Environmental conditions during preharvest influence bioactive compounds in fruits: A review with emphasis on tropical and subtropical species

Las condiciones ambientales en precosecha influencian los compuestos bioactivos en frutos: una revisión, con énfasis en especies tropicales y subtropicales

Helber Enrique Balaguera-López[1*], Gerhard Fischer[1], and Elhadi M. Yahia[2]

ABSTRACT

A healthy diet rich in fruits and vegetables with high contents of bioactive compounds and antioxidants has become an essential habit among the human population, leading to a significant increase in the commercial trade of many fruits, especially of tropical and subtropical origins. The content of phytonutrients in fruits depends on various pre-harvest factors, especially agroclimatic conditions of temperature, light, and air humidity, as well as crop management and fruit maturity stage. Among the essential phytonutrients found in fruits that promote health and prevent diseases are the carotenoids (α-carotene, β-carotene, β-cryptoxanthin, lycopene, lutein, etc.), phenolic compounds (flavonoids, phenolic acids, among others), monoterpenes (*i.e.*, limonene), isoprenoids (*i.e.*, lipophilic vitamins), and ascorbic acid. Factors of temperature, light intensity, UV light, and water stress promote the synthesis of phytochemicals in fruits. In contrast, an excess of these factors can either increase or decrease the accumulation of these compounds in fruits. In addition to different abiotic stresses that result from climatic conditions and have inter- and intra-annual variations, the geographical locations, elevation, and genotype influence the content of bioactive compounds in fruits. There is a strong interest in manipulating changes in climate conditions as a factor in fruit quality, including the phytochemical content, while reducing yield losses. This review aimed to explore how preharvest environmental factors affect accumulation of phytochemicals in fruits, which are important for plant resilience and human health, with an emphasis on tropical and subtropical fruit species.

Key words: phytochemicals, human health, carotenoids, phenolics, vitamins, plant stress, temperature, light.

RESUMEN

Una dieta saludable rica en frutas y verduras con altos contenidos en compuestos bioactivos y antioxidantes se ha convertido en un hábito alimenticio muy importante de la población, conllevando a un incremento significativo en la comercialización de muchos frutos, especialmente de origen tropical y subtropical. El contenido de estos fitonutrientes en frutos depende de los factores precosecha, especialmente de las condiciones agroclimáticas como temperatura, luz y humedad del aire, aparte del manejo del cultivo y de la madurez del fruto, entre otros. Dentro de los fitonutrientes más importantes están los carotenoides (α-caroteno, β-caroteno, β-criptoxantina, licopeno, luteína, entre otros), compuestos fenólicos (flavonoides, ácidos fenólicos, entre otros), monoterpenos (por ejemplo, limoneno), isoprenoides (por ejemplo, vitaminas lipofílicas), y el ácido ascórbico. Factores como temperatura, intensidad lumínica, luz UV y el estrés hídrico promueven la biosíntesis de fitoquímicos en los frutos, mientras que el exceso de estos factores puede aumentar o disminuir la acumulación de estos compuestos en los frutos. Aparte de los tipos de estrés abiótico por las condiciones climáticas, con sus variaciones interanuales e intraanuales, también la ubicación geográfica y elevacional y los diferentes genotipos influyen en los contenidos de compuestos bioactivos de los frutos. Existe un gran interés por aprovechar las condiciones del cambio climático como mecanismo para aumentar la calidad de los productos, incluyendo los contenidos de fitoquímicos, reduciendo al tiempo las pérdidas en los rendimientos de los cultivos. El objetivo de esta revisión fue explorar cómo los factores ambientales en precosecha afectan la acumulación de los fitoquímicos en los frutos, los cuales son importantes para la salud humana y la resiliencia de las plantas, con un enfoque en especies tropicales y subtropicales.

Palabras clave: fitoquímicos, salud humana, carotenoides, fenoles, vitaminas, estrés en plantas, temperatura, luz.

Received for publication: October 8, 2024. Accepted for publication: November 30, 2024. Doi: 10.15446/agron.colomb.v42n3.116951

[1] Universidad Nacional de Colombia, Facultad de Ciencias Agrarias, Departamento de Agronomía, Bogotá (Colombia).
[2] Facultad de Ciencias Naturales, Universidad Autónoma de Querétaro, Querétaro (México).
[*] Corresponding author: hebalagueral@unal.edu.co

Binomial fruit names in this article

Acerola *Malpighia glabra*	Kiwi *Actinidia deliciosa*	Peach palm *Bactris gasipaes*
Annon *Annona cherimola*	Lemon *Citrus limon*	Persimmon *Diospyros kaki*
Apple *Malus domestica*	Lime *Citrus* x *aurantifolia*	Pitanga *Eugenia uniflora*
Avocado *Persea americana*	Mango *Mangifera indica*	Pineapple *Ananas comosus*
Banana *Musa* sp.	Mangosteen *Garcinia mangostana*	Pitahaya *Selenicereus* sp.
Cantaloupe *Cucumis melo*	Orange *Citrus sinensis*	Plantain *Musa paradisiaca*
Cape gooseberry *Physalis peruviana*	Longan *Dimocarpus longan*	Pomegranate *Punica granatum*
Brazilian guava *Psidium guineense*	Loquat *Eriobotrya japonica*	Rambutan *Nephelium lappaceum*
Cactus pear *Opuntia ficus-indica*	Lulo *Solanum quitoense*	Star fruit *Averrhoa carambola*
Cashew *Anacardium occidentale*	Lychee *Litchi chinensis*	Strawberry *Fragaria* × *ananassa*
Chinese plum *Prunus mume*	Macadamia *Macadamia integrifolia*	Sweet cucumber *Solanum muricatum*
Durian *Durio zibethinus*	Mandarin *Citrus reticulata / C. unshiu*	Tangerine *Citrus reticulata*
Goji berry *Lycium barbarum*	Nectarine *Prunus persica* var. nucipersica	Tomato *Solanum lycopersicum*
Grape *Vitis vinifera*	Northern highbush blueberry *Vaccinium corymbosum*	Tree tomato *Solanum betaceum*
Grapefruit *Citrus paradisi*	Papaya *Carica papaya*	Watermelon *Citrullus lanatus*
Guava *Psidium guajava*	Passion fruit *Passiflora edulis*	
Jujube *Ziziphus jujuba*	Peach *Prunus persica*	
	Pear *Pyrus communis*	

