Altitude as a determinant of fruit quality with emphasis on the Andean tropics of Colombia. A review

La altitud como determinante de la calidad del fruto con énfasis en el trópico andino de Colombia. Una revisión

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ABSTRACT

Due to global warming, the highlands of the tropics have become more important for planting fruit trees. The climate at high altitudes is mainly characterized by decreased temperatures and increased solar radiation. A systematic literature review using four bibliographic databases revealed 22 studies that determined fruit quality at two altitudes. With increasing altitude, duration of fruit development was prolonged, and, in most cases, higher fresh weights and sizes were found; however, fruit firmness decreased. The intensity of the fruit color increased because of greater radiation in high areas. Mostly, the total soluble solids of the fleshy fruits augmented with altitude, probably because of an increase in photosynthesis with higher solar radiation. The total acidity did not show a clear trend with increasing elevations. At higher altitudes, the content of antioxidants (mainly phenolics) increased in the fruits, especially in the epidermis as a reaction to the increasing ultraviolet (UV) light. Physiological disorders in the fruits included sunburn and damage caused by low temperatures. Different species and varieties react differently to the conditions of highlands, depending on their origin and whether climatic conditions are optimal for a specific fruit tree. There are no positive effects on fruit quality when altitude is at the limit or above the recommended range for the fruit species.

Key words: UV radiation, temperature, fruit development, physical quality, chemical quality, physiological disorder.

RESUMEN

Debido al calentamiento global, las zonas altas de los trópicos han ganado importancia para la siembra de los frutales. El clima en estas áreas se caracteriza principalmente por tener bajas temperaturas y mayor radiación solar. Mediante una revisión de literatura sistemática en cuatro bases de datos bibliográficas se encontraron 22 estudios que determinaron la calidad de los frutos evaluada en mínimo dos altitudes. A mayor altitud el desarrollo del fruto se prolongó y en la mayoría de los casos, se encontró un mayor peso fresco y tamaño, sin embargo, la firmeza del fruto disminuyó. La intensidad del color del fruto aumentó debido a la mayor radiación en zonas altas. En la mayoría de los casos, los sólidos solubles totales de frutos jugosos se incrementaron con la altitud, probablemente, por el aumento de la fotosíntesis debido a la mayor radiación solar, mientras que la acidez total no mostró una tendencia clara con el incremento de la elevación. Con la altitud ascendente aumentó el contenido de los antioxidantes (principalmente compuestos fenólicos) en los frutos y, especialmente, en su epidermis, como reacción al aumento de luz ultravioleta (UV). Dentro de los desórdenes fisiológicos en los frutos se destacan los golpes de sol y los daños por bajas temperaturas. Las especies y variedades reaccionan de forma diferente a las condiciones de las zonas altas, dependiendo de su origen, y si las condiciones climáticas están dentro de las óptimas para este frutal. No se detectan efectos positivos sobre la calidad del fruto cuando la altitud está en el límite o por encima del rango recomendado para la especie frutal.

Palabras clave: radiación UV, temperatura, desarrollo del fruto, calidad física, calidad química, desorden fisiológico.

Introduction

The tropics have thermal uniformity, without marked temperature seasons. A reduction in temperature with increasing altitudes means that these zones have altitudinal thermal "floors" (Fischer & Orduz-Rodríguez, 2012). Since plants can grow satisfactorily only in certain temperature ranges (Das, 2012), they can only grow in a certain altitude range where the main component is temperature.

Under the colder conditions of the Andean highlands, fruit development is prolonged, and the time to harvest is increased (Mayorga *et al*., 2020), which is why larger and better quality fruits can be generated, as compared to lower

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altitudes, as seen in feijoa (Parra-Coronado *et al*., 2015, 2016, 2017a), banana passion fruit (Mayorga *et al*., 2020), and apples (Fischer *et al*., 2016; Gutiérrez-Villamil *et al*., 2022). In the tropics, each fruit crop has its optimal altitude range for meeting ecophysiological demands (Fischer & Orduz-Rodríguez, 2012).

The phytochemical compounds of fruits are considerably affected by climatic site conditions and the interaction between environmental conditions and varieties (Zeng *et al*., 2020). The environmental conditions of a particular site are crucial for fruit quality and are the basis for the development of commercial crops in a region or country (Fischer & Orduz-Rodríguez, 2012). Fruits and vegetables, which are key parts of a healthy diet, are highly exposed to the magnitude of climate change, where increased temperatures reduce production and quality, especially in the tropics and subtropics (Shukla *et al*., 2019).

However, global warming may also increase fruit production in some areas. Fischer and Melgarejo (2021) and Tito *et al.* (2018) pointed out that an overly high increase in temperature in the Andes, which would affect the growth and development of fruit trees, could be avoided by planting crops in higher altitude areas. In other parts of the world, such as India, the optimum altitudes for apple cultivation of 1,200-1,500 m a.s.l. in the 1980s shifted to 1,500-2,500 m a.s.l. in this century, with maximum elevations even exceeding 3,500 m a.s.l. (Sahu *et al*., 2020). However, Van Leeuven and Darriet (2016) stated that, in the case of wine grapes, the movement of vineyards to higher altitudes as the result of global warming has a high economic and social cost. Of course, there are also the possibilities of choosing species and varieties more adapted to the phenomenon of climate change (Yohannes, 2016) without moving to higher altitudes, apart from plant breeding programs such as the combination of genetic modification of high yield germplasm with proper crop management (Fischer *et al*., 2022). But these topics were not the objective of this review.

Ecophysiological studies are very important for finding adaptation strategies for fruit trees given changing environmental conditions (Sánchez-Reinoso *et al*., 2019). Given the fact that highlands over 1,500 m a.s.l. comprise almost a quarter of the planet's land surface (Mengist *et al*., 2020) and those tropical altitudes can be "escape zones" for global warming, the objective of this review was to characterize the effect of increasing altitudes, with an emphasis on the Andean tropics, on fruit quality to facilitate decisions for future research and for more adaptive production.

