepo-Díaz and Sánchez-Reinoso (2020) stated, the results from recent years that are being used to improve fruit tree productivity need to be reevaluated considering the effects of climate change.

Climate change will strongly affect the high Andean tropics; on the one hand, it will increase precipitation by 20-25%, and, on the other, warming in the mountain region will be more intense than in the lowlands (Marengo *et al.*, 2011). Rain not only predominates because of climate change in the high Andean zone, but precipitation is also the climatic factor that most affects the reproductive phase of plants (73.4%), compared to the influence of air temperature in this phase (19.3%), solar radiation and photoperiod (3.2%), as shown by a study on the phenology of plants in the Neotropics by Mendoza *et al.* (2017). The species more affected by climate change mainly include fruits and vegetables, for which Shukla *et al.* (2019) warned that production and quality will decrease as warming increases, especially in tropical and subtropical regions. Carr (2013) concluded that climate change and variability have impacted growing conditions in passion fruit production regions, which may lead to changes in productivity and commercial viability in these crops. Also, Posada and Ocampo-Pérez (2013) stated that the vulnerability of these crops to climate change will depend on their adaptation capacity in accordance with the genetic plasticity of the species (ecophysiology, genotype x environment). On the contrary, there are also indications that global warming

may increase production in fruit trees in some areas (Devenish and Gianella, 2012), and Tito *et al.* (2018) and Fischer and Melgarejo (2021) assume that a too high rise in the crops growing temperature could be avoided in the Andes by using higher altitude areas (with lower temperatures).

The development of many promising crops that have great potential in international markets is affected by a lack of knowledge on climate impacts on growth, production, and quality (Fischer *et al.*, 2009). There are few studies on ecophysiology in *Passiflora* crops despite the fact that Ocampo (2013) highlighted its importance given that much of the knowledge comes from the observations of fruit growers who cultivate them in different areas of the country (Pérez and Melgarejo, 2015).

Therefore, this article aimed to collect the information on the ecophysiology of passion fruit species cultivated in the Andean region, with an emphasis in Colombia, in order to understand the climatic requirements of each crop and the effects on their physiological processes, which are key to adaptation, management and improvement of the crop.

### Some ecophysiological characteristics of the higher altitude tropics

The Andean region offers growing conditions for numerous fruit species that may thrive up to 3,000 masl or more, whether they are frost-resistant crops or avoid frost during the flowering season or in recently set fruits (Fischer and Orduz-Rodríguez, 2012). For instance, in Colombia frost does not occur below 2,400 masl, and banana passion fruits are found up to an altitude of 3,200 masl (Angulo and Fischer, 1999). Solar radiation in the highlands encourages the thickening of the fruit epidermis and a greater number of parenchyma layers, and the high ultraviolet (UV) radiation results in a greater formation of antioxidants, factors that favor the quality of these fruits (Fischer *et al.*, 2016; Fischer, 2000). Therefore, trellis systems (*sistema de conducción* or *emparrado*) are recommended in areas with excessive radiation (Fischer *et al.*, 2009).

As thermal altitude classification confirms, temperature is the most influential climatic factor, which changes as altitude increases, with a decrease of about 0.6 °C per 100 m of elevation, mainly affecting the duration of growth cycles and the phenology of fruit trees (Fischer *et al.*, 2009).

Likewise, with an increase in altitude, the partial pressure of gases, such as O<sub>2</sub>, CO<sub>2</sub> and N<sub>2</sub>, and air humidity decrease, along with a reduction in precipitation, from the altitude of 1,300-1,500 m (Fischer and Orduz-Rodríguez, 2012). On the contrary, these authors indicated that ultraviolet, visible, and infrared radiation increase with altitude, along with wind speed.