Introduction

A diet rich in fresh fruits and vegetables, abundant in antioxidants, vitamins, minerals, and other phytochemicals, has become a crucial habit among the global population due to its health benefits and role in disease prevention (Kaur *et al*., 2017; Sarkar *et al*., 2023; Yahia, 2018; Yan *et al*., 2021). This growing awareness has increased the global trade of fruits and vegetables, particularly those of tropical and subtropical origin. Consequently, interest in the health-promoting properties of these crops has risen, leading to expanded research on their phytochemical composition and strategies to enhance their consumption (Schreiner *et al*., 2013; Yahia, 2018).

The concentration and metabolism of the bioactive compounds in agricultural crops depend on pre-harvest factors such as agroclimatic conditions, genetics, crop management (especially irrigation and fertilization), biochemical processes of fruit maturation and fruit maturity at harvest, and harvest time, as well as on postharvest factors (Mphahlele *et al*., 2014; Thokar *et al*., 2022; Yahia, 2018). Kader (2007) emphasized that environmental factors significantly impact the nutritional value and overall quality of agricultural crops. However, these factors are difficult to control in field conditions. Meanwhile, Lester (2006) concluded that variability in the bioactive compounds in fruits will always exist due to the interactions between genetic factors and environmental conditions on their synthesis and degradation pathways.

Many bioactive phytochemicals are interrelated with plants and their environment. They act as feeding deterrents, protective compounds against abiotic stresses or pathogens, pollinator attractants, signaling molecules or antioxidants (Schreiner & Huyskens-Keil, 2006). Numerous factors influence the phytochemical profile of fruits. In this regard, Nicola and Fontan (2014) highlight the importance of the geographical area (defined by different environmental conditions), available varieties, and applied cultural practices to crops. Lei *et al.* (2007) also emphasize the importance of the fruit developmental stage, and Yan *et al*. (2021) point out the different postharvest management practices.

Tropical fruits are rich in diverse phytonutrients, potentially preventing diseases and extending productive and active life expectancy in humans (Clevidence, 2010). Yahia, García-Solís, *et al*. (2019) classify these fruit and vegetable ingredients into micronutrients (minerals, vitamins), fiber, and a wide range of other bioactive compounds or phytonutrients that, individually or in combination, benefit human health. There are several reasons why these phytonutrients protect human health, primarily through their functions as antioxidants, anticancer agents, and immunomodulators, among others (Yahia, 2018; Yahia *et al*., 2023; Yahia, García-Solís *et al*., 2019).

Fruits, as a source of antioxidants (phenolic compounds, flavonoids, vitamins, etc.), can preserve cellular components against oxidative damage, reducing the risk of some degenerative diseases related to this type of stress (Stafussa *et al*., 2018). In this regard, Schreiner *et al*. (2013) highlight the current trend of incorporating more fruits and vegetables into the diet, especially considering that global fruit and vegetable consumption is not sufficient to meet daily nutritional requirements for good human health and well-being (Jideani *et al*., 2021). Fruit growers are increasingly aware of the benefits of environmental conditions in promoting the quality and yield of their crops. They are applying technologies to optimize these conditions (Treutter, 2010). However, global warming affects the fruit development cycle by advancing and accelerating flowering and harvest times, which may lead to alterations in fruit quality and yield (García-Pastor *et al*., 2024).

Cervantes *et al*. (2020) point out the complexity of the "fruit quality" concept, which includes organoleptic and functional characteristics highly valued by health-conscious consumers, parameters that can be influenced by environmental changes. Crisosto *et al*. (1997) mention the importance of "orchard quality," which should be maximized through research and understanding of all factors affecting fruit quality. Kyriacou and Rouphael (2018) describe the quality of fruits and vegetables as a dynamic composition of their physicochemical characteristics combined with consumer perception.

The maximal potential of fruit quality can be developed under optimal climatic conditions during cultivation (Fischer *et al*., 2012), when physiological processes such as photosynthesis, translocation of photoassimilates towards sink organs, transpiration, respiration, and other metabolic pathways, which are crucial for both the external and internal quality and postharvest longevity of fruits, are promoted (Ladaniya, 2008). However, adverse conditions can negatively affect fruit quality. Abiotic stress can trigger physiological, biochemical, and molecular alterations through which plants tolerate stressful conditions (Toscano *et al*., 2019). Different types of abiotic stress promote the formation of secondary metabolites, such as phenolic compounds and several other classes that can benefit human health (Toscano *et al*., 2019; Yahia, 2018). Similarly, environmental stresses act as elicitors that induce the biosynthesis of secondary metabolites, commonly known as phytochemicals, many of which are bioactive compounds (Fig. 1) that help plants adapt to stressful conditions and, in turn, may provide significant benefits to human health (Aguirre-Becerra *et al*., 2021; Toscano *et al*., 2019; Yahia, 2018). Among many examples, Fernando *et al*. (2014) report that banana plants counteract oxidative stress from excessive solar radiation and temperature by increasing their antioxidant capacity.

The response of plants to environmental stressors depends on the type of stress, timing, duration of stress, the plant's age and phenological stage, and the various abiotic and biotic factors involved (Ochoa-Velasco *et al*., 2017). Meanwhile, susceptibility to different types of stress can vary significantly among species, varieties, cultivars, and landraces (Días *et al*., 2021; Ochoa-Velasco *et al*., 2017).

