Photosynthesis in fruit crops of the high tropical Andes: A systematic review

La fotosíntesis en los cultivos frutales de trópico alto de los Andes: una revisión sistemática

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ABSTRACT

Commercially grown fruit crops in the high tropical Andes zones from 1,600 to 3,200 m a.s.l. are increasingly important in the world market, mainly because they are exotic fruits, and also because they are produced by hundreds of small growers. Photosynthesis is one of the most important physiological processes involved in the production and quality of fruit crops. However, many aspects of this process are unknown in fruit species grown in the Andean highlands. This systematic review presents the main themes and advances in research on photosynthesis of Andean fruit crops. A systematic literature search was carried out in the Scopus and Web of Science databases using the RStudio Bibliometrix package tool and VOSviewer version 1.6.16 software. Research on this topic has focused on high tropical Andean countries with climatic conditions for the growth of fruit species. Notably, the research addresses themes related to the photosynthesis of Andean highland fruit crops in Brazil and Colombia. The authors cover research topics from horticulture and plant physiology to photosynthesis and leaf anatomy and acclimation, where most research literature currently focuses. In most of the analyzed fruit crops, photosynthetic parameters such as maximum photosynthesis ($A_{\max}$), light compensation point, light saturation point, and apparent quantum yield are known. These are important advances in the knowledge of the fluorescence of chlorophyll *a*, which is mainly used as a tool to characterize the eco-physiological response of these fruit species to different environments.

Key words: gas exchange, chlorophyll fluorescence, light, chloroplasts, ecophysiology.

RESUMEN

Los frutales cultivados comercialmente en las zonas de trópico alto andino, de 1.600 a 3.200 m s.n.m., son cada vez más importantes en el mercado mundial, principalmente porque se consideran frutas exóticas nutritivas, y también porque son producidas por cientos de pequeños cultivadores. La fotosíntesis se considera uno de los procesos fisiológicos más importantes involucrados en la producción y calidad de los cultivos de frutales, pero muchos aspectos de este proceso son desconocidos en las especies cultivadas en los Andes. Esta revisión sistemática presenta los principales temas y avances en la investigación sobre la fotosíntesis de cultivos de frutas andinas. Se realizó una búsqueda sistemática de literatura en las bases de datos Scopus y Web of Science utilizando la herramienta RStudio Bibliometrix y el software VOSviewer versión 1.6.16. La investigación sobre este tema se ha centrado en países de trópico alto andino con condiciones climáticas apropiadas para el crecimiento de estas especies frutales. Se abordan temas relacionados con la fotosíntesis de cultivos de frutas de alta montaña andina centrados en Brasil y Colombia. Los autores cubren temas desde la horticultura y la fisiología vegetal hasta la fotosíntesis, y tópicos como la anatomía foliar y la aclimatación, donde la mayor parte de la investigación se ha realizado recientemente. En la mayoría de los cultivos de frutas analizados, se conocen parámetros fotosintéticos como fotosíntesis máxima ($A_{\max}$), punto de compensación de luz, punto de saturación de luz y rendimiento cuántico aparente, que son avances importantes en el conocimiento de la fluorescencia de la clorofila *a*, la cual se utiliza principalmente como herramienta para caracterizar la respuesta ecofisiológica de estas especies frutales en diferentes ambientes.

Palabras clave: intercambio de gases, fluorescencia de la clorofila, luz, cloroplastos, ecofisiología.

Introduction

Tropical altitude ecosystems are characterized by significant climatic changes in a single day, which can be much more pronounced than between the seasons throughout the year. Due to global warming, these ecosystems are attracting increasing attention (Fischer *et al.*, 2024; Körner, 2007). As an area of primary diversity and richness of plant species, tropical countries provide a great range for the growth of fruit crops, and high tropical Andean regions, especially the Eastern Andes (Barthlott *et al.*, 2005), provide adequate ecological niches for their cultivation (Ligarreto, 2012). The South American Andes are a mountain chain that extends from Chile and the north of Argentina to Venezuela, with an average altitude of 3,000 to 4,000 m a.s.l. (Guerrero *et al.*, 2011). The tropical Andes contain

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15% of the planet's biodiversity (Peyre *et al.*, 2019) due to their very particular environmental conditions which are influenced by their proximity to the equator, unlike other mountain ranges such as the Himalayan mountains. This review focuses on the tropical Andean fruit species which grow well between 1,600 and 3,200 m a.s.l.

Climatic conditions are the main factor in the adaptation of fruit crops to higher elevations, specifically between 1,600 and 3,200 m a.s.l. At these altitudes, the temperature and partial pressure of gases decrease and solar radiation, especially ultraviolet (UV), increases (Fischer, Orduz-Rodríguez *et al.*, 2022; Fischer, Parra-Coronado *et al.*, 2022). Within the spectrum of daylight, UV-B radiation (280-315 nm) has the greatest energy, and its high incidence can damage macromolecules, including DNA (Jenkins *et al.*, 2009). In addition, as reported by Terfa *et al.* (2014), UV-B impacts the morphology, biochemical composition, and molecular response of high tropical Andean plants. For each increase of 100 m of tropical altitude, the temperature descends in a range of 0.6 to 0.7°C (Benavides *et al.*, 2017). This extends the phenological cycles of the fruit crops, allowing the cultivation of other fruit species from subtropical and temperate zones.

The commercially grown fruit species that can adapt to tropical altitude conditions generally originate from the same Andean zone. According to Fischer *et al.* (2024), these include the Solanaceae species, such as tree tomato (*Solanum betaceum*; 1,700-2,600 m a.s.l.), cape gooseberry (*Physalis peruviana*; 1,800-2,800 m a.s.l.), and lulo or naranjilla (*Solanum quitoense*; 1,600-2,400 m a.s.l.) as well as the Passifloraceae fruit species, which includes gulupa or purple passion fruit (*Passiflora edulis* f. *edulis* Sims; 1,600-2,300 m a.s.l.), sweet granadilla (*Passiflora ligularis*; 1,800-2,600 m a.s.l.) and curuba or banana passion fruit (*Passiflora tripartita* var. *mollissima*; 1,800-3,200 m a.s.l.); the Myrtaceae species feijoa (*Acca sellowiana*; 1,800-2,700 m a.s.l.); the Rosaceae species mora or Andean blackberry (*Rubus glaucus*; 1,500-2,600 m a.s.l.); and the Ericaceae species agraz or Andean blueberry (*Vaccinium meridionale*; 2,200-3,200 m a.s.l.). These fruit species, produced mainly in Brazil and the Andes of Colombia, Peru, and Ecuador, are projected to be an important and healthy contribution to global food consumption (Fischer & Miranda, 2021; Viera *et al.*, 2019). They are known as exotic fruits in other parts of the world and are classified as important functional foods (Campos *et al.*, 2018; Moreno *et al.*, 2014). Exported in significant quantities, they are increasingly important for the economy of small producers in the Andean countries, who are mainly responsible for their production (Moreno-Miranda *et al.*, 2019; National Research Council, 1989).

Research on Andean highland fruit crops is less advanced compared to studies on tree fruits from lowland tropical valleys, subtropical, and temperate regions. It has mainly focused on agronomic aspects related to production and quality (Fischer, 2012; Fischer *et al.*, 2016; Fischer, Orduz-Rodríguez *et al.*, 2022; Fischer, Parra-Coronado *et al.*, 2022). Research on physiology, especially photosynthesis, has focused on the improvement of productive systems and abiotic stress (Castañeda-Murillo *et al.*, 2022; Ramírez-Soler *et al.*, 2021; Sánchez-Reinoso *et al.*, 2019). However, research on photosynthesis and related topics on fruit crops from the high tropical Andean has not been consolidated in an article that allows detailed analysis of the advances achieved and the aspects that have still not been investigated.

Photosynthesis is the defining physiological process that determines the maximum achievable yield of crops and drives life on the planet (Vishwakarma *et al.*, 2023). More than 90% of biomass and crop yield derives from photosynthesis, with the rest coming from absorbed and assimilated mineral nutrients (Vishwakarma *et al.*, 2023). This process is vital for the growth and survival of practically all plants during most of their growth cycle (Lambers & Oliveira, 2019). Photosynthesis involves processes of light reactions and carbon fixation. In the first part of the process, light reactions take place in the complexes present in the chloroplast thylakoid. There, photosynthetically active radiation (PAR, 400-700 nm) is absorbed to boost the transport of electrons derived from water photolysis, releasing O_2 and producing NADPH and ATP (Taiz *et al.*, 2017). These molecules are then used in the second part of the process, when the carbon photosynthetic reduction cycle, or Calvin-Benson cycle, takes place in the stroma of the chloroplasts (Silva *et al.*, 2020; Taiz *et al.*, 2017). This synthesizes triose phosphate (Fig. 1), compounds of 3 carbons that are fundamental for producing hundreds of biomolecules in plants.