The leaf thickness increases, and the leaves become smaller when exposed to the UV light, which may be due to the stress caused by increasing altitude (Fischer *et al.*, 2016). In addition, UV radiation affects the production of auxins (Fischer and Melgarejo, 2014). Buchanan *et al.* (2015) stated that UV light causes a lower synthesis of gibberellins in internodes, which means that high-altitude fruit trees reduce the longitudinal growth of the stem, compared to plants in the lower areas.

### Passifloraceae

Rodríguez *et al.* (2020a) and Ocampo *et al.* (2021) reported that South America is the center of diversity for most cultivated *Passiflora* species. The high biodiversity of *Passiflora* in South America puts the continent as a region of great potential for utilization of these species (Hurtado-Salazar *et al.*, 2021). There are about 520 species of passion flowers, and approximately 96% of these are distributed in the Americas, being Colombia and Brazil the centers of the diversity with 30% (Cerqueira-Silva *et al.*, 2014). These species include herbaceous and woody vines, usually with tendrils, and a few are shrubs or trees (Ocampo *et al.*, 2021). The species of this family are native to tropical and subtropical regions of both hemispheres and grow in low- and high-altitude habitats, where temperatures are moderate (Paull and Duarte, 2012). Ocampo *et al.* (2007) stated that the passion fruit plants are originated in the edges of humid forests in tropical valleys, with 20 to 30 °C average air temperature and high environmental humidity and precipitation rates but these conditions does not appear, in all cases, to be optimal for growth and production (Hurtado-Salazar *et al.*, 2021). These are semi-perennial fruit-bearing species of a climbing habit (Primot *et al.*, 2005).

This family, given its permanent production in the interior tropics because of its indeterminate growth habit, requires well-distributed rainfall throughout the year (Fischer *et al.*, 2018). Jackson *et al.* (2010)

recommended areas that are not too cold for these species, with high solar brightness and winds that are not strong. However, as these authors pointed out, regions with very hot summers decrease crop longevity, and frost below -2 °C causes severe damage to plants.

Colombia has the greatest diversity of passion fruit species (Ocampo *et al.*, 2007), where nine species are

cultivated to meet the needs of local markets and export demands (Ligarreto, 2012), with greater production in the departments of Antioquia and Huila, especially for yellow passion fruit, sweet granadilla and gulupa (Fischer *et al.*, 2018). The species requirements for altitude and temperature vary widely. The banana passion fruit plants are well-adapted to the cold climate (Table 1).

**Table 1.** Origin of four important passion fruit trees cultivated in the Andean region.

Species	Zones and countries of origin	Authors
Yellow passion fruit	Amazon region	Blancke, 2016
Sweet granadilla	From Bolivia to Central America	Blancke, 2016
Purple passion fruit	South of Brazil, Paraguay, and North of Argentina	Ocampo <i>et al.</i> , 2020
Banana passion fruit	Mountainous area of South America (Colombia, Ecuador, Venezuela, Bolivia, Peru)	Fischer <i>et al.</i> , 2020

In addition to these four commercially important passion fruits, Colombia has other species of great importance, such as giant granadilla “badea” (*P. quadrangularis*) and stone granadilla “cholupa” (*P. maliformis*) (Rodríguez *et al.*, 2020b).

### Yellow passion fruit

The most cultivated and well-known passion fruit species is the yellow passion fruit (*Passiflora edulis* f. *flavicarpa* Degener), also known as acid passion fruit; it is a product of great commercial and economic importance in Brazil, thanks to the quality of its fruits and its high industrial yield (Faleiro *et al.*, 2020). It can be cultivated between 0-1,300 masl (Table 1), according to Fischer *et al.* (2009), it is the most tropical passion fruit with better adaptation to the lower marginal zone of the coffee region in Colombia.

The yellow passion fruit grows optimally in temperatures between 23 and 25 °C, while in regions with temperatures below 15 °C and a photoperiod with less than 11 h light per day, there is little flowering stimulation (Faleiro *et al.*, 2020) (Table 2). Regions with average temperatures higher than 28 °C, accelerate vegetative growth but with a reduction in production because of dehydration of the stigmatic fluid (Fischer *et al.*, 2009). Cleves (2012)

recommended a minimum of 5 h of direct sunlight on plantations and highlighted that fruits directly exposed to the sun have a higher concentration of ascorbic acid and total soluble solids, with a thinner rind, however, growers always have to avoid sunburn damage.