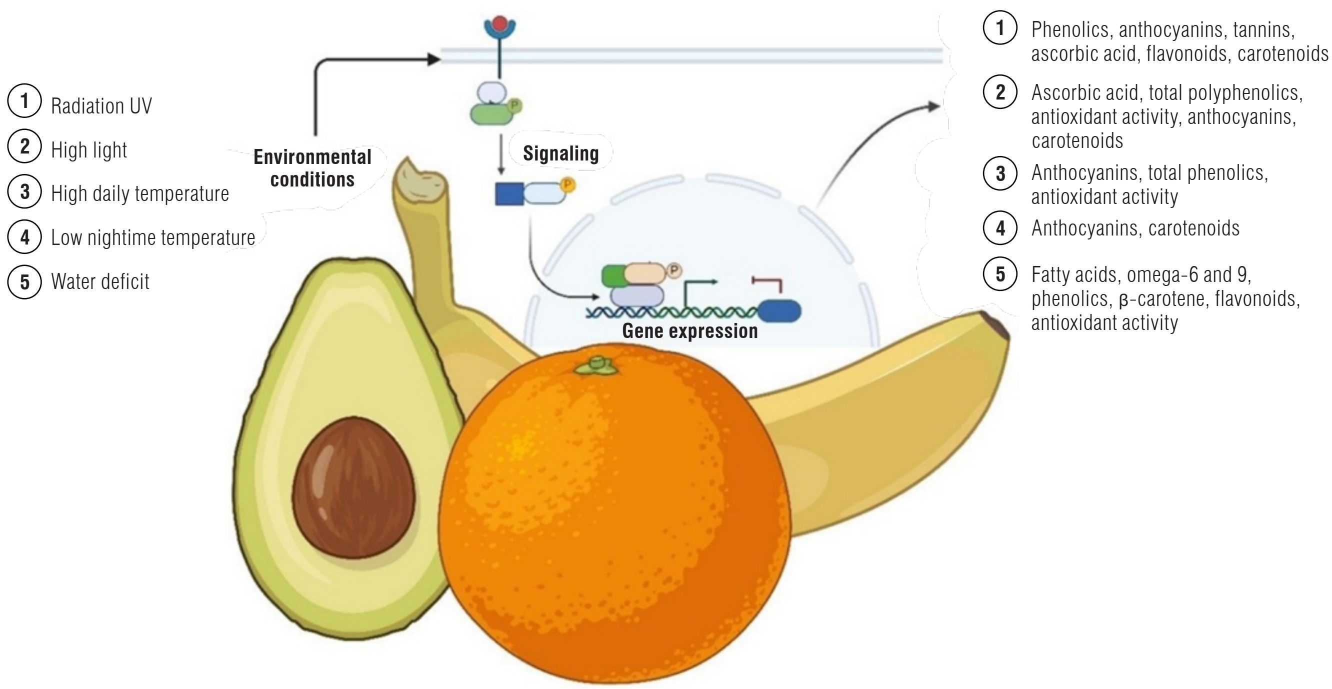

FIGURE 1. Possible role of certain preharvest climatic conditions on increasing contents of bioactive phytochemical compounds in fruits. Superoptimal conditions (that do not cause damage) of temperature, light, UV radiation, and soil water deficit induce the synthesis of various compounds in fruits involved in cell protection and offer health benefits for consumers.

Many environmental effects are currently under study, particularly in harnessing them to increase the content of bioactive phytochemicals in plants (Clevidence, 2010). This literature review explores how preharvest environmental factors such as light, temperature, elevation, water, and carbon dioxide affect fruit phytochemicals, which are essential for plant resilience and human health, focusing on tropical and subtropical species. Additionally, the information in this review can expand knowledge on the impact of climate change on the nutraceutical quality of fruits, providing insights for future research and promoting management practices that modify crop climates to enhance these phytonutrients.

Methodology

The methodology for this literature review consisted of searching for information (articles, book chapters) from various databases following the PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analysis) guidelines according to Flórez-Velazco *et al*. (2024). The keywords used were "phytonutrients," "preharvest," and "fruit," generating 1,030 results from the past 10 years (2014-2024) in the Google Scholar database (75 publications were initially used), 58 results in ScienceDirect (11 were used), and 601 results in Semantic Scholar (92 were used). Additionally, in a second search using the keywords "climate" and "phytonutrients" in Google Scholar, 260 results were found, 4 of which were used. In a final filter, articles, and book chapters repeated across the three databases or that did not explicitly refer to climatic conditions were excluded. More emphasis was placed on publications about tropical and subtropical fruit species, and, in cases where there were not enough examples, some fruits from temperate zones were included. Due to their importance, some publications from before 2014 were also included.

Bioactive compounds in fruits that benefit human health

The insufficient consumption of fruits and vegetables is one of the five most important factors that pose a risk to human health (Harris *et al*., 2021). According to Zakrevskii (2018), the recommended daily intake ranges from 160 to 460 g for fruits, 240 to 402 g for vegetables, and 25 g for dietary fiber. Currently, there are no specific recommended consumption levels for the different groups of fruits and vegetables (Zakrevskii, 2018). Fruits and vegetables promote protective functions against chronic diseases such as cerebrovascular, cardiovascular, neurological, and ocular diseases, as well as diabetes, cancer, blood-related diseases, hypertension, and strokes (Jideani *et al*., 2021, and references therein; Yahia, 2018).

Due to the wide variety of bioactive compounds that promote health, fruits, and vegetables have a high potential for preventing cancer (Tab. 1) and cardiovascular diseases (Schreiner & Huyskens-Keil, 2006). Fruits contain thousands of phytochemicals (Yahia, 2018; Yahia, García-Solís, *et al*., 2019). Many phytochemicals have antioxidant activity, induce upregulation of detoxification enzymes, cell-to-cell communication, and regulate angiogenesis and apoptosis (Clevidence, 2010).

TABLE 1. Some phytochemicals from tropical and subtropical fruits with cancer-preventive properties (modified from Yahia, García-Solís *et al*. (2019)).