Methods

Information from different databases was used following the PRISMA guide (Preferred Reporting Items for Systematic Reviews and Meta-Analysis), applying the modified methodology of Page *et al*. (2021). The keywords "altitude" and "fruit quality" were used, in English and Spanish, which generated 500 article titles in the "Google Academic" database, of which 74 were used (14.8%). The SciELO database only had 19, with 3 (15.8%) used. ScienceDirect listed 565 titles, of which 28 (15.8%) were used, and the Redalyc had 4,268 articles, with 57 (1.3%) useful for this review. To ensure better topicality, greater emphasis was placed on publications from 2015 onwards; however, some studies from previous years were included because of their importance.

In a second filter, research conducted at only a single altitude was excluded, with a final total of 22 studies that compared fruit quality at least two different altitudes.

Tropical altitude and climatic characteristics

Since the tropics have thermal uniformity, the largest fluctuation occurs in the highlands during the 24 h cycle of a day, where daytime can be described as summer, and night can be described as winter (Fischer, 2000).

Climatic changes with increasing tropical altitudes that affect the growth, development, and quality of fruit trees include a reduction in temperature, about 0.6 to 0.7°C per 100 m (Benavides *et al*., 2017), and partial pressure of gases such as CO_2, O_2, and N_2 and water vapor (Fischer & Orduz-Rodríguez, 2012). There is also reduced precipitation which has an inverse relationship with radiation (Benavides *et al*., 2017), while the visible UV, infrared radiation, and wind increase with altitude (Fischer & Orduz-Rodríguez, 2012). Since the atmospheric layer that filters solar rays is thinner in high areas, UV radiation increases between 10 to 12% with each increase of 1,000 m in altitude (Benavides *et al*., 2017). This greater incidence of solar radiation at high elevations increases soil temperature (Fischer *et al*., 2022), favoring plant growth. In addition, the microclimate of a particular site can vary because of other factors, *e.g*., the gradient of decreasing temperature with altitude can be modified by location, time of day (Benavides *et al*., 2017), and cloudiness (Paull & Duarte, 2011).

This reduction in temperature with increasing altitude leads to zones that are suitable for fruit cultivation, classified in altitudinal thermal floors as described by Paull and

Duarte (2011) in the equatorial zone as: (1) the hot zone (0-1,000 m a.s.l.; "warm climate altitudinal zone"); (2) the temperate zone (1,000-2,000 m a.s.l.; "temperate climate altitudinal zone"); and (3) the cold zone (>2,000 m a.s.l.; "cold climate altitudinal zone"). These authors pointed out that, in these zones, the temperature depends on latitude, wind pattern, and precipitation, among other factors.

For a specific area such as Colombia, there are recommended altitude ranges for fruit trees (Tab. 1). These ranges can even be specific to the varieties of a certain fruit species, *e.g.*, the optimal altitude ranges in the Department of Boyacá in Colombia for the 'Anna' apple are 1,700 to 2,800 m a.s.l. (Fig. 1) (Gutiérrez-Villamil *et al.*, 2022), for the 'Triunfo de Viena' pear 2,400 to 2,800 m a.s.l., for the Japanese plum 'Beauty' 2,600 to 2,800 m a.s.l. (Fischer, 2000), and for feijoa 1,800 to 2,700 m a.s.l. (Parra-Coronado *et al.*, 2019). Likewise, there are recommendations for a narrower range, such as those in Table 1, which may have better production results, for example, cape gooseberry at 2,200 to 2,400 m a.s.l. (Fischer & Orduz-Rodríguez, 2012), purple passion fruit at 1,700 to 2,000 m a.s.l. (Ocampo *et al.*, 2020), fig at 2,400 to 2,500 m a.s.l. (Fischer, Almanza-Merchán & Piedrahíta, 2012), and feijoa at 2,100 to 2,600 m a.s.l. (Duarte & Paull, 2015). On the other hand, at greater proximity to the equator, temperatures increase, which is why fruit trees grow at higher altitudes there. For example, in Ecuador, there are cape gooseberry, tree tomato, and Andean blackberry crops up to an altitude of 3,300; 3,000, and 3,200 m a.s.l., respectively (Carrillo-Perdomo *et al.*, 2015).

It is important that crops are located within altitude limits because this guarantees good physiological and productive performance, *e.g.*, in an ecophysiological study on

TABLE 1. Recommended altitude ranges for Colombian Andean fruit cultivation.

Plant family	Species	Altitudinal range (m a.s.l.)	
Passifloraceae	Yellow passionfruit[1]	0	1300
	Purple passionfruit[1]	1,600	2,300
	Sweet granadilla[1]	1,800	2,600
	Banana passionfruit[1]	1,800	3,200
Solanaceae	Lulo[2]	1,600	2,400
	Tree tomato[3]	1,700	2,600
	Cape gooseberry[4]	1,800	2,800
Myrtaceae	Guava[5]	0	2,000
	Feijoa[6]	1,800	2,700
	Champa[7]	800	1,600
Ericaceae	Blueberry[8]	2,200	2,800
	Andean blueberry[9]	2,200	3,200
Rosaceae	Apple[2]	1,700	2,800
	Pear[2]	1,800	2,800
	Peach[2]	2,000	2,600
	Japanese plum[2]	1,800	2,800
	Strawberry[2]	1,800	2,700
	Andean blackberry[2]	1,500	2,600
Annonaceae	Cherimoya[2]	1,500	2,200
Lauraceae	Avocado[10]	1,200	2,600
Moraceae	Fig[11]	800	2,500
Cactaceae	Pitaya[12]	1,500	1,900

[1]Fischer and Miranda (2021); [2]Fischer and Orduz-Rodríguez (2012); [3]Bonnet and Cárdenas (2012); [4]Fischer and Melgarejo (2020); [5]Fischer and Melgarejo (2021); [6]Parra-Coronado *et al.* (2019); [7]Balaguera-López *et al.* (2022); [8]Cleves (2021); [9]Medina *et al.* (2015); [10]Carvalho *et al.* (2015); [11]Fischer, Almanza-Merchán and Piedrahíta (2012); [12]Corredor (2012).