Relative humidity below 30% reduces pollination and fruit development (Faleiro *et al.*, 2020); these very dry conditions inhibit photosynthesis by closing stomata and burning the tender shoots of plants (Fischer *et al.*, 2009). Faria *et al.* (2020) irrigated yellow passion fruit seedlings with 25, 50, 75 and 100% of the capacity of the pot substrate, and found that, in 50%, the plant height and the stem diameter were very similar to those plants with greater amounts of water (up to 175%) and stated that the plants possibly have water reserves in the stem and roots. Likewise, these authors observed that the number of leaves, the transpiration and the biomass of the plants constantly increased up to 100% of the capacity of the pot substrate.

Yellow passion fruit plants do not tolerate waterlogging for more than four days, which especially affects roots and stem growth (Basso *et al.*, 2019). As shown in Table 3, flooded yellow passion fruits increase the relative water content, but the photosynthetic and transpiration rates

**Table 2.** Climatic factors for the growth and production of passion fruits in Colombia (modified according to Fischer *et al.*, 2018)

Climate factor	Yellow passion fruit ( <i>P. edulis</i> f. <i>flavicarpa</i> )	Sweet granadilla ( <i>P. ligularis</i> )	Purple passion fruit ( <i>P. edulis</i> f. <i>edulis</i> )	Banana passion fruit ( <i>P. tripartita</i> var. <i>mollissima</i> )
Temperature (°C)	15-28 (opt. 23-25)	15-23 (opt. 18-20)	15-22 (opt.15-18)	13-16 (opt. 12-16)
Altitude (masl)	0-1,300	1,800-2,600	1,600-2,300	1,800-3,200
Precipitation (mm year <sup>-1</sup> )	800-1,500	1,500-2,500	1,800-2,300	1,000-1,500
Relative humidity (%)	70	60-80	60-70	70-80
Solar radiation	>11 h sunshine per day	1,500-1,600 h sunshine per year	7-9 h sunshine per day	7-8 h sunshine per day
Authors	Cleves <i>et al.</i> , 2012; Faleiro <i>et al.</i> , 2020	Miranda, 2020	Ocampo and Posada, 2012; Ocampo <i>et al.</i> , 2020	Campos and Quintero, 2012; Fischer <i>et al.</i> , 2020

decrease, along with the stomatal conductance (Govêa *et al.*, 2018; Faria *et al.*, 2020). Nonetheless, because of the formation of an aerenchyma in the cortex of flooded plants (Govêa *et al.*, 2018), passion fruits have

mechanisms of adaptation to higher humidity conditions in the root environment for a time; thus, Faria *et al.* (2020) classified this fruit as moderately sensitive to water excess in the soil.