The photosynthetic process requires an adequate supply of water, nutrients, and CO_2, as well as favorable temperature and light conditions (Lambers & Oliveira, 2019; Silva *et al.*, 2020). When these conditions are unfavorable for the photosynthesis process, photochemical quenching (QP) occurs, and the plant must activate several mechanisms to protect the photosynthetic device (Castañeda-Murillo *et al.*, 2022). Several of these mechanisms involve the functioning of photosystem (PSII); these include the dissipation of excess energy in heat or non-photochemical quenching

(NPQ), or dissipation in the form of fluorescence, with a greater wavelength and lower energy than is dissipated by chlorophyll *a* (Lambers & Oliveira, 2019). Knowledge of these energy dissipation mechanisms has been fundamental in elucidating the physiological status of plants and is considered a key tool for the diagnosis and management of biotic and abiotic stress in different crops, including fruit plants (Castañeda-Murillo *et al*., 2022; Chávez-Arias *et al*., 2019, 2020; Sánchez-Reinoso *et al*., 2019).

Given the above, this review aims to systematically analyze the state of knowledge of the process of photosynthesis in high tropical Andean fruit crops, enabling the consolidation of research progress on this subject and the determination of priorities for future studies. This approach will facilitate continued advancement in the improvement of the productive systems of these fruit species. Moreover, according to Li *et al*. (2018), the regulation of photosynthesis can provide novel solutions to increase yields.

Bibliometric analysis

A systematic review was carried out in the Scopus and Web of Science (WoS) databases. The search equation was defined as TITLE-ABS-KEY (“cape gooseberry” OR “passion fruit” OR “lulo” OR “tree tomato” OR “feijoa” AND photosynthesis AND NOT “yellow passion fruit”, following Pullin and Stewart (2006). Yellow passion fruit (*Passiflora edulis* f. *flavicarpa*) was omitted due to its growth in the Colombian tropical warm climate of the Andean lowlands. The search terms were then evaluated. The downloaded Scopus and WoS databases were combined into a single Excel file and, using the RStudio Bibliometrix package tool, the bibliometric parameters were analyzed. The timespan with the most scientific contributions in photosynthesis and development of high tropical Andean fruits was 2000-2023. The VOSviewer version 1.6.16 software types were used to determine bibliometric networks such as co-occurrence maps.

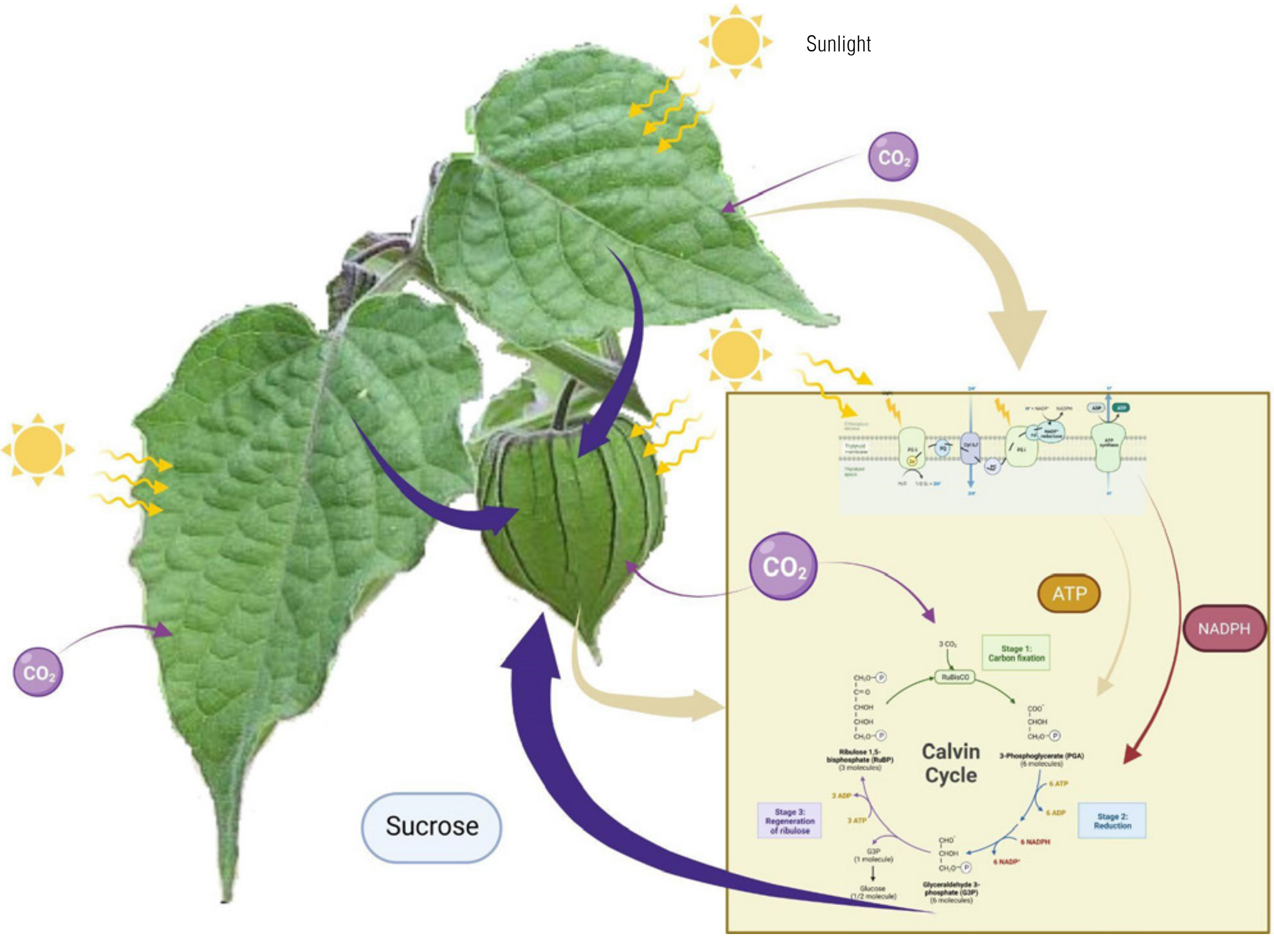

FIGURE 1. General schematic photosynthesis process illustrated for cape gooseberry (*Physalis peruviana* L.), a high-altitude tropical fruit plant. In this species, the calix covers the fruit during development and can perform photosynthesis. In the photo phase, NADPH and ATP are produced, which will then be used in the Calvin cycle to synthesize sugars.

Scientific publications per country

Figure 2 shows Brazil as the most significant producer of scientific publications on photosynthesis in the Andean fruit crops. The blue colors indicate that the People's Republic of China ranks second in research on this topic. Colombia was third place in scientific publications on the Andean highland fruits. Finally, Germany and Egypt have been important contributors to research in foliar gas exchange in Andean fruit species. It is interesting to note that Ecuador, an important country in the production of Andean fruits, is not included in this statistic, suggesting that the results of their studies are not frequently published in international journals.

Co-occurrence and centrality analysis

Network analysis helps to depict and graphically visualize the structure of a relationship in social networks, natural phenomena, and biological systems (Bilen *et al*., 2022). In this study, the network map shows three groups of interrelated keywords. The blue node groups themes concerning the leaf anatomy, native fruits, and acclimatization. The green node associates themes related to water absorption, solar radiation, roots, and water use efficiency. Finally, the red node associates themes related to plant physiology, horticulture, and salt stress (Figs. 3 and 4).

Research on leaf photosynthesis of Andean fruit species was subjected to bibliometric analysis for the period from 2000 to 2023 (Fig. 5). The themes of plant physiology, horticulture, and salt stress first appeared in early 2014. By 2022, the focus had shifted to solar radiation, mulching, water use efficiency, water absorption and roots, while for 2023 the scientific focus was related to leaf anatomy, native fruits, and acclimatization.

The ranks of centrality and density are important tools for analyzing keywords of authors (Herrera-Viedma *et al*., 2016). Centrality is the degree of interaction of the topic of interest with other research topics, while density is the internal strength of the research topic (Salleh & Bushroa, 2022). Figure 5 shows the author keywords divided into four main clusters. The first cluster, namely plant leaf, genetic variation, and plant hormone, had a low density and high centrality (Basic Themes Quadrant), which indicates weak development; however, these were important topics in the research field. The second cluster, photosynthesis, article, and biosynthesis had high centrality and density (Motor Themes Quadrant). These are the most developed and important topics in the field of photosynthesis in Andean fruit crops. The third cluster, *Passiflora*, metabolism, and light, had developed internal links (high density) but low centrality, that is, of limited importance for the field (the Niche Themes quadrant) (Della Corte *et al*., 2019). Finally, the fourth cluster, *Passiflora edulis*, physiological response, and fruit, had low centrality and density, indicating weak and marginal development in the field.