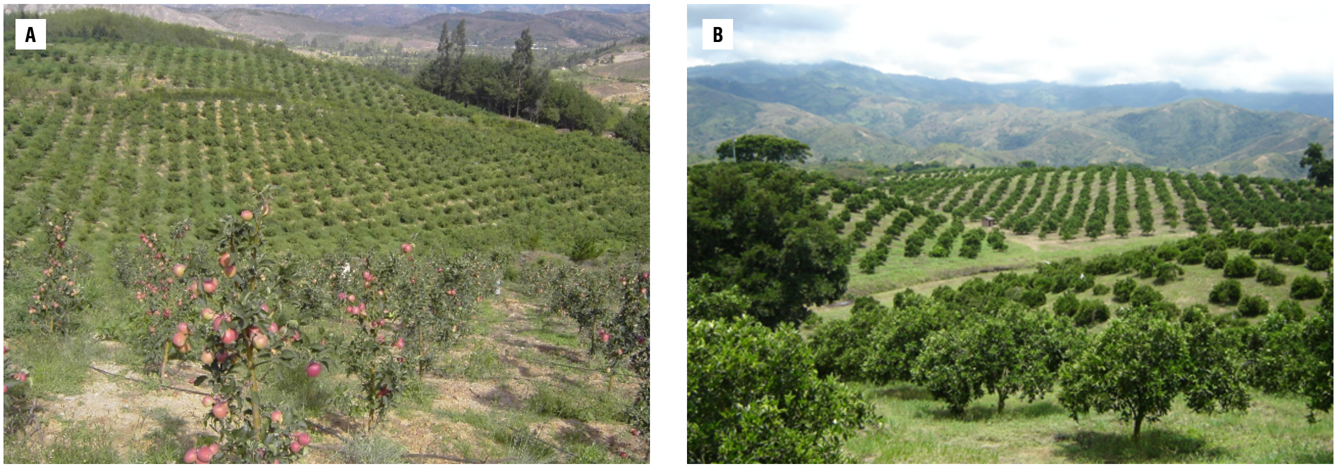

FIGURE 1. Apple orchards in the A) Boyacá highlands and B) citrus fields in the Valle department of Colombia.

passion fruit in the Department of Huila (Colombia) grown at 2,060 and 2,270 m a.s.l., the predawn values of the maximum photochemical efficiency of photosystem II (*Fv/Fm* >0.86) confirmed that the plants were not exposed to stress conditions and the two altitudes are suitable for the cultivation of passion fruit in this region (Fernández *et al*., 2014). Fruit cultivars outside their optimal altitude range do not generate economic profitability, and plants at a higher altitude grow too slowly, with lower yields and qualities. At too low altitudes, they grow too fast, without developing their typical and stable post-harvest quality (Fischer & Parra-Coronado, 2020).

Adaptation of fruit trees to highland conditions

Cultivars originating from regions near the equator and/or higher altitudes, as the case of Andean fruit crops, may have developed a greater tolerance to UV-B radiation (Caldwell *et al*., 1980). A good example of the adaptation of fruit trees to higher altitudes is the study by Voronkov *et al.* (2019), who found that the levels of phenolic substances and polyunsaturated fatty acids increased in the skin of apples with altitudes increasing from 300 to 1,200 m a.s.l. in the Caucasus. This increase in phenols protects fruits against high UV radiation because of their powerful antioxidant effects, while unsaturated fatty acids retain the fluidity of the fruit's cell membranes within the physiological range (Voronkov *et al*., 2019).

In cape gooseberry plants, Fischer *et al.* (2007) found that plants formed a more superficial root system at a higher altitude (2,690 m a.s.l.) in Boyacá (Colombia) than at 2,300 m a.s.l. to take better advantage of soil warming by the midday sun. In addition, this species, which originated in the Andean highlands, can increase the number of leaf stomata at higher altitudes to compensate for the lower concentrations of CO_2 and O_2 at these conditions (Fischer & Melgarejo, 2020), along with dense pubescence in all aerial organs to counteract the high UV radiation and nocturnal cooling of the atmosphere (Fischer *et al*., 2021).

Plants at high elevations develop a lower height because UV light decreases auxin production (Fischer & Melgarejo, 2014) and affects the synthesis of gibberellins in the internodes (Buchanan *et al*., 2015). In addition, fruit trees develop a smaller leaf area because of the greater solar radiation and increased temperature resulting from climate change (Fischer, Almanza-Merchán & Ramírez, 2012). Moreover, the cuticle as well as the leaves becomes thicker because of the increased number of parenchyma layers that better resist UV light (Fischer & Miranda, 2021). Within this context, varieties with higher photosynthetic performance and lower susceptibility to photoinhibition are better adapted to high elevation belts (Fischer *et al*., 2016).

For plant breeders, climatic adaptation is the requirement that a new variety must meet, and fruit trees are continuously modified through genetic selection to adapt to new environments, such as light intensity, photoperiod, cold and heat, type of soil, and moisture condition. Many of these requirements change with altitude and latitude (Sherman & Beckman, 2003). It is noteworthy to mention the existence of a genotype-by-environment interaction, as shown in the case of guava fruits, where a significant genotype × environment interaction was found for sugar and organic acid content in four genotypes at different altitudes in the department of Santander in Colombia (Solarte *et al*., 2014).

Effect of altitude on fruit quality

In general, for the comparison of different altitudes, the intrinsic characteristics of each site must be considered, *e.g.*, slope, acidity, and organic matter content of the soil, among others, along with the climatic factors (Brenes-Gamboa, 2017). Table 2 shows some studies (22) that compare the effect of different altitudes on the physical and chemical components of fruits. Pérez and Melgarejo (2015) confirmed that the environmental conditions must be very close to the optimum to achieve the highest possible yields and qualities on fruit plantations, which are determined by the genetic potential of the species.

The physical characteristics of fruits

Physical features, such as weight, size, shape, firmness, and color, along with the duration of the reproductive phenological phase, depend first of all on the genetics of the species and variety; the potential is expressed to the maximum under optimal climatic conditions of the crop (Fischer, Ramírez & Almanza-Merchán, 2012), which favor physiological processes, such as photosynthesis, transpiration, translocation of photoassimilates, respiration, and metabolism, which are crucial to the internal and external quality and postharvest longevity (Ladaniya, 2008).