Phytochemical	Fruit species
Dietary fiber	Most fruits
Carotenoids	Cantaloupe, kiwi, mango, papaya
α-carotene	Orange-flesh-fruits (cantaloupe, mango, orange, papaya, persimmon,
β-carotene	pineapple, cape gooseberry)
Lycopene	Brazilian guava, papaya, watermelon, red grapefruit
Xanthophylls (β-cryptoxanthin, lutein, zeaxanthin)	Cantaloupe
Phenolics	
Anthocyanidins (cyanidin, malvidin, delphinidin, pelargonidin, peonidin, petunidin)	Red, blue, and purple fruits
Flavanones (hesperetin, naringenin, eriodictyol)	*Citrus* (oranges, grapefruits, lemons, limes, tangerines)
Flavones (luteolin, apigenin, chrysin)	Guava
Flavonols (kaempferol, myricetin, quercetin, rutin)	Berries
Phenolic acids	
Hydroxycinnamic acids (caffeic acid, ferulic acid, sinapic acid, chlorogenic acid, coumaric acid)	Orange, lemon, grapefruit
Monoterpenes	
Limonene	*Citrus* (grapefruit, tangerine)
Isoprenoids (lipophilic vitamins)	
Vitamin E (tocopherols)	Avocado, macadamia

Table 2 shows some tropical and subtropical fruits that contain significant amounts of carotenoids. Carotenoids are notable for having conjugated double bonds in their structure, with antioxidant effects through singlet oxygen quenching and their ability to neutralize peroxyl radicals (Leite *et al*., 2024; Yahia *et al*., 2019). Some of these molecules have been reported to possess antitumor properties (breast and prostate cancer) involving antioxidant functions, immune modulation, and antiproliferative effects (Leite *et al*., 2024; Yahia *et al*., 2018; Yahia, García-Solís *et al*., 2019). The high carotenoid content in many tropical and subtropical fruits, as shown in Table 2, suggests that incorporating them into the diet can significantly contribute to the intake of carotenoids necessary for good health (Phillips *et al*., 2014).

Sarkar *et al*. (2023) reported health benefits (including anticancer, recovery from cardiovascular diseases, antioxidants, anti-inflammatory effects) by consuming tropical fruits lychee, guava, star fruit, tree tomato, rambutan, pepino melon, mangosteen, loquat, durian, persimmon, longan, passion fruit, annon, and pitahaya.

Environmental factors influencing the accumulation of bioactive compounds in fruits

Climatic conditions during the crop growth cycle, especially temperature, light, air and soil composition, and humidity, affect fruit development, such as the duration of cell division, photosynthesis, transpiration, respiration, carbohydrate metabolism and translocation (Burgos *et al*., 2021; Fischer, Parra-Coronado *et al*. 2022; Siddiqui, 2018). These factors include not only the size of the fruits but also their internal and external characteristics and storage potential (Ladaniya, 2008; Siddiqui, 2018). Kader (2007) highlights that light intensity and temperature have a powerful impact on the nutritional quality of fruits and vegetables. The climate is generally interconnected with various factors, especially the geographic location of the orchard and the season, making climate a complex phenomenon (Días *et al*., 2021; Zhao *et al*., 2024). Treutter (2010) notes that the secondary metabolism of plants is highly dependent on the site's environmental conditions.

Environmental stress, especially from drought, high solar radiation incidence (ultraviolet (UV) and photosynthetic active radiation (PAR)), high heat load, and salinity, constitutes the four most detrimental types of stress for agricultural productivity (Brito *et al*., 2019), with significant synergistic effects on growth, quality, and fruit production (Fischer, Orduz-Rodriguez *et al*., 2022). To prevent plants from producing an excess of reactive oxygen species (ROS) and potentially experiencing cell death due to different types of stress, higher plants can activate an antioxidant defense system that includes both non-enzymatic and enzymatic components (Godoy *et al*., 2021). Several classes of phenolic compounds, such as flavonoids,

TABLE 2. Carotenoid content (µg 100 g^{-1} fresh weight-FW) in tropical and subtropical fruits.

Fruit species	Country	α-carotene	β-carotene	β-cryptoxanthin	Lycopene	Lutein	Zeaxanthin	References
Orange	Costa Rica	23.1	41.8	47.3	nd	312	nd	Monge-Rojas and Campos (2011)
Mandarin	Spain	<ld	213	843	<ld	<ld	<ld	Beltrán *et al*. (2012)
Lemon	Spain	<ld	0.4	14.4	nd	2.5	1.2	Olmedilla *et al*. (2005)
Cape gooseberry 'Sudáfrica'	Colombia	3	335	17	nd	nd	nd	Fischer *et al*. (2000)
Cape gooseberry 'Colombia'*	Colombia	-	~115	-	-	~10	-	Etzbach *et al*. (2018)
Loquat	Brazil	nd	38.1	54.8	nd	6.4	nd	Faria *et al*. (2009)
Acerola	Brazil	60	1220	95	nd	115	nd	Porcu *et al*. (2005)
Guava 'Regional Roja'	Colombia	nd	155	nd	2316	7	nd	González *et al*. (2011)
Cactus pear	Mexico	nd	9733	nd	nd	14133	nd	Jaramillo-Flores *et al*. (2003)
Tree tomato	Ecuador	nd	nd	1350	nd	98	59	Mertz *et al*. (2009)
Mango 'Tommy Atkins'	Costa Rica	19.4	838	12.4	27.1	40.9	nd	Ornelas-Paz *et al*. (2008)
Papaya 'Formosa'	Brazil	nd	548.6	3798.6	3137.5	nd	nd	Oliveira *et al*. (2010)
Cashew 'Native'	Costa Rica	109	935	137	nd	56	nd	Monge-Rojas and Campos (2011)
Passion fruit	Brazil	nd	284	24	nd	nd	nd	Wondracek *et al*. (2011)
Pitanga	Brazil	nd	380	1150	1660	100	nd	Burgos *et al*. (2012)
Peach palm 'Colombia'	Costa Rica	120	1590	Nd	nd	nd	nd	Jatunov *et al*. (2010)
Lulo	Ecuador	-	57.93	-	-	-	-	Llerena *et al*. (2019)

nd: no data; <ld: below detection limit. * Expressed in µg g^{-1} dry weight-DW and in all-E isomer.

and several carotenoids play a pivotal role in eliminating excess hydrogen peroxide caused by environmental stress (Hinojosa-Gómez *et al*., 2020). Due to their ecological and physiological relevance, phenolic acids and flavonoids are among plant´s most significant bioactive compounds (Ochoa-Velasco *et al*., 2017). Their content is influenced by climatic and other factors (Cetinkaya *et al*., 2016). Zoratti *et al*. (2014) reported that the genetic origin of plants primarily determines the level of phenolic compounds in their tissues. Still, external factors can qualitatively or quantitatively modify the composition of these phytochemicals.