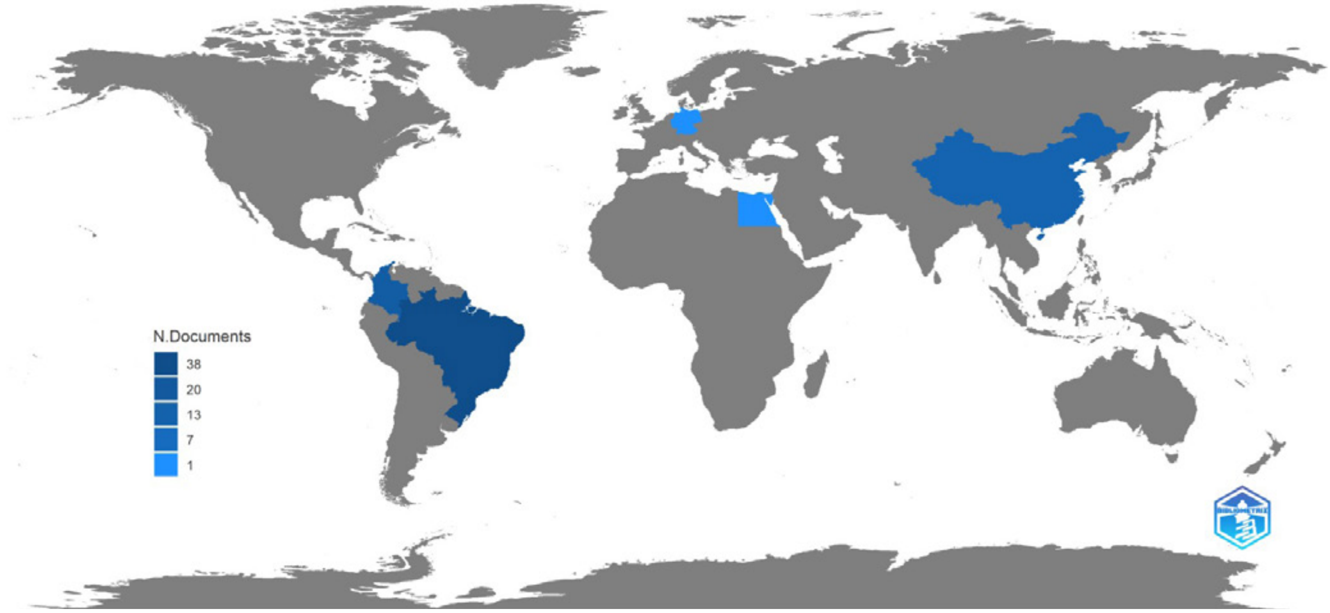

FIGURE 2. Country scientific production in topics related to photosynthesis in high tropical Andean fruits. The intensity of the blue color indicates a higher number of articles published during the 2000-2023 period.

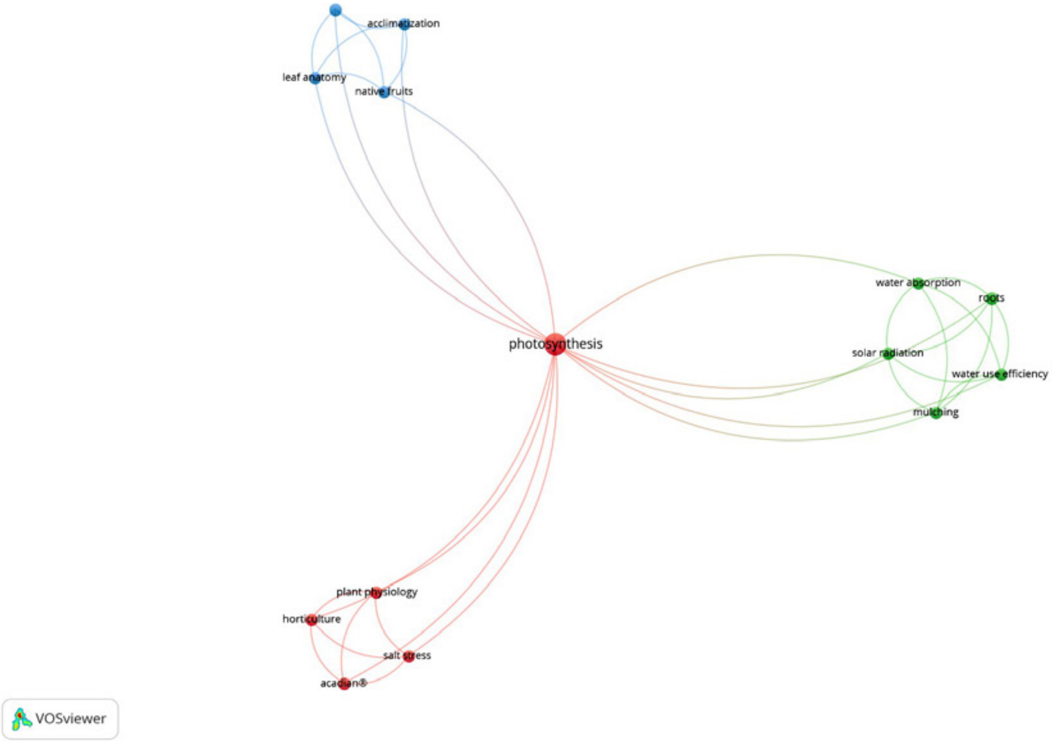

FIGURE 3. Network map based on co-occurrence of terms on titles and abstracts related to photosynthesis in high tropical Andean fruits. Colors indicate clusters of related terms identified by VOSviewer.

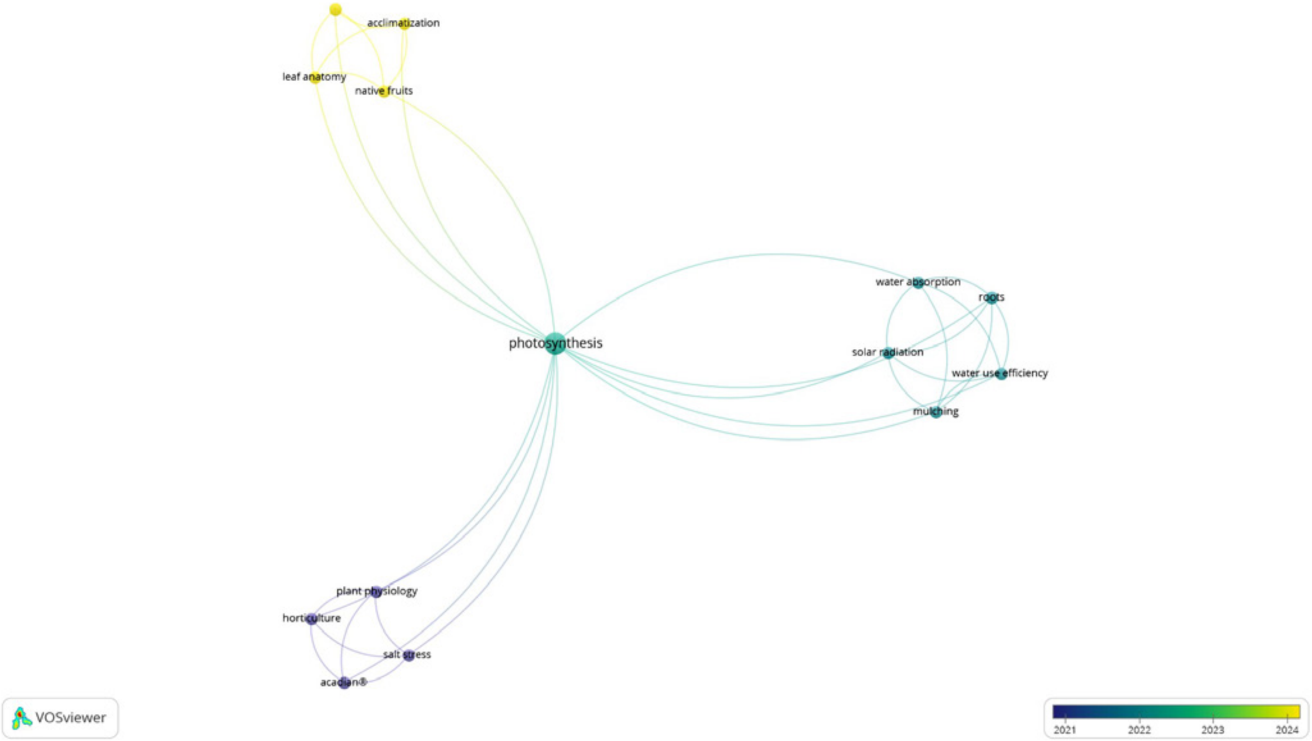

FIGURE 4. Network map based on co-occurrence over time of the terms presented on titles and abstracts related to photosynthesis in high tropical Andean fruits.