The duration of fruit development until physiological maturity depends to a high degree on the temperature of the cultivation site; the lower the temperature during the growing season, the later the fruit will ripen (Moretti *et al*., 2010). Thus, feijoas at 1,800 m a.s.l. and an average temperature of 18.3°C took 155 d, while at 2,580 m a.s.l., (12.3°C) they took 180 d (Parra-Coronado *et al*., 2015); cape gooseberries took 66 and 75 d at 2,300 (17.4°C) and 2,690 m a.s.l. (12.5°C), respectively (Fischer *et al*., 2007). Posnette (1980) reported that the growth cycle of 'Lacatan' banana fruits in Jamaica increased by 1 month with each 100 m increase in altitude. Temperature, as one of the most important climate variables, affects the growth and development of fruit trees by regulating the length of the different phenological stages, *i.e*., fruit development is prolonged at higher altitudes because of decreased temperatures (Parra-Coronado *et al*., 2015; Mayorga *et al*., 2020). Ramírez *et al*. (2018) stated that the length of fruit development is highly dependent on climatic differences and particularly on the temperature. These authors mentioned that higher mean temperatures enhance fruit growth rates and decrease the time to maturity, whereas lower average temperatures tend to extend time necessary for fruit growth and maturity. Fischer, Ramírez and Almanza-Merchán (2012) emphasized that carbohydrate transport to the fruits and the rate of biochemical reactions catalyzed by enzymes (Moretti *et al*., 2010) are highly temperature-dependent.

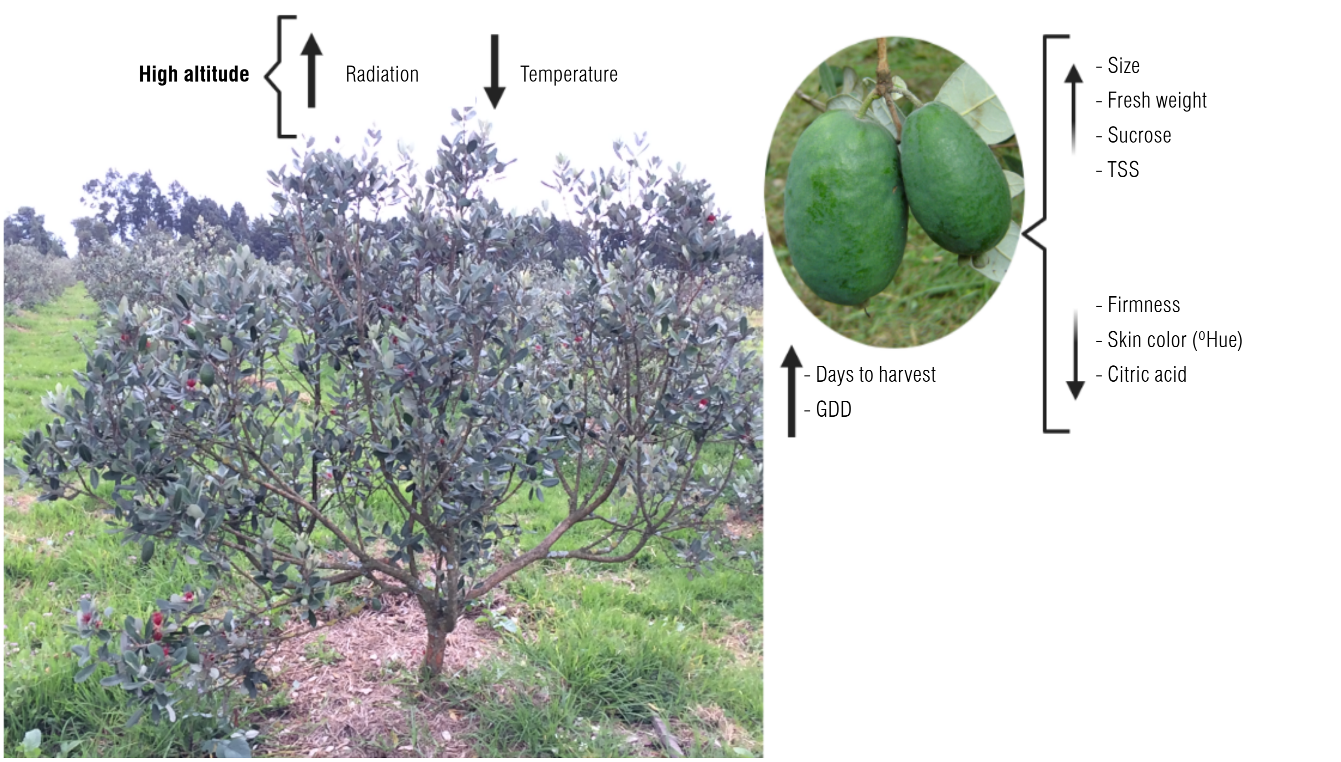

FIGURE 2. Representation of the effect of a higher altitude (2,580 *vs.* 1,800 m a.s.l.) on development and quality characteristics of feijoa (*Acca sellowiana*) fruits (Parra-Coronado, Fischer & Camacho, 2015; Parra-Coronado *et al*., 2017a, 2019, 2022). GDD: growing degree days; TSS: total soluble solids.

Several researchers compared growing degree days (GDD) during fruit development at different altitudes, with more physiological data and better adaptation to the temperature of the site, *e.g.*, feijoa at 1,800 m a.s.l. requires 2,965±113 GDD (167.5 ± 4.97 calendar days) from flower bud to harvest and, at 2,580 m a.s.l., requires 2,337±124 GDD (210.25 ± 10.08 calendar days) (Parra-Coronado *et al*., 2015) (Fig. 2). Bugaud *et al*. (2006) found that for bananas, at higher elevations (300 m a.s.l. *vs*. 50 m a.s.l.), the sum of temperatures (measured in GDD) was higher, which is why fruit fingers developed with greater thickness and density (Tab. 2), and the green life was shorter.

Of the 22 studies in Table 2, the fresh weight (FW) and size of the fruit increased in 12 studies (*e.g*., feijoa, banana passion fruit, Andean blackberry, lime, cactus pear) with increasing altitude, while in five studies, these properties decreased (*e.g*., cape gooseberry, guava, kiwi); the conditions of the sites must be within the optimal range required by these fruit species (Fischer *et al*., 2016), especially for temperature, precipitation and solar radiation (Fischer, Ramírez & Almanza-Merchán, 2012). In this regard, Viera *et al*. (2019) indicated that the effect of location on fruit weight and blackberry production was due to climate and soil characteristics.