The accumulation of carotenoids in chromoplasts depends on three climatic factors: temperature, light, and air humidity (Dhunique-Mayer *et al*., 2009). Oranges grown in Mediterranean climate develop a significantly higher content of total carotenoids (up to 10 times more) than those grown in tropical or subtropical regions (Benkeblia *et al*., 2011). In contrast, Dhunique-Mayer *et al*. (2009) observed that the 'Star Ruby' grapefruit produced higher levels of carotenoid lycopene in tropical and subtropical areas than in Mediterranean regions.

Inter-annual and intra-annual variations are observed in fruit´s functional and organoleptic parameters, which also depend significantly on genotype, as Cervantes *et al*. (2020) reported in five strawberry varieties. Among these, 'Sabrina' and 'Cadonga' demonstrated greater inter-annual and intra-annual stability in fruit functional quality. Mean and minimum air temperatures and relative air humidity only partially explained the variation in fruit quality across the five strawberry varieties (Cervantes *et al*., 2020).

Moretti *et al*. (2010), Fischer, Parra-Coronado *et al*. (2022), and Fischer, Melgarejo *et al*. (2022) suggest that, due to climate change, fruit production and quality, especially in tropical and subtropical regions, will have to contend with non-optimal conditions for crop growth such as increased temperature, drought, solar radiation, and CO_2 contents in the air.

Light

Exposure to light depends on the fruit's position on the branch and the tree canopy (Fischer & Parra-Coronado, 2020; Lechaudel & Joas, 2007). The intensity and quality of light significantly influence the contents of many secondary metabolites in plants, often positively affecting the fruit quality (Días *et al*., 2021), as Li and Cheng (2008) find for the level of carotenoids in apple fruit skin. Lester (2006) also highlights that light intensity and quality significantly impact the vitamin content in different fruits.

Additionally, the intensity of light the plant receives affects the level of ascorbic acid produced in fruits (Nicola & Fontan, 2014). Gruda (2019) clarifies that light is a regulatory factor for L-ascorbate (vitamin C) synthesis, a potent antioxidant for plants and animals.

Kim *et al*. (2022) observe in Satsuma mandarins that, as sun damage increases (from mild to severe), total polyphenols and antioxidant activity are more significant compared to fruits that do not suffer from sunburn or have moderate sunburn, while the contents of chlorophyll (*a*, *b*, and total) in the skin and of carotenoids in the pulp decrease with the severity of damage. Meanwhile, 'Keitt' and 'Reynal' mangoes in full sun field-grown conditions with air temperatures reaching 36°C present epidermis temperatures up to 47°C and higher concentrations of total polyphenols and anthocyanins compared to fruits grown under shade (Kagy *et al*., 2024). Additionally, hot water (55°C for 50 min) and hot air (47°C for 20 min) treatments increase heat shock proteins HSP 17.4 two- to six-fold in fruits of both mango varieties exposed to direct sunlight compared to those maintained in the shade (Kagy *et al*., 2024).

In Chinese plum (greengage) fruits, a period of sunshine followed by increased air humidity significantly influences the different biosynthetic pathways of phenylpropanoids (Liu *et al*., 2022). Specifically, radiation, in addition to air humidity and temperature, affects the polyphenol content in these plums during different stages of fruit ripening. In particular, the structures of flavanols and flavanones depend on radiation and temperature (Liu *et al*., 2022).

The effect of ultraviolet (UV) light on fruit quality is undeniable. UV radiation, which is part of the electromagnetic spectrum, can be grouped into three ranges based on wavelength: UV-C, with short wavelengths of high frequency (100-280 nm); UV-B, with medium frequency long wavelengths (280-320 nm), and UV-A, with low-frequency long wavelengths (320-400 nm) (Peng *et al*., 2022). UV light induces a phenomenon known as hormesis, which affects morphological, metabolic, and molecular processes that enhance the phytochemical characteristics of fruits (Pataro *et al*., 2015). UV radiation between 200 and 300 nm is strongly absorbed by phenolic compounds, which protect fruits from this harmful radiation (Felicetti & Schrader, 2008; Oliveira *et al*., 2019), such as in the flavanols that protect against UV light and scavenge free radicals (Zoratti *et al*., 2014).

According to Ávila-Sosa *et al*. (2016), UV light affects plant tissues through three associated pathways: (1) UV photoreceptors, which control growth and development by influencing the expression of many genes involved in various processes for the production of secondary metabolites in plants; (2) the activation of enzymes such as chalcone synthase, anthocyanidin synthase, and phenylalanine ammonia-lyase, which are involved in the production of secondary metabolites through metabolic pathways of malonic acid, methylerythritol 4-phosphate, shikimic acid, and mevalonic acid; and (3) the production of ROS such as hydroxyl radical, superoxide radical, alkoxy radical, singlet oxygen, and hydrogen peroxide, and antioxidant enzymes such as catalase, superoxide dismutase, and glutathione reductase, among others. Peng *et al.* (2022) characterize the effect of UV-B radiation on plants as the promoter of secondary metabolism, increasing naturally active substances and inducing disease resistance mechanisms.