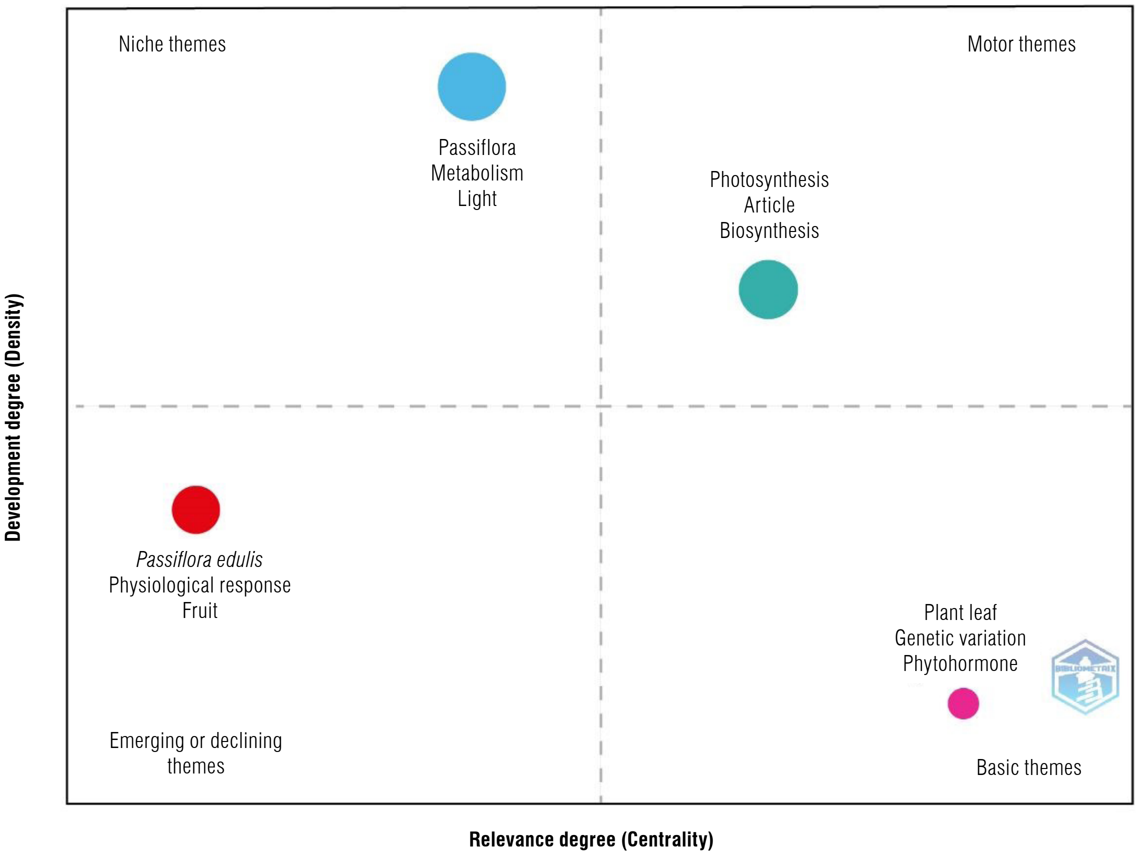

FIGURE 5. Cluster of the author keywords related to photosynthesis in high tropical Andean fruit species. Each bubble represents a network cluster, and the bubble position is set according to the cluster's Callon centrality and density.

Main aspects of photosynthesis in Andean highland fruit crops

Solanaceae fruits

Cape gooseberry

The cape gooseberry (*Physalis peruviana* L.) is native to the South American Andes. In Colombia, the widely planted material is the regional ecotype known as Ecotipo Colombia. Two important commercial varieties are also reported, Agrosavia Dorada and Agrosavia Andina (Nuñez-Zarantes *et al.*, 2024). The cape gooseberry is a C3 photosynthetic metabolism plant. It belongs to the Solanaceae family (nightshade) but also develops and is produced under direct sun, as is the case for commercial plantations in Colombia (Fischer *et al.*, 2024; Fischer & Melgarejo, 2020). For this reason, Carrillo-Perdomo *et al.* (2015) cataloged it as a light-demanding plant. A special characteristic of this fruit is the calyx that covers it throughout its development and in its green state, together with the two adjacent leaves; these are the most important sources for the production and translocation of carbohydrates to the fruit during its development (Fischer *et al.*, 2015). As tropical altitude increases, cape gooseberry plants develop a greater number of leaf stomata per leaf area to better compensate for the reduced partial gas pressure (CO_2, O_2) at higher elevations. In Colombia, this plant grows between 1,800 and 2,800 m a.s.l. (Fischer *et al.*, 2024; Fischer, Parra-Coronado *et al.*, 2022) and, in Ecuador, it grows at elevations up to 3,300 m. Its temperature and precipitation range are 13°C - 16°C and 1,000-1,800 mm per year, respectively (Fischer & Melgarejo, 2020).

Under open field conditions in Bogotá, Colombia (2,556 m a.s.l.), Fischer and Melgarejo (2020) reported an average rate of maximum photosynthesis A_{max} = 10.545 µmol CO_2 m^{-2} s^{-1}. This rate was measured within the range of 0 to 1,500 µmol photons m^{-2} s^{-1} (to 18°C and 400 ppm CO_2), using the Light Curve methodology (Light response curve methodology *A*/PFFD). Multiple measurements were made on leaves close to the source-sink, with an A_{max} between 8 and 15 µmol CO_2 m^{-2} s^{-1}; light compensation point I*c* = 13.645 µmol CO_2 m^{-2} s^{-1}; light saturation constant = 416 µmol photons m^{-2} s^{-1}; dark respiration Rd = 0.6496 µmol

CO_2 m^{-2} s^{-1}; and photosynthetic efficiency $\varphi = 0.03011$ µmol CO_2 µmol^{-1} photons (Tab. 1). Therefore, areas with solar radiation from 900 to 1,500 µmol photons m^{-2} s^{-1} are suitable for the cultivation of cape gooseberry, allowing high photosynthesis rates and, with optimal crop management, high yields and fruit quality (Fischer & Melgarejo, 2020).

In the above-mentioned study, the plants and leaves of the cape gooseberry in Bogotá (Colombia), with response curves of net photosynthesis to CO_2 concentrations between 0 to 600 Ci, had a maximum carboxylation rate of Rubisco V_{cmax} = 75.70 µmol CO_2 m^{-2} s^{-1} and a maximum regeneration rate of ribulose-1.5-bisphosphate, controlled by electron transport J_{max} = 288.09 µmol CO_2 m^{-2} s^{-1} (Fischer & Melgarejo, 2020). Additionally, through the measurements of the fluorescence of chlorophyll *a* under the same conditions, the cape gooseberry had a maximum potential quantum efficiency of PSII (*Fv/Fm*) of 0.82. This shows that there is no damage to photosystems and that the plant performed well in energy transduction, with no photoinhibition (Maxwell & Johnson, 2000). Other values of chlorophyll *a* fluorescence parameters include an electron transport rate (ETR) around 8.3 µmol electrons m^{-2} s^{-1} and QP close to 0.77 (Tab. 2) (Chávez *et al.*, 2019).

Several studies on the cape gooseberry measured photosynthesis and/or fluorescence of chlorophyll to elucidate its response to stress conditions. Barbosa *et al.* (2019), applying irrigation indices of 50, 100, 125 and 150% of the reference evapotranspiration (ETo) in cape gooseberry plants, found that 125% and 150% of the ETo led to a lower stomatal restriction with a higher assimilation rate of CO_2, foliar transpiration and intrinsic water use (WUEi) than with a lower volume of irrigation. Segura-Monroy *et al.* (2015) reported for cape gooseberry that water deficit caused reductions in the chlorophyll index and stomatal density and an increase in the trichome density, while foliar application sprays with kaolin improved *Fv/Fm* and water use efficiency by reducing the leaf transpiration rate and the leaf temperature (Segura-Monroy *et al.*, 2015).

TABLE 1. Photosynthetic parameters of various high tropical Andean fruit crops. Light compensation point (I*c*) (µmol photons m^{-2} s^{-1}), light saturation point (I*s*) (µmol photons m^{-2} s^{-1}), photosynthetic rate at light saturation (A_{max}) (µmol CO_2 m^{-2} s^{-1}), and efficiency of photosynthesis (ΦPPFD) measured under Colombian high-altitude conditions.

Species and conditions	I*c*	I*s*	A_{max}	ΦPPFD	Reference
Physalis peruviana, vegetative phase, Bogotá (2556 m a.s.l.)	13.65	~416	10.55	0.03011	Fischer & Melgarejo (2020)
Solanum betaceum, vegetative phase, Bogotá (2556 m a.s.l.)	35.1	-	6.8	-	Ramírez-Soler *et al.* (2021)
Passiflora edulis Sims, flowering, Tena municipality (2090 m a.s.l.)	13.37	419.54	19.93	0.042	Pérez Martínez & Melgarejo Muñoz (2015)
Passiflora edulis Sims, flowering, Granada municipality (2230 m a.s.l.)	15.31	1161.44	15.84	0.024	Pérez Martínez & Melgarejo Muñoz (2015)
Passiflora ligularis Juss., vegetative phase, Santa María municipality (2060 m a.s.l.)	39.63	285.04	19.44	0.036	Rodríguez-Castillo & Melgarejo (2015)
Passiflora ligularis Juss., reproductive phase, Santa María municipality (2060 m a.s.l.)	34.66	661.38	23.61	0.044	Fernández *et al.* (2014)
Passiflora tripartita var. *mollissima*, reproductive phase, Pasca municipality (2498 m a.s.l.)	19.07	584.78	16.09	0.031	Mayorga (2016)

TABLE 2. Parameters of chlorophyll *a* fluorescence of different high tropical Andean fruit crops measured in Colombia. *Fv/Fm*: maximum potential quantum efficiency of PSII, QP: photochemical quenching, NPQ: non-photochemical quenching, ETR: electron transport rate, ϕPSII: PSII operating efficiency.