Possibly, the development of fruits with a smaller size and lower weight at lower elevations occurs because of accelerated development driven by high temperatures, as compared to higher elevations of the same species. Therefore, there is a shorter time for accumulation of photoassimilates, along with a smaller daylight integral, as observed by Mayorga *et al*. (2020) in banana passion fruit. The increase in fruit weight may be highly related to cooler nights at high altitudes (Fischer *et al*., 2016) which reduce maintenance respiration in fruits and energy costs, favoring carbon balance and dry weight (DW) accumulation in these organs (Gariglio *et al*., 2007).

Apart from temperature, precipitation and soil moisture play the most important role in fruit filling because of their direct effect on the rate of fruit growth and translocation of carbohydrates to the fruit (Fischer, Ramírez & Almanza-Merchán, 2012). According to Mendoza *et al*. (2017), precipitation and soil moisture promote the reproductive phase of crops in the Andes to a greater degree (73.4%), as compared to temperature (19.3%) and solar radiation or photoperiod (3.2%). In cape gooseberries, a decrease in precipitation (837 *vs*. 302 mm year^{-1}) with the increase of altitude (2,300 *vs*. 2,690 m), could also have contributed to smaller fruits, number of fruits, and yield per plant (Tab. 2), although there was additional irrigation (Fischer *et al*., 2007). In the case of feijoa, Parra-Coronado *et al*. (2017a) found an opposite behavior for the size and quality of fruits, which were greater at higher altitudes (1,800 *vs*. 2,580 m a.s.l.) and with less rainfall (1,493 *vs*. 765 mm year^{-1}) although plants were near the upper recommended altitude limit at 2,700 m (Tab. 1).

TABLE 2. Effect of increasing altitude on the physical and chemical properties of fruits grown in various countries at the time of harvest.

Species	Common name / variety	Country (region) / altitude (m a.s.l.)	Physical property	Chemical property	Author
Acca sellowiana	Feijoa / clone 'Quimba'	Colombia (Cundinamarca) / 1800, 2580.	Increase of FW and size; decrease of firmness and hue angle.	Increase of TSS and sucrose; decrease of citric acid; without effect on TTA, malic acid, glucose and fructose.	Parra-Coronado, Fischer and Camacho (2015); Parra-Coronado *et al*. (2017a, 2019, 2022)
Actinidia chinensis	Kiwi / 'Hayward'	Turkey (Ardesen district of Rize) / 20, 210, 446, 610.	Decrease of FW, diameter, length and firmness.	Decrease of TSS and pH.	Zenginbal and Ozcan (2018)
Citrus latifolia	Lime / 'Tahití'	Colombia (Espinal, Villavicencio, Lebrija) / 335, 336, 1038.	Increase of size, color intensity and green coloration; decrease of firmness.	Increase of TTA; decrease of juice content.	García-Muñoz *et al.* (2021)
Citrus reticulata	Mandarine / 'Fremont'	Indonesia (West Java) / 500, 650, 800.	Increase of orange color; without effect on firmness.	Increase of vitamin C and TTA; without effect on TSS and TSS/TTA ratio.	Susanto *et al.* (2013)
Citrus sinensis	Orange / Mousambi	Nepal (Dadeldhura district) / 1400, 1700, 2000.	Increased peel thickness; decreased FW and diameter.	Increase of vitamin C, but TSS only at 1,700 m a.s.l.; decrease of juice content.	Ayer and Shrestha (2018)

to be continued

Species	Common name / variety	Country (region) / altitude (m a.s.l.)	Physical property	Chemical property	Author
Fragaria × *ananassa*	Strawberry / 'Capitola'	Venezuela (Lara, Trujillo and Aragua) / 1200, 1800, 2800.	Increase of size and dark red color; decrease of firmness.	Increase of TSS, vitamin C and anthocyanins; decrease of TTA and total polyphenols.	Pérez de Camacaro *et al.* (2017)
*Malus domestic*a	Apple / 'Red Gold'	India (Himachal Pradesh) / 1400, 1800.	Increase of FW, length and diameter; without effect on firmness and color (−L*, −a*, +b*).	Increase of TTA, glucose, total phenols and antioxidant activity; decrease of fructose, sucrose, ascorbic, malic and citric acids; without effect of TSS.	Kumar *et al.* (2019)
Musa acuminata	Banana / 'Grande Naine'	French West Indies (Martinique) / 50, 300.	Increase of diameter, firmness, % FW, density and peel hardness.	Increase TSS, citrate and Zn; decrease of P; without effect on K, Mg, Ca, Fe and Mn.	Bugaud *et al.* (2006)
Olea europaea	Olive/ 'Nabali'	Jordan (Soum and Om Al-Dananeer) / 400, 700.		Decrease of oil, oil acidity, peroxide and unsaturated fat/saturated fat ratio.	Freihat *et al.* (2008)
Opuntia ficus-indica	Cactus pear / 'Gialla', 'Rossa'	Italy (Sicily) / 301-350, 351-450, 451-550, 551-650	Increase of FW.	Increase of TSS; without effect on TTA, pH and % pulp.	Inglese *et al.* (2010)
Passiflora tripartita	Banana passion-fruit / var. *mollissima*	Colombia (Cundinamarca) / 2006, 2498.	Increase of FW, diameter, length, color: tone (ºH), brightness and saturation (chroma); without effect on firmness.	Increase of TTA, ascorbic and citric acid; decrease of malic and oxalic acids.	Mayorga *et al.* (2020)
Persea americana	Avocado / 'Hass'	Colombia (Antioquia) / 1340-2420.	Increase of FW, length, diameter and % DW; decrease of % humidity.	Increase of % of oil, oleic oil, % palmitoleic and linoleic acids.	Carvalho *et al.* (2015)
Physalis peruviana	Cape gooseberry / ecotypes 'Colombia', 'Kenya', 'South-Africa'	Colombia (Boyacá) / 2300, 2690.	Decrease of accumulated DW, diameter, fruit number/ plant, and yield/plant; without effect on fruit FW.	Decrease of sucrose and β-carotene; without effect on glucose, fructose, total carbohydrates, citric and ascorbic acids.	Fischer *et al.* (2000, 2007)
Prunus armeniaca	Apricot / 162 genotypes	India (Trans-Himalayan Ladakh) / 3006-3346.	Decrease of FW, diameter, length, humidity; without effect on blush area.	Increase of TSS.	Naryal *et al.* (2020)
Prunus avium	Cherry / 'Tragana'	Greece (Prefectures of Pieria, Imathia, and Pella) / 59, 216, 490.	Increase of FW and color at 216 m a.s.l. (L*, a*, b*).	Increase of total phenols antioxidant capacity; decrease of TTA; without effect on TSS.	Faniadis *et al.* (2010)
Prunus persica	Peach / 'June Gold'	Greece (Imathia and Kozani) / 72, 495.	Increase of % red blush surface, redness (a*) and lightness (L*); without effect on firmness.	Increase of anthocyanins and in fruit epidermis: antioxidant capacity, total phenols, flavonoids and carotenoids; without effect on TSS and TTA.	Karagiannis *et al.* (2016)
Psidium guajava	Guava / 'Reg. Blanca', 'Guavatá Victoria', 'Ráquira Blanca'	Colombia (Santander) / 1570, 1720, 1890.	Decrease of FW, color change from green to yellow.	Increase of glucose and organic acids; without effects on sucrose.	Solarte *et al.* (2014)