In fruits, light is a key factor for accumulating some phenolic compounds, including flavonoids, such as anthocyanins, and chlorophyll pigments (Yahia & Carrillo-López, 2019). Since UV-B radiation increases the concentrations of flavonoids such as quercetin and kaempferol in kale (Zhang *et al.*, 2003), whilst Clevidence (2010) suggests that a reduction in flavonoid content is an undesirable consequence of growing vegetables in greenhouses, which are covered to protect against UV radiation. Gil *et al.* (2015) also recommend that farmers cultivate crops in open fields rather than in greenhouses to increase phytochemical levels in fruits, where bioactive compounds are typically lower due to the combined effect of low light intensity and high temperatures. However, Fischer, Orduz-Rodriguez *et al.* (2022) state that high levels of UV-B radiation can cause harmful effects at morphological, physiological, and biochemical levels in plant tissues (Brito *et al.*, 2019).

In various fruit crops, such as watermelon, blueberry, papaya, mango, guava, and mandarins, UV-B or UV-C radiation has been used to increase the content of secondary metabolites and antioxidant capacity in fruits (Ochoa-Velasco *et al.*, 2017, and references therein). In tomatoes, both UV-C and UV-B increase the concentration of phenolic compounds such as flavonoids, lycopene, and β-carotene, as well as the antioxidant capacity (Bravo *et al.*, 2012; Liu *et al.*, 2011; Pérez *et al.*, 2009). Peng *et al.* (2022) note that UV-B and UV-A radiation are typically applied for several hours to days. UV-C radiation is a method where effective doses can be achieved in a shorter time, from 10 s to a few minutes.

Light influences the expression of genes related to pigment biosynthesis and the control of light signaling pathways (Azari *et al.*, 2010; Qiu *et al.*, 2023). According to Benkeblia *et al.* (2011), purple or bright red skin pigments in tropical fruits may indicate the presence of anthocyanins, with many genes related to the flavonoids that are co-regulated to enhance anthocyanin synthesis, which depends on environmental and other factors (Shi *et al.*, 2023). Color is essential to consumers, who associate it with the taste of various fruits. For this reason, plant breeders strive to develop varieties with striking colors and high anthocyanin content in some fruits (Benkeblia *et al.*, 2011).

It is important to note that the effects of solar radiation do not only depend on its intensity but also, in many cases, are specific to fruit variety or species and its developmental stage, as reported Bernjak and Cristl (2020) and Zoratti *et al.* (2015) regarding the stimulation of flavonoid synthesis in fruits. On the other hand, pruning or eliminating the leaves that cover the fruits allows for greater light interception, increasing fruit size, color, and quality. However, fruit growers should consider the type of fruits (including the thickness and other properties of the epidermis) and avoid exposing fruits for an excessive time close to harvest, especially in very elevated locations with intense UV light (Fischer, Orduz-Rodríguez *et al.*, 2022). In peach (cv. TA-170), with 50% and 75% pruning of branches, maintains significantly higher concentrations of ascorbic acid in the fruits after harvest compared to non-pruned trees, with the higher pruning percentage having a more significant effect on the concentration of ascorbic acid (Choudhury *et al.*, 2021).

In several crops, fruit pre-harvest bagging is used to protect against diseases and pests and also from sunburn due to high solar radiation found at high elevations or during extended summer periods (Fischer, Orduz-Rodríguez *et al.*, 2022). Usually, this high radiation is combined with excessive air temperatures and low relative humidity or, in many cases, with a deficient number of leaves covering the fruits (Baiea *et al.*, 2018). In the case of "sunburn browning", caused by increased solar radiation and temperatures between 46.0 and 49.8°C, the lesions result from severe degradation of chlorophylls and carotenoids, leading to a bronze-brown-yellowish coloration (Muñoz & Munné-Bosch, 2018). It should be considered that light also accompanies high temperatures caused by light intensity.

Results regarding the effect of bagging on fruit phytochemicals are variable. Hossain *et al.* (2020) report higher vitamin C content in unbagged mangoes (29.7 mg 100 g^{-1}) as compared with bagged fruits. Lima *et al.* (2013) observe similar results in peach varieties, where bagged fruits had lower levels of vitamin C, phenolics, and organic acids. On the other hand, bagging mangoes with brown and white paper, UV-selective plastic bags (transparent to UV light) or muslin fabric effectively increases the level of β-carotene compared to the non-bagged fruits (Islam *et al*., 2017).

For varieties with intense color, such as red fruits, removing the bag from the fruits before harvest is essential. This is the case with the 'Mantianhong' pear (*Pyrus pyrifolia*), which develops its red color quickly, where the key regulator PyMYB10 promotes anthocyanin synthesis in response to light (Qian *et al*., 2013).

Similarly, the color and material of shade netting affect fruit quality (Fischer, Orduz-Rodríguez *et al*., 2022; Siddiqui, 2018). According to Tinyane *et al*. (2018), this is mediated by photoreceptors such as phytochromes, cryptochromes, and phototropins, which involve the upregulation of specific genes during fruit development, such as those involved in the synthesis of phenolic compounds. UVB is also sensed by the receptor UV Resistance Locus 8 (UVR8) cellular component, and this radiation may enhance the synthesis of phenolics and terpenoids in plants (Miao *et al*., 2020; Qaderi *et al*., 2023).

Temperature

Crops develop within an optimum temperature range that guarantees, among other growing conditions, maximum yield until growth is limited (Hewett, 2006). Tropical and subtropical fruit trees are exposed to cold and freezing when grown in temperate climates, except if grown under protected conditions in this geographic location (Hewett, 2006). Temperature changes during fruit growth and development significantly affect fruit composition and quality, especially their phytochemical contents (Yahia, 2018). Crop environment temperature greatly influences fruit production, color, aroma, and carbohydrate biosynthesis through its effect on photosynthesis and, consequently, on maturation and ripening processes (Yahía, Gardea-Béjar *et al*., 2019b). Temperature should always be within the range for the cultivated species to ensure optimal photosynthesis, avoiding a more significant respiratory loss of carbohydrates, so night temperatures should be lower, such as under conditions that provide tropical altitudes (Flórez-Velasco *et al*., 2024).