**Table 3.** Effect of waterlogging on the physiological response of yellow and purple passion fruits.

Crop	Physiological response to waterlogging	Reference
Yellow passion fruit	<ul style="list-style-type: none"> <li>- Plants tolerate waterlogging up to 4 days.</li> <li>- Root and stem biomass were mainly affected.</li> <li>- With increased waterlogging, the hydration of the plant increased.</li> <li>- Waterlogging of <math>\geq 5</math> days caused irreversible negative effects on the plant.</li> </ul>	Basso <i>et al.</i> (2019)
Yellow passion fruit	<p>In plants watered for 22 days with 100, 125, 150 and 175% of the capacity of the pot substrate:</p> <ul style="list-style-type: none"> <li>- The height of the plant and the diameter of the stem were not affected, while the biomass was reduced.</li> <li>- The transpiration was reduced with the increase of the water starting at 118% of the substrate capacity.</li> <li>- The relative water content of the plant increased with irrigation.</li> </ul>	Faria <i>et al.</i> (2020)
Yellow passion fruit	<p>In seedlings kept with soil moisture at field capacity, soil pre-immersed in water or flooded, for 7 days:</p> <ul style="list-style-type: none"> <li>- Waterlogging reduced the photosynthetic rate, stomatal conductance and intracellular CO<sub>2</sub>.</li> <li>- There were no differences in the water potential or the proline content of the leaves.</li> <li>- Plants in pre-submerged and flooded soil increased the diameter of roots, epidermis, cortex and endodermis of the root system, also forming an aerenchyma.</li> </ul>	Govêa <i>et al.</i> (2018)
Purple passion fruit	<ul style="list-style-type: none"> <li>- Mycorrhized seedlings tolerated waterlogging better because of higher leaf retention, proline and chlorophyll production, but lower synthesis of carotenoids and total soluble sugars.</li> <li>- In non-mycorrhized plants, the nitrogen and phosphorus contents in the leaves were reduced faster.</li> <li>- Waterlogging reduced mycorrhizal colonization of the roots.</li> </ul>	Chebet <i>et al.</i> (2020)

### Sweet granadilla

In Colombia, the sweet granadilla crop (*Passiflora ligularis* Juss.) is the second one in species of the genus *Passiflora* because of its economic importance (Ocampo *et al.*, 2015). It adapts well to elevations between 1,800 and 2,600 masl, with optimal temperatures between 18 and 20 °C (Table 1) (Miranda, 2020). Temperatures higher than 23 °C cause thermal stress, and those between 15 and 18 °C increase the duration of the production cycle but decrease the productivity (Miranda, 2012). As this author affirmed, there are problems with temperatures below this range, namely those between 12 and 15 °C, which increase the abortion of flowers, reduce fecundation, and cause cracking of recent set fruits. Rivera *et al.* (2002) reported that below 1,800 masl, the incidence of insect-pests increases, and smaller fruits develop. Also, below 1,500 masl, the viability of pollen is low.

In the municipality of Santa María, Department of Huila (Colombia), Fernández *et al.* (2014) ecophysiologicaly characterized sweet granadilla *in situ* at 2,060 masl (average temperature 17.15 °C, PAR (photosynthetic active radiation) 1,186.2  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ ) and at 2,270 masl (16.24 °C, PAR 470.9  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ ). At 2,060 masl, the maximum photosynthetic rate ( $A_{\text{max}}$ ) 23.6  $\mu\text{mol m}^{-2} \text{s}^{-1}$  of  $\text{CO}_2$ , the darkness respiration rate (DR) 2.24  $\mu\text{mol m}^{-2} \text{s}^{-1}$  of  $\text{CO}_2$ , and the compensation point per light ( $I_c$ ) 34.6  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , were higher than at 2,270 masl (17.5  $A_{\text{max}}$ ; 1.34 DR and an  $I_c$  of 21, respectively), while for the two locations, the foliar water potential (about -0.2 MPa), the edaphic one (about -0.01 MPa) and the predawn values of maximum photochemical efficiency of photosystem II (Fv/Fm; >0.86) indicated that the plants did not suffer any stress, concluding that both sites are suitable for the commercial cultivation of sweet granadilla (Fernández *et al.*, 2014).

Among the physiological disorders of sweet granadilla, sunburn is the most important physiopathy, caused by excess solar radiation in fruits unprotected by leaves, accentuated after pruning of branches in the fruitful part of the plant or by a drought that also reduces the leaf area (Rivera *et al.*, 2002). Fruit cracking is a physiopathy related to sudden changes in day to night temperature but can also be caused by a high Ca deficiency (Miranda, 2020), irrigation or a heavy rain after a prolonged dry

season that increases the senescence of the epidermis and its extensibility (Fischer and Orduz-Rodríguez, 2012).