to be continued

Species	Common name / variety	Country (region) / altitude (m a.s.l.)	Physical property	Chemical property	Author
Punica granatum	Pomegranate / 'Helow'	Omán (Al-Hajar Mountains) / 1540, 1876, 2019.	Increase of FW, length, diameter and red color of aril and peel.	Increase of TSS, SST/TTA ratio and juice volume.	Al-Kalbani *et al.* (2021)
Rubus glaucus	Andean blackberry	Colombia (Cundinamarca) / 1882, 2200, 2410, 2647.	Increase of FW, DW, firmness, humidity and consistency; Decrease of L* and chroma.	Increase of TSS; decrease of TTA.	Vergara *et al.* (2016)
Rubus idaeus	Raspberry / 'Golden Bliss', 'Heritage'	Brazil (Mantiqueira Mountains) / 918, 1628.	Increase of FW, length, diameter and L*; without effect on ºhue and humidity.	Increase of total sugars and TSS/TTA ratio; decrease of TSS and TTA.	Maro *et al.* (2014)
Vaccinium ashei	Rabbiteye blueberry / 'Brightwell'	China (Provinces of Zhejiang, Jiangsu, Hubei, Guizhou, Yunnan) / 37-2010.		Increase of TSS, TSS/ATT ratio, flavonoids, phenols and anthocyanins; decrease of TTA.	Zeng *et al.* (2020)
Vitis vinifera	Grape / 'Syrah'	Brazil (Pernambuco and Bahia) / 350, 1100.		Increase of TSS, malic and succinic acids; decrease of glucose, fructose, citric and tartaric acids; in peel increase of anthocyanins and tannins and decrease of trans-resveratrol.	De Oliveira *et al.* (2019)

FW: fresh weight; DW: dry weight; TSS: total soluble solids; TTA: total titratable acidity.

An increase in altitude only increased fruit firmness in two studies, *e.g.*, in blackberry (Vergara *et al*., 2016), while in four studies, firmness decreased (*e.g.*, in strawberry; Pérez de Camacaro *et al*., 2017). Four authors observed no effect on this property (*e.g.*, in mandarin; Susanto *et al*., 2013). This non-uniform effect of altitude on firmness could be because this quality characteristic depends on various factors, such as fruit morphology, cell wall composition, Ca concentration, starch concentration, ethylene production, respiratory intensity, and enzymatic activity related to softening, among others (Yahia & Carillo-López, 2019), factors that can be differentially regulated depending on altitude and crop management (fertilization, irrigation).

Two studies looked at the thickness of the epidermis, as in the case of oranges (Ayer & Shrestha, 2018) and the hardness of the epidermis in bananas (Bugaud *et al*., 2006), which increased with higher altitude (Tab. 2), possibly promoted by higher solar radiation in these sites, which increases the number of parenchyma layers and cuticle for greater resistance against UV light (Fischer & Miranda, 2021). Additionally, Osterloh *et al.* (1996) pointed out an increase in the firmness of deciduous fruits growing in mountainous regions, which shortens the ripening processes and leads to a longer shelf-life and better aroma than those from valleys. In the case of the 'Kristal' guava in Indonesia, fruits from altitude (550 m a.s.l.) stood out as being "crispier", while those from a valley (200 m a.s.l.) were softer and heavier (Musyarofah *et al*., 2020).

These observations coincide with the increase in the quality of the 'Anna' apple at 2,500 m a.s.l. *vs*. lower elevations in Duitama (Colombia), with a thicker cuticle and epidermis, making the fruits less susceptible to pathogens and insect pests, along with a better red coloration because of increased anthocyanin synthesis (Fischer *et al*., 2016). This reaction agrees with the report by Campos and Quintero (2012) for banana passion fruit grown in the Colombian highlands (Tab. 1), which developed a thicker epidermis and was more resistant to anthracnose than fruits from lower sites.

Fruit color changes with increases in solar radiation at higher altitudes (Fischer & Orduz-Rodríguez, 2012); a greater intensity of color and green coloration were found in Lima Tahiti (Tab. 2) (García-Muñoz *et al*., 2021), probably because of the role of light in the biosynthesis of chlorophylls. In another citrus, mandarin cv. Fremont, the orange color increased (Ayer & Shrestha, 2018) because of the mentioned parameter. The higher altitude was also responsible for a greater increase in the intensity of red color in strawberries (Pérez de Camacaro *et al*., 2017) and pomegranates (Al-Kalbani *et al*., 2021) because of the increase in the concentrations of anthocyanins that, apart from these two crops mentioned, have also been found in peaches (Karagiannis *et al*., 2016), blueberries (Zeng *et al*., 2020) and grapes (Oliveira *et al*., 2019) (Tab. 2). Light is a determining factor in the accumulation of pigments (carotenoids and anthocyanins) in fruits (Yahia & Carrillo-López, 2019). It has been shown that light is an important component that affects the expression of genes related to the synthesis of pigments and also regulates their accumulation by controlling the light signaling apparatus (Azari *et al*., 2010; Ruiz-Sola & Rodríguez-Concepción, 2012).