Aril coloration in seeds of pomegranate fruits change inversely with seasonal temperature (Borochov-Neori *et al*., 2011). For apples, nighttime temperatures around 10°C stimulate red coloration in the fruit skin due to anthocyanin accumulation (Musacchi & Serra, 2018), especially when combined with daytime temperatures of around 18 to 24°C that promote fruit growth, depending on the species and variety (Fischer & Orduz-Rodríguez, 2012). Consequently, high nighttime temperatures in the weeks before harvest decrease the accumulation of red pigments in apple fruit skin (Treutter, 2010).

In some varieties of grapes, lower temperatures than the optimal range can increase the content of phenolic compounds (Yahia, Gardea-Béjar *et al*., 2019). For grape berries, cool nights enhance coloration (Fischer *et al*., 2016), being delphinidin an essential precursor of the anthocyanin pigments of this berry, which synthesis is promoted by low temperatures (Yahia, Gardea-Béjar *et al.,* 2019). The enhancement of fruit coloration by night temperatures lower than daytime temperatures is because these conditions activate the gene expression of chalcone synthase. This enzyme participates in the synthesis of anthocyanins (*i.e*., cyanidin, pelargonidin, naringenin, and malvidin, etc.) in fruits of oranges, grapefruits, grapes, red apples, and strawberries (Yahia, Gardea-Béjar *et al*., 2019).

Fruit epidermis temperatures can rise significantly during the day under clear skies (Konno & Sugiura, 2024) in the skin of Satsuma mandarins and apples, with temperatures at least 15°C higher than the average air temperature in Tsukuba, Japan. High temperatures in strawberries (25-30°C per d) increase the content of anthocyanins and total phenolics and enhanced antioxidant activity in the fruits (Wang *et al*., 2006). Toscano *et al*. (2019) report that elevated temperatures can increase antioxidant concentrations, which help protect the cell membrane from breakdown and peroxidation. In turn, Wahid *et al*. (2007) indicate that plants under heat stress may increase the contents of bioactive compounds such as betaine, proline, and sugar alcohols related to stabilizing enzymes/proteins and the membrane bilayer structure of plant tissues. High temperatures directly affect plant metabolism and influence enzymatic activities (Yahia, Gardea-Béjar *et al*., 2019). Pivotal processes affected by heat stress are phenylpropanoid synthesis pathways and photosynthesis (Toscana *et al*., 2019). By high-temperature stress, ROS can accumulate, which activates detoxification systems and causes buildup by preserving the cell membrane from peroxidation and breakdown (Toscana *et al*., 2019).

Due to changes in the microclimate caused by the production system, such as plastic mulch with row covers, Fan *et al*. (2017) find a significant increase in total phenol content and overall antioxidant capacity in the strawberry variety 'SJ8976-1' compared to the standard matted row system (wide rows with straw). Fan *et al*. (2017) attribute this effect mainly to the increase in the surrounding temperature of the soil and plants (Fischer, Cleves-Leguizamo *et al*., 2022). With multivariate techniques, such as principal component analysis and heat maps, Moreno-Medina *et al.* (2024) find a close relationship between the accumulation of phenolic compounds and the photosystem II (PSII) of photosynthesis, which favors the adaptation of Andean blackberries to adverse conditions of low temperature and high radiation in Colombian highlands.

Altitude

Each fruit species is adapted to an elevation range that matches its ecophysiological demands in the tropics and subtropics. It is known that, as elevation increases, solar radiation (especially UV) increases, while temperature, partial gas pressure (CO_2, O_2, N_2), precipitation, and water vapor decrease (Benavides *et al*., 2017; Fischer, Parra-Coronado *et al*., 2022), depending on the microclimatic conditions, because interestingly, in Colombian páramos, the relative humidity is close to 100%. Adapting crop varieties to higher elevations depends, in particular, on their photosynthetic performance and reduced susceptibility to photoinhibition (Fischer, Parra-Coronado *et al*., 2022). Additionally, the adaptation of fruit species to elevational conditions depends on anatomical, morphological, and biochemical characteristics, mainly in fruits and leaves (Fischer *et al*., 2024).

Species and cultivars of fruit plants originating from inner tropical regions, especially Andean fruit species from higher elevations, are noted for their better tolerance to UV-B radiation according to Caldwell *et al.* (1980). With increasing elevation, the level of antioxidants, often phenolics, increases in fruits, particularly in the epidermis, in response to increased UV light (Fischer, Parra-Coronado *et al*., 2022). In the fruit skin of apples growing between 300 and 1,200 m a.s.l. in the Caucasus, Voronkov *et al.* (2019) find increased concentrations of phenolic compounds, many potent antioxidants protecting fruits against excess UV radiation. Similarly, in Italy, the content of phenolic compounds, such as ellagic acid and flavanols in ‘Elsanta’ strawberries, is higher at 1,500 m a.s.l. than at lower elevations (Andreotti *et al*., 2014). In addition, in pomegranate, Mphahlele *et al.* (2014) conclude that elevation may adjust certain climatic factors that significantly affect the biosynthetic pathway of phenolic compounds.

Oliveira *et al.* (2019) find an increase in anthocyanins and tannins in the skin of ‘Syrah’ grapes with increasing elevation, while Karagiannis *et al.* (2016) observe an increase in anthocyanins, total phenolics, carotenoids, flavonoids, and antioxidant capacity in the skin of ‘June Gold’ peaches. Similarly, rising elevation results in stronger red coloration in the skin of pomegranate fruits (Al-Kalbani *et al*., 2021) and strawberries (Pérez de Camacaro *et al*., 2017) due to increased levels of anthocyanins. Additionally, in mandarin pulp (Susanto *et al*., 2013), orange (Ayer & Shrestha, 2018), and strawberry (Pérez de Camacaro *et al*., 2017), there is an increase in vitamin C levels at higher elevations. In contrast, in cape gooseberry, which is enclosed in an enlarged calyx, β-carotene concentration decreases with higher elevation (2,690 respect to 2,300 m a.s.l.) (Fischer *et al*., 2000).