Species and conditions	*Fv/Fm*	QP	NPQ	ETR (µmol electrons m^{-2} s^{-1})	PSII operating efficiency (ϕPSII)	Reference
Physalis peruviana	0.82	-	-	-	-	Fischer and Melgarejo (2020)
Physalis peruviana, vegetative phase, Bogotá (2556 m a.s.l.)	~0.77	~0.77	~1	~8.3	-	Chávez-Arias *et al.* (2019)
Solanum betaceum, vegetative phase, Bogotá (2556 m a.s.l.)	0.81	-	-	-	-	Ramírez *et al.* (2021)
Solanum quitoense, vegetative phase, Bogotá (2556 m a.s.l.)	~0.79	~0.47	~1.7	-	-	Castañeda-Murillo *et al.* (2022)
Passiflora edulis Sims, vegetative phase, Bogotá (2556 m a.s.l.)	0.81	-	-	-	~0.5-0.8	Cárdenas-Pira *et al.* (2021)
Passiflora ligularis Juss., reproductive phase, Santa María municipality (2060 m a.s.l.)	0.87	-	-	-	~0.35-0.55	Fernández *et al.* (2014)
Passiflora tripartita var. *mollissima*, reproductive phase, Pasca municipality (2498 m a.s.l.)	0.825	-	-	-	0.580-0.600	Mayorga (2016)

In cape gooseberry plants flooded for 4, 6 or 8 d, stomatal conductance (*gs*), photosynthetic pigments, chlorophyll fluorescence parameters (*Fv/Fm*, ETR, and QP) decreased as the waterlogging period increased. These effects were more pronounced in plants inoculated with *Fusarium oxysporum* f. sp. *physali*, indicating a low acclimatization to flooding conditions greater than 6 d in soils with *Fusarium* (Chávez-Arias *et al*., 2019). In another study on cape gooseberry stressed by inoculation with *Fusarium*, Chávez-Arias *et al*. (2020) observed that three applications of brassinosteroids, salicylic acid, and jasmonic acid promoted chlorophyll fluorescence, contents of photosynthetic pigments, *gs*, water potential (Ψw), proline synthesis, and plant growth.

Lulo

To date, two varieties of this plant have been reported. The first is *Solanum quitoense* var. *septentrionale*, which is a variety with thorns adapted to understory conditions. The second is *Solanum quitoense* var. *quitoense*, a thornless variety that adapts to areas with greater sun exposure (Ardila *et al*., 2015; Jaime-Guerrero *et al*., 2022). According to Jaime-Guerrero *et al*. (2022), the lulo (or naranjilla) grows better under shading and can present modifications in photosynthetic capacity when exposed to full sun. Excess solar radiation can cause photoinhibition (Fig. 6) (Sogamoso Alape, 2020). Under temperate conditions of Central Europe, supplemental lighting in winter increased flower and fruit numbers but not yield (Messinger & Lauerer, 2015). Under tropical Andean conditions, lulo plants grow well in ranges of 1,600-2,400 m a.s.l., temperatures between 16 and 24°C and precipitation ranging from 1,000 to 2,800 mm per year (Jaime-Guerrero *et al*., 2022; Paull & Duarte, 2012).

The lulo is a C3 photosynthetic plant that derives minimal benefit from additional light above 500 µmol m^{-2} s^{-1} of photonic flow (Ardila *et al*., 2015). Medina Cano *et al*. (2006) obtained net photosynthesis averages close to 8 µmol CO_2 m^{-2} s^{-1} during the first 84 d after transplanting. These same authors reported that the contents of chlorophyll

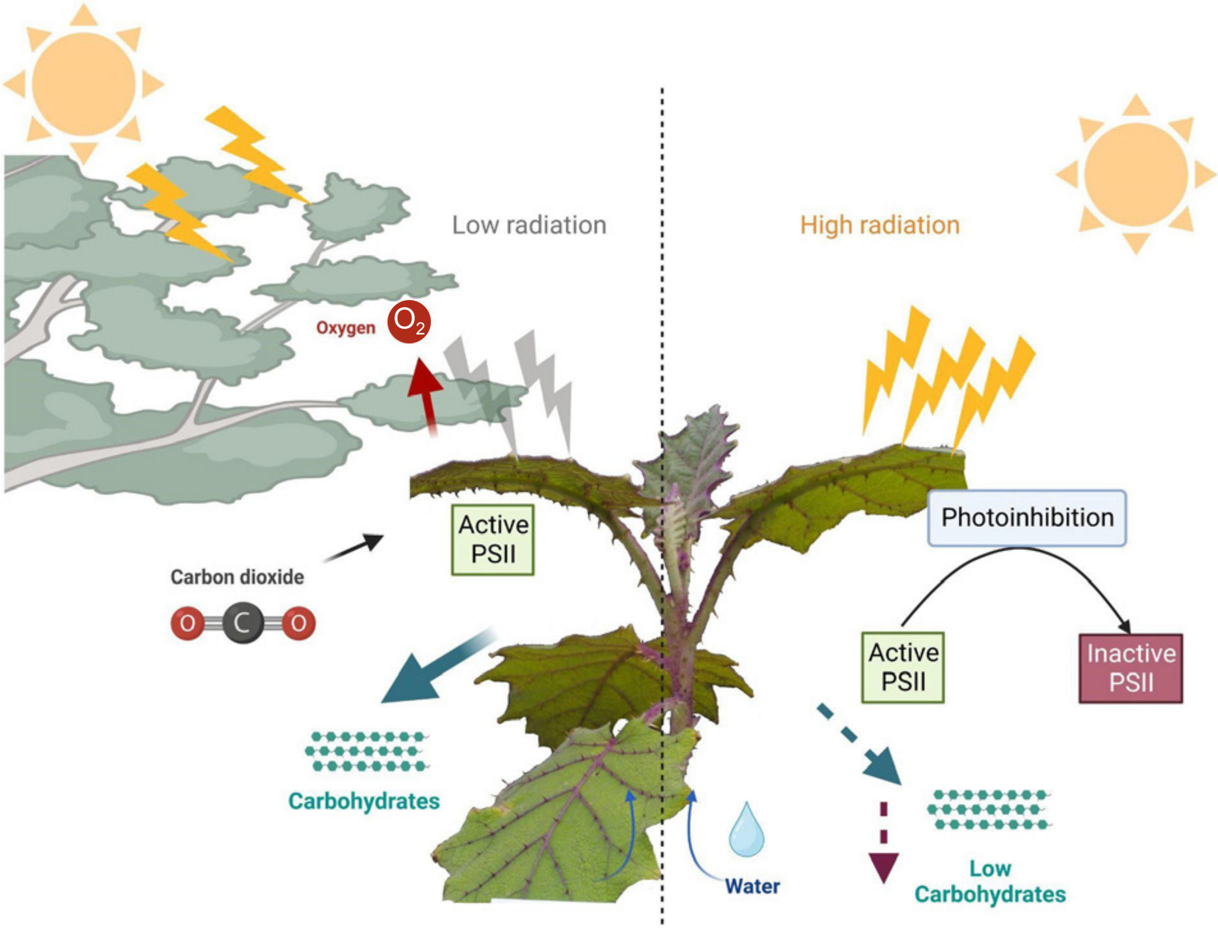

FIGURE 6. Schematic overview of photosynthesis process in lulo or naranjilla (*Solanum quitoense*) plants. Left side: Shadow condition available photosynthesis process, active PSII drives electron to ATP and NADPH for Calvin cycle reactions and carbohydrate synthesis. Right side: Light excess in non-shading conditions causes photoinhibition and reduces photosynthetic rates.

a, chlorophyll *b*, and total chlorophyll in lulo plants are higher in the transplanting stage (4.24, 1.14, and 4.33 mg g^{-1} of fresh weight (FW), respectively) than in production (1.66, 0.58, and 2.98 mg g^{-1} FW, respectively). This higher chlorophyll content during transplanting is attributed to the plants having a small photosynthetic area with high chlorophyll concentrations. Shade-grown plants, when transferred to high-radiation conditions, decrease their chlorophyll *a* content (Medina Cano *et al.*, 2006).