Apart from light, temperature is a key factor for the red color of fruits; day temperatures around 18-24°C promote fruit growth (Fischer & Orduz-Rodríguez, 2012), depending on the species and variety, while cool night temperatures (*e.g*., 10°C) promote red coloration by anthocyanins in the fruit epidermis, as reported by Musacchi and Serra (2018) for the case of red apples, while Fischer *et al*. (2016) mentioned that cool nights promote the coloration of wine grape berries. These temperature contrasts can easily be found at tropical altitudes.

Parra-Coronado *et al*. (2017a) measured color during the growth of feijoa (cv. Quimba) fruits as a function of hue angle (H°), which varies from 180° for the pure green color to 0° for the pure red color, and found that feijoa remained a green fruit, with small decreases in H° for the two altitudes (1,800 and 2,580 m a.s.l.), with values at the time of harvest of 122.9 ± 2.0 and 125.0 ± 2.1 Hº, respectively. Although an increase in temperature with a decrease in altitude accelerates the ripening process, degradation of chlorophyll and reduction of Hº in the skin of feijoa fruits do not change its color because of the genetics of the fruit, which only varies within a color tonality.

Chemical characteristics of fruits

Total soluble solids (TSS), mainly soluble sugars, organic acids, and vitamins, increased in nine fruit species (*e.g*., feijoa, Andean blackberry, and cactus pear) at increased altitudes, as seen in Table 2. In two fruit species, kiwi (Zenginbal & Ozcan, 2018) and raspberry (Maro *et al*., 2014), they decreased with increasing altitude. The increase in TSS may be related to the increase in photosynthesis with altitude because of the higher luminosity (Mayorga *et al*., 2020) if the temperature is still in the optimal range of the crop and/or with the lower respiratory carbohydrate loss as a result of the lower night temperature at high elevations (Fischer *et al*., 2016). For the reduction of total soluble solids (TSS) in kiwi, Zenginbal and Ozcan (2018) found that the conversion of starch into sugar decreased due to lower temperatures at altitude of 610 m a.s.l. Temperature can influence total sugar content in yellow and purple passion fruit that are grown at different altitudes and temperature conditions (Viera *et al*., 2022). In addition, low night temperatures can limit the transport of carbohydrates to fruits (Fischer, Almanza-Merchán & Ramírez, 2012), as seen by Tombesi *et al*. (2019) in grapevines exposed to a night temperature of 15°C as compared to 25°C.

The total titratable acidity (TTA), which is the quantification of the organic acids contained in the cell juice, decreased in five species at increased altitude, especially in the berries (blackberry, raspberry, blueberry) (Tab. 2). In four species (lime, mandarine, apple, banana passionfruit), the TTA increased with elevation, possibly because the lower temperature limited the respiration rates of fruits that use organic acids as a substrate (Batista-Silva *et al*., 2018). In strawberries, blackberries, and blueberries, increases in TSS were recorded in association with a decrease in TTA with increased altitude, and the TSS/TTA ratio (maturity index) increased (Tab. 2), which could be related to the conversion of organic acids into sugars by the gluconeogenesis process (Famiani *et al*., 2015).

In apple, cherry, peach, and blueberry, increases in phenols were detect at higher altitude; in the latter three species, an increase in flavonoids was also reported (Tab. 2), which is a very important protection mechanism against UV radiation (Cheynier *et al*., 2013). On the other hand, total phenol contents decreased with higher altitude only in strawberries (Pérez de Camacaro *et al*., 2017). These secondary metabolites are essential phytochemical substances in the plant, which are activated by the light spectrum, acting as defense compounds and protectors against UV radiation (Salazar-García *et al*., 2016).

Likewise, the antioxidant capacity and activity increased with increased altitude in peaches (Karagiannis *et al*., 2016) and apples (Kumar *et al*., 2019), possibly generated by the increase in phenols, flavonoids, and ascorbic acid (especially in citrus fruits, strawberries, and banana passion fruit) (Tab. 2). These secondary metabolism substances are powerful antioxidants (Ouzounis *et al*., 2015).

In two (Tahiti lime and orange) of the three citrus species studied (Tab. 2), a decrease in juice content was found with increasing altitude, *e.g*., a 14.8% lower juice content was produced in Tahiti lime fruits at 1,038 m as compared to 336 m altitude (García-Muñoz *et al*., 2021). Possibly, this occurred because the climatic conditions were not adequate for the juiciness of the fruit, taking into account the multidimensionality of climatic factors in a given site (Zandalinas *et al*., 2021). The volume of juice also increased in pomegranates, according to the increase in weight and size of the fruits with altitude (Al-Kalbani *et al.*, 2021) (Tab. 2).

In fruits with high lipid content, such as the olive tree, the oil content decreased (Freihat *et al.*, 2008), while it increased in avocados (Carvalho *et al.*, 2015) with rising altitude (Tab. 2). In the latter fruits, the contents of oleic, palmitoleic, and linoleic fatty acids increased at higher elevations. Environmental factors at different altitudes influence the respiration pattern of avocados during ripening on the tree, affecting the metabolism of the fruit that is responsible for the composition and quantity of fatty acids (Carvalho *et al.*, 2015). The increase in altitude to values above 2,300 m a.s.l. was reported by Henao-Rojas *et al.* (2019) as a favorable one for the fruit quality of this species, while Ramírez-Gil *et al.* (2018) mentioned the altitude range for avocado is between 1,400 and 2,600 m a.s.l.

There are very few studies that reported a lack of an effect from increasing altitude on fruit quality; one on highbush blueberries, comparing elevations of 217 and 636 m a.s.l. in Portugal, found no statistical differences for the concentrations of free sugars, organic acids and vitamin C (Correia *et al.*, 2016).

In the two studies that evaluated the content of antioxidants in the epidermis of fruits, such as total phenols, flavonoids, and carotenoids in peaches (Karagiannis *et al.*, 2016) and anthocyanin and tannins in grapes (Oliveira *et al.*, 2019), antioxidants increased with increasing altitude, confirming the importance of these protective substances in the skin of fruits that attenuate excessive UV radiation (Caldwell *et al.*, 1998). Interestingly, in bilberries (*Vaccinium myrtillus*), a direct relationship was found between altitude and antioxidant activity; in the range between 900 and 1,450 m a.s.l., the relationship between altitude and total anthocyanins was inversely proportional, while the dependence became proportional from 1,500 m a.s.l. (Papanov *et al.*, 2021).