The best quality with the highest levels of alkaloids, flavonoids, amino acids, and vitamins in dragon fruit (pitahaya) cv. Jindu1 in Guizhou Province, China, is reached at the highest altitude of 650 m a.s.l., while at the lower altitude (356 m a.s.l.), the fruits have the highest content of phenolic acids (Zhao *et al*., 2024). Likewise, ‘Golden Delicious,’ ‘Royal Delicious,’ and ‘Red Gold’ apples in northern India produce higher total phenolic content and increased overall antioxidant activity at 1,800 m a.s.l. compared to 1,400 m a.s.l. (Kumar *et al*., 2019).

Water

Water is one of the most critical factors influencing fruit crop growth, development, productivity, and quality. Drought is one of the most destructive abiotic stresses for crop productivity (Devin *et al*., 2023; Ochoa-Velasco *et al*., 2017). Water deficit in crops significantly affects the synthesis and accumulation of bioactive compounds in fruits (González-Chavira *et al*., 2018), considering that the stimulation of secondary metabolism in plants also depends on genetic factors and seasonality, as well as the duration and intensity of the water deficit (Ripoll *et al*., 2014).

Moderate water stress or regulated deficit irrigation (RDI) increases some phytochemicals and flavor compounds in fruits (González-Chavira *et al*., 2018). Production of avocado fruits under deficit irrigation conditions in a subtropical Mediterranean climate results in smaller fruit size but increased content of unsaturated fatty acids (oleic acid), omega-6, and omega-3 fatty acids (Durán *et al*., 2021). Navarro *et al.* (2015) observe that moderate water stress increases grapefruit phenolic compounds, β-carotene, and flavonoid contents but decreased lycopene levels. Additionally, in blueberries, a low irrigation regime in plastic tunnels increases the content of total flavanols (by 30%), delphinidin-3-acetyl hexoside (by 54%), and antioxidant activity (by 10%), depending on the cultivation system and genotype (Cardeñosa *et al*., 2016). In goji berries, irrigation deficit (up to 50% of the evapotranspiration) concentrates most of the health-related metabolites in the fresh fruits. It increases the concentration of total phenolics and carotenoids (+15.5%) and β-carotene (+19.6%) based on dry mass (Breniere *et al*., 2024).

In passion fruit cultivated at 2,260 m a.s.l. during two production cycles in southern Colombia, the second cycle, characterized by high precipitation, elevated relative humidity, and lower solar radiation during the first third of the reproductive period, exhibits a 28% decrease in ascorbic acid content and a 67% reduction in antioxidant capacity compared to the drier preceding cycle (Muñoz-Ordoñez *et al*., 2023). Nectarines grown under long-term regulated irrigation deficit has significantly increase vitamin C content (21-42% in pulp, 20-69% in skin), soluble phenolics (7-11% in pulp, 22-31% in skin), and antioxidant capacity (22-27% in pulp, 8-19% in skin) compared to fruits grown under optimal irrigation (Falagán *et al*., 2015).

Dzomeku *et al*. (2020) find the highest carotenoid levels of three banana cultivars in Ghana during the dry season, which coincides with periods of high UV-B radiation. These authors attribute the high carotenoid content in bananas to increased UV-B radiation under clear sky conditions. Although watermelon yields are reduced by irrigation deficit, lycopene content and fruit quality remain high (Bang *et al*., 2003).

In olives, irrigation deficit regimes produce higher values of phytonutrients and antioxidant capacities, with significant increases in polyphenol content (150-317%), phenylalanine ammonia-lyase (PAL) activity (128-164%), and antioxidant activity (139-292%), depending on the water regime, although these differences tend to decrease as the fruits matured (Machado *et al*., 2013). In contrast, in pomegranates (cvs. Sefri and Wonderful), irrigation deficit at 50% and 70% according to evapotranspiration in a Mediterranean climate in Morocco markedly reduces total phenolic content and antioxidant activity, while an increase in hydrolysable tannin content is observed in both cultivars. However, epicatechin concentrations in both cultivars and caffeic acid in cv. Sefri are not affected by soil water conditions (Adiba *et al*., 2024).

Carbon dioxide concentration in the air

The scenarios of climate change driven by increased atmospheric CO_2 concentration have positive effects on fruit trees, related to enhanced photosynthetic activity, efficient water use, growth, and accumulation of biomass (Fischer, Melgarejo *et al*., 2022), which also affect the production of phytonutrients. Wang *et al*. (2003) observe that increasing CO_2 concentration to 300 or 600 ppm above ambient levels increases flavonoids such as anthocyanin levels in strawberries. Additionally, Wang *et al*. (2003) find that elevated CO_2 concentrations led to higher oxygen-free radical absorbance activity in the fruits. However, Sun *et al*. (2012) observe that increasing CO_2 concentration to 720 mg L^{-1} in growth chambers reduces the total antioxidant capacity of strawberries despite increases in total sugars and fruit dry weight. Loladze *et al*. (2019) report in a meta-analysis that high levels of ambient CO_2 generally decrease carotenoid content by about 15%, and only when plants were stressed by abiotic factors do carotenoid levels increase. Conversely, CO_2 applications in greenhouse vegetable production can increase the edible part´s total flavonoids, phenolics, ascorbic acid, and antioxidant capacity (Dong *et al*., 2018).

Conclusions

Fruit consumption offers numerous health benefits since the fruit's phytochemical contents, including carotenoids, phenolics, monoterpenes, and isoprenoids, prevent various diseases, such as cancer and cardiovascular conditions.

Several critical environmental factors promote the content of phytochemicals in fruits, such as temperature, light quality and intensity, and water deficit. However, excessive levels of these factors can be counterproductive. Besides abiotic stress from climatic conditions, including inter-annual and intra-annual variations, factors such as geographic and elevational location, genotypes, fruit ripening process, and crop management influence the bioactive phytochemical compounds in fruits. Significant interest is in leveraging climate change to enhance product quality while reducing crop yield losses due to adverse conditions.

Conflict of interest statement

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

Author's contributions

HEBL: conceptualization, visualization, writing, and editing. GF: conceptualization, visualization, writing, editing, and supervision. EMY: writing, editing. All authors have read and approved the final version of the manuscript.

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