Regarding the water factor, a commercial sweet granadilla plantation requires rainfall between 1,500 and 2,500 mm year<sup>-1</sup> and an atmospheric humidity of 60 to 80%, which favors the activity of pollinators, while higher humidity increases the incidence of fungal pathogens (Rivera *et al.*, 2002; Miranda, 2020). As in other passion fruit species, water stress in the reproductive stages, from the pre-flowering stage to the filling of the fruit, causes the abscission of the floral structures and considerably reduces yield (Miranda, 2020). Likewise, this detrimental effect in the reproductive phase is related to the deficiency of nutrients, such as P, K, Ca and B. Under a moderate water stress in sweet granadilla plants generated a decrease in leaf area, number of leaves and longitudinal growth of branches, while the root/aerial ratio of the plants increased with the duration of water stress (Casierra-Posada and Roa, 2006).

According to Table 2, the light in a technical cultivation of sweet granadilla requires 1,500 to 1,600 h year<sup>-1</sup> of sunshine (Miranda, 2020) because this luminosity highly encourages the differentiation of floral primordia, flowering and fruit coloration (Miranda, 2009).

On the other hand, excessive winds are detrimental to this passion fruit species since they affect pollination agents, bees and bumblebees, and can damage flowers and pollen germination as a result of drying of the stigmatic surface, while calm environments ensure better fruit set (Miranda, 2009).

### Purple passion fruit

While Blancke (2016) confirmed that the purple passion fruit (*Passiflora edulis* f. *edulis*) is cultivated not only in the subtropics but also in high Andean areas, in Colombia, Ocampo *et al.* (2020) reported that crops are found from 1,600 to 2,300 masl, avoiding very steep slopes, with the best results in terms of production and quality found in areas from 1,700 to 2,000 masl. Ocampo and Posada (2012) specified this as the optimal range to develop good genetic vigor, good pollination and fecundation, and low incidence of pests and diseases. Interestingly, Rodríguez *et al.* (2019), who studied 50

purple passion fruit genotypes at two different altitudinal locations, Pasca (Cundinamarca, 1,800 masl, 18 °C) and Susacón (Boyacá, 2,500 masl, 13.1 °C), found that the 34 landraces had a better adaptive physiological response at the higher altitude than the commercial genotypes, which is because they are more suitable for plant breeding programs in the current climate change scenario. Carr (2013) observed that the purple passion fruit can be cultivated up to 3,000 masl in the tropics.

Optimal temperatures for purple passion fruits are in the range of 15-22 °C day and 12-14 °C night (Table 2) (Pérez and Melgarejo, 2012), tolerating temperatures ranging between 10 and 24 °C (Ocampo *et al.*, 2020). In their ecophysiological study at three different locations in Cundinamarca (Colombia), Pérez and Melgarejo (2015) concluded that climatic conditions similar to those in the municipality of Granada (2,230 masl, 15 °C), which has a day/night temperature of 18/13 °C, a vapor pressure deficit close to 0.05 kPa and radiation that does not exceed 1,000  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ , greatly favor the physiological performance of purple passion fruits. Temperatures over 30/25 °C day/night affect flower production (Jiménez *et al.*, 2012); adult plants resist low temperatures but can be damaged by temperatures between -1 and -2 °C (Paull and Duarte, 2012).

Sunlight from 7 to 9 h day<sup>-1</sup> favors fruit quality (Pérez and Melgarejo, 2012), while Ocampo and Posada (2012) stated that excessive cloudiness during fruiting delays ripening, and decreases the content of soluble solids (° Brix) and the quality of the juice. The purple passion fruit is very susceptible to changes in solar radiation because they affect the productivity of plants; thus, cloudy days decrease growth, induction of flower buds and flower opening. A reduction of light of 1-4 weeks decreases flowering and plant production. Besides, an excess radiation generates sunburning on fruits and decreases normal plant development (Jiménez *et al.*, 2012).