Lulo with thorns presents higher contents of total protein and greater activity of Rubisco and PEP carboxylase compared to lulo without thorns (Medina Cano *et al.*, 2006). During the development of these two types of lulo, the photosynthesis rates were similar. Greater photosynthesis rates were observed up to 84 d after transplanting to the field. These rates then decreased dramatically, followed by small increases. However, interestingly, photosynthesis was greater in the two upper leaf strata of the plants, which received more PAR, than the lower strata of the plants (Medina Cano *et al.*, 2006). However, there are no reported photosynthetic parameters obtained from light curves in lulo.

The use of algae-based bio-stimulants in lulo plants is recommended. These treatments, both to the soil and soil + foliar, can increase the net photosynthesis rate to close to 6 µmol CO_2 m^{-2} s^{-1}, almost twice that reported for control plants. Bio-stimulants also generated a positive effect on *gs*, transpiration rate, efficient use of water (WUE), *Fv/Fm*, and chlorophyll content in leaves (Díaz-Leguizamón *et al.*, 2016).

Regarding the light phase of photosynthesis, Sánchez-Reinoso *et al.* (2019) found that measuring chlorophyll *a* fluorescence is a useful tool to characterize the lulo seedlings under stress conditions in terms of maximum quantum efficiency of the PSII, the effective photochemical quantum yield of PSII and the QP. Castañeda-Murillo *et al.* (2022) report control values of *Fv/Fm* close to 0.79, QP~0.47 and NPQ~1.7 for lulo plants (Tab. 2).

Several factors affect photosynthesis in lulo plants, mainly those related to availability of soil water and light. Lulo is susceptible to waterlogging conditions, and this stress condition generates reductions in shoot length, stomatal conductance, plant transpiration, and leaf chlorophyll pigments (Flórez-Velasco *et al.*, 2015). In addition, lulo plants are more susceptible to waterlogging stress than to shading as waterlogging leads to damage at the level of PSII and a decrease in the chlorophyll content. Plants with waterlogging stress under shading tolerated the stress more than those cultivated in full light (Sánchez-Reinoso *et al.*, 2019). Interestingly, foliar N applications helped to mitigate the negative effects of waterlogging by increasing leaf chlorophyll concentration, *Fv/Fm* value, and nitrogen use efficiency (Flórez-Velasco *et al.*, 2015).

Under water deficit conditions, for example, during the dry seasons of the year, lulo plants present a reduction in *Fv/Fm* ratio, leaf gas exchange properties, total biomass, and relative water content (Castañeda-Murillo *et al.*, 2022). This indicates that water stress is a condition that negatively affects lulo plants, necessitating alternatives that mitigate these effects. In this regard, DI-31 (brassinosteroid analog) sprays enhance the photochemical efficiency of PSII, plant growth, and the concentration of photosynthetic pigments, and reduce lipid peroxidation of membranes under drought conditions (Castañeda-Murillo *et al.*, 2022).

Tree tomato

The Solanaceae tree tomato (*Solanum betaceum* Cav.) is an important crop native to South America (Ramírez & Kalla-rackal, 2019). The best conditions for its commercial cultivation in Colombia are altitudes between 1,800 and 2,600 m a.s.l., temperatures between 13 and 20°C, and precipitation between 1,500–2,000 mm per year (Bonnet & Cárdenas, 2012). In subtropical zones, the crop can be grown down to sea level (Blancke, 2016). The plant does not resist prolonged drought, which particularly affects flowering due to its very superficial root system (Carrillo-Perdomo *et al.*, 2015; Ramírez & Kallarackal, 2019). Additionally, warm temperatures affect the reproductive phases of this plant (Carrillo-Perdomo *et al.*, 2015). Ramirez and Kallarackal (2019) mentioned different cultivars of tomato tree, including cv. Mora, cv. Mango, cv. Common, and cv. Common crossed with cucubo (*Solanum ovalifolium*).

A study conducted in Pasca (Cundinamarca, Colombia) at 2,452 m a.s.l. with tree tomato plants in the juvenile phase of growth using light curve methodology found a maximum photosynthesis rate of 17.477 µmol CO_2 m^{-2} s^{-1}, a light compensation point of 54.42 µmol photons m^{-2} s^{-1}, a saturation constant (K) of 613.08 µmol photons m^{-2} s^{-1}, and dark respiration of -0.0008 µmol CO_2 m^{-2} s^{-1} (Niño & Cotrino, 2015). Lower values in some of these parameters were observed in plants grown under the conditions of Bogotá (Colombia), with an A_{max} of 6.8 and a light compensation point of 35.1 µmol photons m^{-2} s^{-1}. However, in the photo phase, an *Fv/Fm* of 0.81 was reported (Tabs. 1 and 2) (Ramírez-Soler *et al.*, 2021), indicating ecophysiological factors that affect the photosynthetic responses, which remain largely unexplored in tree tomato plants.

The growth of tree tomato plants could be affected by low nitrogen levels. A nitrogen concentration of 10 mg N L^{-1} results in an *Fv/Fm* ratio of 0.5 and a chlorophyll index (in SPAD units) of 12.7, while a level of 150 mg N L^{-1} results in a higher *Fv/Fm* ratio of 0.62 and a SPAD value of 37.5 (Betancourt-Osorio *et al*., 2016). In this same study, 5-d flood periods caused a 75% reduction in the leaf area and a 50% reduction in the nitrogen use efficiency; however, the flooding increased the partition of photoassimilates to the stem.

Potassium (K) is the second most important mineral nutrient absorbed by the tree tomato plants after nitrogen (N) (Clark & Richardson, 2002). Clavijo-Sánchez *et al*. (2015) found that tomato tree plants maintained with an optimal nutritional level of K^+ (applying 2.5 mm KCl) had better acclimatization to drought conditions since their WUE did not fall drastically despite having stomatal conductance and low transpiration. Also, Ramírez-Soler *et al*. (2021) confirmed the importance of K for the correct physiological functioning of the tree tomato plants, as deficient K (without KCl and KNO_3 in the nutrient solution) reduced the $A_{\max}$ (66%), Ic, transpiration rate (E), *Fv/Fm*, and the contents of chlorophylls *a*, *b*, and total chlorophyll, but increased the stomatal resistance and the thickness of the upper and lower epidermis of the leaves. Lu *et al*. (2016) suggest that K deficiency decreases the photosynthetic rate due to the lower activity of Rubisco and the activation of the pyruvate kinase.

Passifloraceae fruits

Gulupa

Several ecophysiological studies in gulupa (purple passion fruit, *Passiflora edulis* f. *edulis* Sims) and other passion fruits confirm the adaptability of these to the climatic conditions of tropical regions (Mayorga *et al*., 2020; Rodríguez *et al*., 2019). In Colombia, this fruit species is well adapted to 1,600–2,300 m a.s.l., 15-22°C temperature and 1,800–2,300 mm precipitation per year (Ocampo & Posada, 2012; Ocampo *et al*., 2020).

Sánchez *et al*. (2013) found a positive correlation in gulupa between stomatal opening and temperature and solar radiation, while observing a negative correlation between relative humidity and stomatal opening. On average, they found 107 stomata per mm^2 leaf surface. The stomata are responsible not only for the control of the entry of CO_2 for photosynthesis but also for the optimization of WUE (Bergmann & Sack, 2007). In another study on the purple passion fruit "maypop" (*P. incarnata*), García-Castro *et al*. (2017) observed an exponential decrease in the photosynthetic rate when soil water potential becomes more negative than -1.0 MPa, although the plants promptly reestablished their gas exchange after being watered at 100%. Lozano-Montaña *et al*. (2021) showed that the gulupa plant prevents water loss under progressive drought stress by stomata closure, modulation of growth, and accumulation of proline and sugars in leaves, while promoting root growth, although total chlorophyll content in leaves decreased. These authors suggest that their results should be complemented by future studies on gas exchange analysis and measurements of fluorescence of chlorophyll *a*. The gulupa is classified as moderately tolerant to water stress (Crane *et al*., 2019) and displays isohydric behavior, avoiding water loss as a response strategy (Lozano-Montaña *et al*., 2021). Also, Jiménez-Bohorquez *et al*. (2024) found a reduction in *gs* in gulupa grafted on *Passiflora maliformis* when irrigation was reduced to 50% and 25%, while *Fv/Fm* was not affected.

Mineral nutrition is one of the most important factors that affect photosynthesis (Lambers & Oliveira, 2019; Rengel *et al*., 2023). Cárdenas-Pira *et al*. (2021) conducted a study using the missing element methodology on gulupa seedlings. They found that the seedlings subjected to Fe deficiency had the lowest $A_{\max}$ with 1.72 µmol CO_2 m^{-2} s^{-1}. They also found that a deficiency of Mg generated the least apparent quantum efficiency (0.008 µmol CO_2 µmol $photons^{-1}$), while the lack of P induced the lowest maximum photochemical efficiency values of photosystem II, *Fv/Fm* (0.69). The nutrient deficiencies, mainly of Fe or Mg, negatively affected photosynthesis in gulupa plants at the vegetative stage of growth (Cárdenas-Pira *et al*., 2021).