In general, if the highest altitude of studied sites was very close to or above that recommended for the crop (Tab. 1), the physical and chemical components of the fruit quality decreased or there were no differences between the sites, as observed in the case of cape gooseberries at 2,690 *vs.* 2,300 m a.s.l. in Colombia (Tab. 2) (Fischer *et al.*, 2000, 2007).

In feijoa, the accumulated solar radiation during fruit growth (8,918 *vs.* 11,082 W m^{-2}) at the two altitudes (1,800 *vs.* 2,580 m a.s.l.) affected its size and quality at harvest (Fig. 2) (Parra-Coronado *et al.*, 2017a). At higher altitudes (greater accumulated solar radiation), the feijoa fruits presented a larger size, higher content of TSS and less firmness of the epidermis. According to Parra-Coronado *et al.* (2017a), the higher content of TSS, and greater FW produced at higher altitudes could be explained by "the higher rate of transpiration related to greater irradiance, which would provide a prolonged entry of water and nutrients to the fruit", indicating that the greater availability of light increases and extends the transport stream from the xylem to the fruits. Furthermore, photosynthesis in adjacent and well-illuminated leaves near the fruit is promoted by the attraction of photoassimilates from the fruit (Fischer, Almanza-Merchán & Ramírez, 2012).

Physiological disorders of fruits at high altitudes

Fruit trees grown at altitudes above their optimal range can suffer abiotic stress, especially from low temperatures (chilling and freezing stress, Fig. 3A), and oxidative stress from high UV radiation, which can cause large production losses (Madani *et al.*, 2019). On clear nights, the surface of the outer tissues of plants and fruits cool below air temperature because of heat exchange, leading to damage to cell membranes and intracellular compartments (Voronkov *et al.*, 2019). In addition, sudden changes in temperature between day and night at altitudes can generate physiological disorders, such as fruit cracking (Fischer, Balaguera-López & Álvarez-Herrera, 2021), as reported by Miranda (2020) for sweet granadilla.

During recent decades, radiation has increased steadily, especially UV-B (280-320 nm) (Van Leeuwen & Dariet, 2016). Fruit trees, growing at higher altitudes and especially near the equator, suffer from prolonged solar radiation affecting the epidermis of the fruit, as observed in crops such as mango, kiwi, pineapple, avocado, sweet granadilla (Fig. 3B) and deciduous fruit trees (Fischer, 2000; Fischer & Orduz-Rodríguez, 2012), and from a higher concentration of potentially harmful UV-B (Benavides *et al.*, 2017).

Fruit sunburns which are common at altitude sites are further promoted by prolonged dry periods due to climate change and the effect of "El Niño" in northern South America (Fischer *et al.*, 2016). Damage caused by photoinhibition results when the chlorophylls in the thylakoid membrane of the chloroplasts absorb more light energy than the photosynthesis process can use and induce damage to the photosystem II and degradation of D1 protein (Casierra-Posada, 2007).

Direct solar radiation increases not only the temperature but also evapotranspiration through the fruit surface,

FIGURE 3. A) Chilling injury in feijoa (*Acca sellowiana)* and B) sunburn in sweet granadilla (*Passiflora ligularis*) in Colombian highlands.

causing an accelerated loss of moisture and increasing susceptibility to fruit cracking (Ikram *et al*., 2020; Fischer, Balaguera-López & Álvarez-Herrera, 2021). For example, in the case of Japanese plums (*Prunus salicina*), excessive radiation manifests itself as a brown to yellow discoloration on the surface of the fruits, which, in severe cases, can result in necrotic spots and cracking of the fruit epidermis (Makeredza *et al*., 2018).

In sensitive plants, prolonged UV-B radiation affects photosynthetic activity and plant growth by damaging DNA, membranes, proteins, and lipids (Hideg *et al*., 2013). However, normal (natural) levels of UV-B radiation can reduce abundant vegetative growth and the incidence of pathogens, and favor secondary metabolism from greater synthesis of anthocyanins, carotenoids, and flavonoids, improving flavor, aroma and color in the case of grapes (Fischer *et al*., 2016).

Fruits are capable of developing protection mechanisms against high UV-B radiation, such as increased synthesis of phenylpropanoids (flavonoids, *e.g*., anthocyanins) in the epidermis that can absorb this radiation and serve as antioxidants (Caldwell *et al*., 1998).

Conclusions

In this review of most information from Colombia, higher altitudes are characterized by decreased temperatures and increased solar radiation. Because of global warming, highlands will become important for planting fruit trees. The effect of altitude on the quality components of fruit trees depends, firstly, on the species and variety and, secondly on whether the climatic conditions are within the range of optimal conditions for the fruit crop growth.

In the 22 studies found in the systematic review of four bibliographic databases that compared fruit quality at least two altitudes, increased altitudes showed prolonged fruit development in most cases, and increased fresh weight and size, while, in some fruit species, fruit firmness decreased. In general, the higher radiation in the upper zone promoted the intensity of the fruit color. The total soluble solids content of the fruits increased with altitude in most cases, probably because of the increase in photosynthesis resulting from higher solar radiation. For total titratable acids, there was no clear trend for altitude, and it depended more on the fruit species and the site conditions. In various fruit species, increasing altitude means the content of antioxidants (mainly phenolics) is increased in the fruit flesh and epidermis as a reaction to increasing UV light. Physiological disorders in the highlands include stress caused by high UV radiation (oxidative stress) and too low temperatures (chilling and freezing stress).

In general, if altitude is at or above the recommended range for a fruit species, there are no positive effects on fruit quality. Varieties with higher photosynthetic performance and lower susceptibility to photoinhibition are better adapted to high altitudes.

The authors suggest undertaking more studies in different altitudes of the Andean region with all fruit species and varieties in correlation with the climatic conditions for a better understanding of fruit production and quality. These results, in the face of climate change, would serve as an input for new plant breeding programs and improved management of these crops.

Conflict of interest statement

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

Author's contributions

GF wrote the initial draft and carried out the final revision of the manuscript. APC wrote and carried out the revision of the manuscript. HEB wrote and carried out the revision of the manuscript.

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