Ocampo *et al.* (2020) recommended relative humidity (RH) between 60 and 70% for cultivation, which sustains effective pollination and fecundation, so the stigmas remain hydrated and adhesive. Rain during flowering affects the functionality of pollen because it can burst and cause abscission of flowers (Jiménez *et al.*, 2012). Carr (2013) reported that rain up to 2 h after pollination

prevents fruit set. Sánchez *et al.* (2013) found a negative correlation between RH and stomatal opening on a purple passion fruit plantation, but positive correlations between solar radiation and temperature with stomatal opening.

According to Ocampo *et al.* (2020), well-distributed rainfall between 1,800 and 2,300 mm year<sup>-1</sup>, is favorable for the growth and production of the purple passion fruit, while for the reproductive phases, i.e. between the sprouting of flower buds and fruit enlargement, water stress causes very small fruits or aborted fruits (Jiménez *et al.*, 2012). Paull and Duarte (2012) reported that a water stress less than -1.3 MPa leads to a strong reduction in the development of the foliar area, flowering and plant yield, pointing out that the lack of water can be one of the environmental factors responsible for production fluctuations in these passion fruits.

In another purple passion fruit maypop (*P. incarnata*), García-Castro *et al.* (2017) found a moderate tolerance to short water deficit periods because of its stomatal mechanism and other non-stomatal factors (up to 10% of evapotranspiration, ET), with an exponential reduction in the photosynthetic rate with a water stress more negative than -1.0 MPa; however, the plants quickly recovered their gas exchange properties when they were irrigated again at 100% ET. Also, Crane *et al.* (2019) classified passion fruits as moderately water-stress tolerant plants that can withstand this stress for several days but with reduced plant growth and yield. Carr (2013) observed that the production of new leaves ceases at a leaf water potential -2.0 MPa, and the expansion of new leaves is considerably reduced to -1.5 MPa in *P. edulis*.

In general, the purple passion fruit, like the other passion fruits, does not resist periods of waterlogging (Crane *et al.*, 2019); however, Chebet *et al.* (2020) found that mycorrhized plants (with a mixture of *Glomus caledonium*, *G. etunicatum*, *Gigaspora margarita* and *Scutellospora* sp.) better tolerate this adversity, producing more osmoprotectant proline and chlorophyll and thus, retaining their leaves and foliar N and P for longer than non-mycorrhized ones (Table 3).

Strong winds affect pollinating insects, which do not fly at high wind speeds (Fischer and Orduz-Rodríguez,

2012) and can damage flower structures and dehydrate pollen and stigma, along with damage to plantations and conduction systems (Ocampo *et al.*, 2020).

### Banana passion fruit

The banana passion fruit (*Passiflora mollissima* f. *tripartita*) is favored by altitude because UV radiation promotes the thickness of the epidermis, increasing resistance to diseases, mainly anthracnose (Campos and Quintero, 2012). There are commercial plantations between 1,800 and 3,200 masl in Colombia (Fischer *et al.*, 2020), with the best conditions between 2,000 and 3,000 masl (Angulo, 2003). In countries such as Bolivia and Peru, there is cultivation up to 3,300 and 3,400 masl (Blancke, 2016; National Research Council, 1989). Mayorga *et al.* (2020) studied banana passion fruits at altitudes of 2,498 and 2,006 m in Pasca (Cundinamarca, Colombia), observing that, in the higher altitude, larger fruits were formed, with higher levels of citric and ascorbic acid but with less total soluble solids ( $^{\circ}$ Brix), and recorded temperature and photosynthetic active radiation (PAR) as the climatic factors that exerted the greatest effect on plant development. To resist large fluctuations in temperature and high radiation (UV) in high Andean zones, plants develop soft hairs on the entire vegetative part (Angulo and Fischer, 1999). Sunlight between 1,300 and 1,600 h year<sup>-1</sup> are necessary to guarantee favorable growth and production conditions for plants (Angulo, 2003).