Salinity considerably affects the growth of *P. edulis* plants. With a dose of 150 mm of NaCl, growth was reduced due to negative effects on gaseous exchange parameters such as net photosynthetic rate (*A*), E and *gs*, and the synthesis of chlorophyll (Lima *et al*., 2020). Interestingly, *P. mucronata* exhibited better salt tolerance and maintenance of photosynthesis, conductance and stomatal functionality (Lima *et al*., 2020). Therefore, this species has a potential for use in improvement programs or as a rootstock for commercial passion fruit crops.

Rodríguez Castillo *et al*. (2020) described landraces of gulupa in Colombia characterized by minimal branching and longer internodes, requiring less pruning. In addition, the location of their leaves, with longer internodes, above the trellis system, provides better exposure of the canopy to sunlight and, thus, greater photosynthetic capacity. Also, in Cundinamarca, some gulupa landraces showed better adaptation to conditions in the high-elevation municipality of Susacón (2,500 m a.s.l.) than those in Pasca (1,800 m a.s.l.). Photosynthesis measurements confirmed these varieties' broad adaptive response to the highest zone, an important result given the need to cultivate gulupa at higher altitudes due to global warming (Rodríguez *et al*., 2019). Likewise, the authors concluded that these genotypes, under high-altitude tropical conditions, must present not only high efficiency in the use of water but also in photosynthesis, so that they adapt better to these colder and drier sites, compared to those of medium-sized elevations that are more humid and warmer.

Pérez Martínez and Melgarejo Muñoz (2015) compared three sites of gulupa cultivation in Cundinamarca (Colombia) and concluded that the municipality of Granada (2,230 m a.s.l., 15°C average temperature) offers conditions for optimal physiological performance due to differences in soil moisture content, vapor-pressure deficit (VPD) and temperature (day/night 18/13°C), as well as solar radiation $\leq$1,000 µmol photons m^{-2} and 0.5 kPa VPD. These conditions support the recovery of the foliar water status and photosystems, particularly when combined with a low VPD in the daytime. The cultivation sites affected the photosynthetic parameters (Tabs. 1 and 2), indicating the great importance of the environment for the physiology of gulupa. However, photosynthetic parameters also vary depending on the phenological stage of this fruit species (Pérez Martínez & Melgarejo Muñoz, 2015).

In addition, Tominaga *et al*. (2018) evaluated the overestimation of calculated $C_{i(c)}$ without stimulating stomatal closure. The researchers measured gas exchange and $C_{\mathrm{i(m)}}$ simultaneously in hypostomatous leaves of gulupa. They concluded that direct measurement of C_{i} is a more accurate estimate than the calculation when stomatal gas transport is restricted (Tominaga *et al*., 2018).

Sweet granadilla

Miranda (2020) reported that sweet granadilla (*Passiflora ligularis*), native to tropical America, has various ecotypes, including Criolla, Pecosa, Valluna, Urrao, Cascara de huevo, and Huila. In Colombia, sweet granadilla best adapts to elevations of 1,800-2,600 m a.s.l. (Miranda, 2020), with growth temperatures of 15-23°C and precipitation between 800 and 1,500 mm per year. Research on sweet granadilla aiming to characterize its ecophysiology at different altitudes in the Huila department (Colombia) found $A_{\max}$ of 23.6 µmol CO_2 m^{-2} s^{-1}, I*c* of 34.6 µmol m^{-2} s^{-1} (Tab. 1) and dark respiration of 2.24 µmol CO_2 m^{-2} s^{-1} with average temperature conditions of 17.15°C, and photosynthetically active radiation (PAR) of 1,186.2 µmol photons m^{-2} s^{-1} at altitudes of 2,060 m a.s.l. However, an altitude of 2,270 m a.s.l. reduced the photosynthetic performance of sweet granadilla, with A_{max} of 17.5 µmol CO_2 m^{-2} s^{-1}, dark respiration of 1.34 µmol CO_2 m^{-2} s^{-1}, and I*c* of 21 µmol m^{-2} s^{-1}, observed in plants without stress (Fernández *et al*., 2014).

These photosynthetic parameters are not only affected by the area in which the sweet granadilla is cultivated but also by the phenological state as well as the time of day. For more details on this, refer to Rodríguez and Melgarejo (2015).

Banana passion fruit

In Colombia, commercial banana passion fruit (*Passiflora tripartita* var. *mollissima*) cultivation is found in zones of 1,800–3,200 m a.s.l., with temperatures of 13-16°C, and precipitation between 1,000 and 1,500 mm per year. The main variety is Castilla (Campos & Quintero, 2012; Fischer *et al*., 2020a). The ecophysiology of banana passion fruit is not well studied (Mayorga, 2016). As in several other fruit species, the banana passion fruit shows an increase in total soluble solids in the fruits with the increase in altitude, which could be related to the higher photosynthetic activity in the leaves adjacent to the fruits due to the high luminosity at these elevations (Mayorga *et al*., 2020). Therefore, the temperature must be within the optimal range of the species and/or the respiratory loss of carbohydrates must be lower due to the lower night temperature at these altitudes (Fischer *et al*., 2016).

Mayorga (2016) compared photosynthesis and efficient water use in banana passion fruit plants at two altitudes in Pasca (Cundinamarca) of 2,498 m a.s.l. (13.9°C, PAR of 680 µmol photons m^{-2} s^{-1}) and 2,006 m a.s.l. (17.8°C, PAR of 620 µmol photons m^{-2} s^{-1}). This study found that the banana passion fruit in the vegetative phase developed greater photosynthetic rates, while during flowering the plants showed high water-use efficiency, low transpiration, large water potentials, and high *Fv/Fm* (Tab. 2) compared to the fructification phase, which had lower photosynthetic rates and lower water-use efficiency. At 2,006 m a.s.l., the *Fv/Fm* was higher in plants in a vegetative stage of growth, and at 2,498 m a.s.l. it was higher during fructification. In the higher zone, the transpiration rate of the plants was reduced, which increased the WUE and water potentials. Due to the higher temperature in the lower zone, the banana passion fruit reached each of its phenological stages in less time compared to those of the higher zone, but with smaller fruits. These results suggest that the high zone better favors the development of the plants; however, each of the two sites affected the phenology and physiology differently due to climatic factors. The parameters of the light curve reported by Mayorga (2016) are included in Table 1.

Applications of N, K, and Mg to banana passion fruit at the amounts zero, low, and high resulted in the accumulation of plant dry matter (DW) only at a high amount of N. This finding aligns with the Thornley model, with accumulation of DW in the roots and its subsequent partition to above-ground plant parts (Lizarazo *et al.*, 2013). This result confirms the importance of N and its foliar level, which is closely related to the content of chlorophyll, Rubisco activity, the quantum performance of photosynthesis, and the electron transport rate, processes that directly affect photosynthetic efficiency (Sanclemente & Peña, 2008).

Myrtaceae fruits

Feijoa

Feijoa (*Acca sellowiana*), native to South America, has a high degree of adaptation to the agroecological conditions of the tropical Andean area (Naizaque *et al.*, 2014). Different varieties and clones have been reported, as detailed in Parra-Coronado and Fischer (2013). In Colombia, it is commercially grown at altitudes between 1,800 and 2,700 m a.s.l., with average temperatures between 13 and 21°C and precipitation of 700-1,200 mm per year (Fischer *et al.*, 2020; Fischer & Parra-Coronado, 2020). Feijoa requires a base temperature of only 1.76°C from fruit set to harvest (Fischer & Parra-Coronado, 2020; Parra-Coronado, Fischer *et al.*, 2015). In temperate and subtropical regions of the world, feijoa restarts its growth, sprouting of branches, and formation of floral buttons when temperatures increase in spring, but in the tropics it grows and produces fruits throughout the year, favored by the rainy season or irrigation (Fischer, 2003).

Solar radiation is a very important factor in the development, production, and quality of feijoa fruits. In Colombia (Cundinamarca), a study during two harvest seasons comparing average radiation of 11,082 W m^{-2} at 2,580 m a.s.l. and 8,918 W m^{-2} at 1,800 m a.s.l. found that the higher elevation generated fruits of greater weight and higher content of soluble solids (Parra-Coronado, Fischer, Camacho *et al.*, 2015) and sucrose (Parra-Coronado *et al.*, 2022). The authors concluded that the higher temperature at the lower site led to greater respiration and loss of sugars in these fruits.

This differential reaction of the feijoa to solar radiation was also found by Silva *et al.* (2024) in feijoa saplings. These saplings had optimal growth under direct light or shade up to 30%, but when exposed to a shade of 80%, they developed larger leaves with lower thickness, reduced rate of CO_2 assimilation and electron transport and greater quantum performance of photosystem II. As in the other Andean fruit crops, the fruits unprotected by foliage suffer sunburn, stomatal closure, and photoinhibition, especially if the high-radiation periods, particularly of UV light, are extended (Fischer, Orduz-Rodríguez *et al.*, 2022).