This species is the commercial passion fruit most adapted to cold tropical and subtropical regions (Blancke, 2016). Mayorga *et al.* (2020) established the base (minimum) temperatures for the growth of primary branches, flower buds and fruits as 4.3, 3.1 and 0.01 °C, respectively. Zones with temperatures between 13 and 16 °C are recommended for cultivation, but temperatures below 0 °C can affect flower buds, flowers, fruit set and non-lignified vegetative parts of the plant (Campos and Quintero, 2012). Given that this fruit grows at altitudes higher than the frost limit, *P. mollissima* f. *tripartita* lines have formed tolerance to temperatures of -5 °C for a short time (National Research Council, 1989).

Rainfall of 1,000 to 1,500 mm year<sup>-1</sup>, well-distributed throughout the year, is optimal for commercial crops (Fischer *et al.*, 2009); therefore, supplying moisture

in dry periods with artificial irrigation is necessary, especially in the reproductive phases. Climatic events such as prolonged rain (waterlogging), intense droughts and hail can affect the cultivation and production of plants (Fischer *et al.*, 2020). Campos and Quintero (2012) recommended a relative humidity between 70 to 80%, which favors pollination and pollen germination; considering that drier airs increase the risk of frost in the high Andean zone, while a higher atmospheric humidity benefits some diseases, especially anthracnose. Light winds facilitate the transport of pollen through the air and the flight of pollinating insects, which are necessary since the banana passion fruit is an allogamous plant. Strong winds must be controlled by planting windbreak barriers using native plants (Fischer *et al.*, 2020) that also protect against flower fall (Angulo, 2003).

The cultivation of passion fruit plants in Colombia reveals a positive impact of plastic roofing oriented over the plant rows with a PE plastic (175  $\mu$ m thickness) 1.50 m wide, which is placed on a "T" type structure located at 2.2 m above the ground. This structure protects the plants from heavy rains and direct solar radiation and regulates the circulation of air inside the canopy, reducing relative humidity. These factors improve the production and quality of the fruits and contribute to reduce the incidence of critical fungal diseases, such as *Alternaria* sp. and *Cladosporium* sp. Nevertheless, the use of this technique is still scarcely reported since it is necessary to carry out physiological studies of these crops that explain the variables of yield and quality of the fruit production.

### CONCLUSIONS

The temperature requirements for the studied passion fruit species are, generally, between 15 and 23 °C; only the banana passion fruit requires a temperature range between 13 and 16 °C. For altitude requirements, the yellow passion fruit is the most "tropical" species, growing at the elevations between 0 and 1,300 masl, and the banana passion fruit is the most "Andean" one, which is found between 1,800 and 3,200 masl.

Sufficient solar radiation and PAR are crucial for flower induction and flowering, while a relative humidity between 60 and 80% favors pollination and fecundation. Sweet granadilla and purple passion fruit plants require



precipitations rates between 2,300-2,500 mm year<sup>-1</sup>. On the other hand, a new technology consisting in the plastic cover placed over the rows of purple passion fruit plants protects the plants against heavy rains and the fruits against direct sunlight. This technology allows for a lower incidence of pests and diseases and, therefore, provides a higher fruit quality and production; however, there is a lack of studies to understand better these beneficial effects.

These crops are moderately sensitive to waterlogging, having a resistance mechanism of aerenchyma and, on the other hand, the mycorrhizal plants better tolerate this abiotic stress. The passion fruit plants withstand a moderate water shortage; however, very dry conditions at reproductive stages, starting from the pre-flowering up to the fruit filling, cause the abscission of the floral structures and can considerably reduce the yield.

In addition to hailstorms, strong winds are very harmful to *Passiflora* plants, since affect the activity of pollinating insects and can damage flower structures and dehydrate pollen and stigma along with the damage produced to plantations and conduction systems.

The current climatic variability affects the physiology of plants and orchards and requires the implementation of new agronomic practices for special management of the temperature and precipitation effects.

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