Naizaque *et al.* (2014) studied the reception of light by the different strata of the canopy of feijoa trees and observed, in the leaves of the upper stratum, a higher rate of transpiration and higher number of stomata per unit of leaf area (91 stomata/mm^2) than in the lower stratum (78 stomata/mm^2). In their study, foliar transpiration directly increased with the temperature (being higher in the upper stratum than in the lower one) and with a higher irradiance, leading to increased transpiration as relative humidity decreased. When comparing the incident solar radiation in the two strata of the feijoa, Martínez-Vega *et al.* (2008) measured an average of 90% radiation in the upper stratum, while in the lower interior stratum only 35% of the incident radiation was found. This shows that pruning and training of this cone-shaped plant with horizontal side branches guarantee maximum photosynthesis throughout the canopy (Fischer *et al.*, 2020).

Germanà and Continella (2004) found that feijoa grown under the climatic conditions of Sicily had a low photosynthetic rate (on average between 4 and 6 μmol CO_2 m^{-2} s^{-1}), with a high energy demand during the bloom. Under these conditions, the feijoa plants, due to the high stomatal transpiration and low stomatal resistance, presented a WUE of only 1/3 that of the avocado and the custard apple.

Observing the behavior of several varieties of feijoa in southern Russia with subtropical climate, where the development of the fruits coincides with the dry season, Omarova *et al.* (2020) found that, in the Dagomyskaja variety, the intensity of respiration exceeds photosynthesis. This finding suggests that adaptation to drought abiotic stress depends considerably on the genotype. Also, Peña Baracaldo and Cabezas Gutiérrez (2014) reported in a study in Colombia at 2,450 m a.s.l. that feijoa plants without additional irrigation developed lower leaf area index, compared to the largest index with 50% irrigation. This reduced leaf area index would greatly limit the ability of the plants to capture light and restrict the production of photoassimilates in these non-irrigated plants.

Despite the advances mentioned in feijoa research, we did not find reports that indicate the characterization of parameters of photosynthesis in this species, such as fluorescence of chlorophyll *a* and gas exchange.

General discussion

This review consolidates the main advances in the current knowledge of photosynthesis in high tropical Andean fruit crops. This knowledge of photosynthesis should be used as a priority to generate strategies focused on increasing yield (Li *et al.* 2018) and quality at harvest. In the high tropical Andean areas, an increase in photosynthesis due to the higher solar radiation can favor fruit quality parameters, such as soluble solid contents, as has been observed in feijoa and banana passion fruit (Fischer *et al.*, 2024; Mayorga *et al.*, 2020).

The reviewed studies report important advances in the understanding of fluorescence of chlorophyll *a* and gas exchange, with a good part of these studies carried out in the main fruit producing countries, Brazil and Colombia (Fig. 2). However, these advances lag behind those achieved in species of the low tropics, subtropical, and temperate areas. This is evidenced in the modest number of articles published on these topics. The greatest number of studies have been done on cape gooseberry and gulupa, high-altitude species that are most exported. The above shows that the progress in research is related to the economic importance of fruit crops.

Fluorescence of chlorophyll *a*

As expected, the most frequently characterized parameter in the high tropical Andean fruit crops has been *Fv/Fm* (Tab. 2), mainly because it is an indicator widely used to determine the physiological status of the plants. In the reported fruit crops, *Fv/Fm* ranges from ~0.77 to 0.87 in non-stress conditions (Tab. 2). To a lesser extent, parameters such as QP, NPQ, ϕPSII, and ETR have been used. These parameters have been used as indicators of the physiological behavior of fruit plants in different agroecological zones, providing insight into the most appropriate areas for crop, as mainly reported for sweet granadilla and banana passion fruit (Fernández *et al.*, 2014; Mayorga, 2016). However, these indicators have been most utilized in studies of physiological response of the fruit crops to biotic stress conditions (e.g., *Fusarium*) and abiotic stress conditions. In the latter case, experiments have focused on characteristic conditions of climatic variability, such as water deficit, waterlogging, nutrient deficit, and even overshading (Cárdenas-Pira *et al.*, 2021; Castañeda-Murillo *et al.*, 2022; Chávez-Arias *et al.*, 2019; Sánchez-Reinoso *et al.*, 2019; Segura-Monroy *et al.*, 2015). The trend indicates that the fluorescence of chlorophyll *a* has been mainly used as a tool to characterize the ecophysiological response of these fruit crops.

It is important to investigate further the response of the photo-phase of the photosynthesis in the high tropical Andean fruit crops under conditions of salinity stress, one of the most important types of stress in agriculture (Eswar *et al.*, 2021). It should also be noted that there is very little information on the tree tomato, a fruit crop with an important cultivated area (Ramírez *et al.*, 2021), and feijoa, a fruit crop that is grown in several countries in the world (Fischer & Parra-Coronado, 2020).

Gas exchange

Significant contributions are evidenced through light response curves (Tab. 1) for cape gooseberry, tree tomato, gulupa, sweet granadilla, and banana passion fruit (Fernández *et al.*, 2014; Figueiredo *et al.*, 2021; Fischer & Melgarejo, 2020; Mayorga, 2016; Pérez Martínez & Melgarejo Muñoz, 2015, Ramírez-Soler *et al.*, 2021). The main purpose of this research has been to identify the photosynthetic performance of the plants in different ecophysiological conditions to select optimal cultivation areas. It is recommended to extend these studies of light response curves to lulo and feijoa. These studies have also included gaseous exchange measurement across times of day and in several phenological stages and are frequently complemented with measurements of fluorescence of chlorophyll *a* and plant water potential (Fernández *et al.*, 2014; Pérez Martínez & Melgarejo Muñoz, 2015).

Gas exchange parameters (*A*, *E*, *gs*, *C*i (intracellular carbon concentration)) have generally been evaluated in the high tropical Andean fruit species (Fernández *et al.*, 2014; Lima *et al.*, 2020; Pérez Martínez & Melgarejo Muñoz, 2015; Ramírez-Soler *et al.*, 2021), but these studies are scarce and do not yet provide enough detailed understanding of the photosynthetic performance of the fruit species in the various edaphoclimatic conditions of the high Andean areas. There is also a lack of CO_2 response curves of photosynthesis, with few reports available (Fischer & Melgarejo, 2020). Such curves are necessary for the current conditions of climatic variability. In addition, as atmospheric concentration of CO_2 rises in tropical highlands, plants living in 'thinner' air (low partial pressure) may benefit from increased CO_2 since leaf photosynthesis in plants rises when supplied with extra CO_2, potentially enhancing growth (Körner, 2023).

Finally, it is important to mention that there is almost no research on the morphological, biochemical, and molecular levels of the photosynthetic processes of these fruit crop species in the high tropics of the Andes. The effects of UV light, wind, relative air humidity, and temperature on the indirect features associated with photosynthesis – density of stomata, size of stomata, morphology and size of leaves, number of leaves – should be studied with priority.

Conclusions and recommendations for future research

The fruit crops produced in Andes, considered exotic fruits and important functional foods, are gaining increasing global importance. Most research into these fruit species has been carried out by producing countries to improve their productive systems. Photosynthesis is one of the most important physiological processes that determines the production and quality of crops. This review presented the main aspects and advances of research in photosynthesis of the high tropical Andean fruit crops. Bibliometric analysis shows that research on the topic has focused on the countries with the climatic conditions for the growth of these fruit species, namely Brazil and Colombia. In the past, research topics focused on horticulture and plant physiology, evolving to photosynthesis, and more recently, leaf anatomy and the acclimation process. In aspects of the photosynthetic process, in most of the analyzed species, the photosynthetic parameters such as A_{max}, I_c, I_s, and ΦPPFD are derived from light curves. Important advances in the knowledge of the fluorescence of chlorophyll *a* have been made, which are mainly used as a tool to characterize the ecophysiological response of these fruit crops.

Despite the progress reported, the understanding of the photosynthetic process in the high tropical Andean fruit species remains limited. The main findings are related to instrumental measurement under specific ecophysiological conditions, often focusing on climatic variability.

We suggest that future research be focused on elucidating the biochemical, genetic, and molecular aspects of photosynthesis. We also recommend using photosynthesis as a tool to evaluate improvements in the production system including fertilization, irrigation, pruning and training, planting densities and arrangements, bioregulators, protected cultivation, and shading nets, among others. In addition, the evaluation of new genetic materials for varieties and rootstocks is crucial. It is also necessary to study photosynthesis related to climate change, ideally in controlled conditions (phytotrons, growth chambers or free air CO_2 enrichment (FACE) chambers), varying temperature of the air and soil, solar radiation, concentration of CO_2, relative air humidity, atmospheric pressure, and other variables. Currently, there are no published reports on these aspects of photosynthesis for the high tropical Andean fruit species.

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Conflict of interest statement

The authors declare that there is no conflict of interests regarding the publication of this article.

Author's contributions

NFV: conceptualization, research, writing - original draft, visualization, writing, and editing. GF: conceptualization, writing, and supervision editing. HEBL: conceptualization, visualization, writing, and editing. All authors have read and approved the final version of the manuscript.

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