

Review

A Current Review on the Impact of Environmental and Biological Stresses on the Production of Bioactive Compounds in Berries

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Abstract: In recent years, interest in functional foods has grown due to increasing consumer awareness of the link between diet, health, and nutrition. Berries are a source of bioactive compounds, including particularly secondary metabolites such as polyphenols, flavonoids, and anthocyanins, which are bioactive compounds valued for their antioxidant properties and their potential for producing functional food ingredients. However, berry production faces challenges from environmental stressors, including drought, salinity, and extreme temperatures (either heat or low), which can negatively affect the biosynthesis of these compounds. Such stressors have become more frequent and intense due to climate change. Biological stressors, such as herbivory and pathogens, also threaten berries, triggering complex defense responses that activate secondary metabolic pathways involved in bioactive compound production. These bioactive compounds play a critical role in plant defense and offer potential health benefits, making berries an appealing model for studying plant metabolic responses under stress. Native berries, such as those found in Chile, offer a unique yet underexplored opportunity to investigate how environmental and biological interactions shape metabolite accumulation. Therefore, this review explores how environmental and biological stresses influence bioactive compounds, particularly secondary metabolite production in berries, highlighting their functional potential and emphasizing the importance of understanding these responses to support sustainable use in agri-food industries and human health. This review also highlights recent advances in pre-harvest stress management and emerging food processing technologies, which offer promising approaches to sustainably enhance and valorize bioactive compounds. These insights may guide the development of functional foods and nutraceuticals, fostering innovation in the agri-food sector and informing evidence-based public health policies.

Keywords: antioxidants; bioactive compounds; environmental stress; native berries; pathogens; polyphenols; secondary metabolites



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1. Introduction

In recent decades, the interest in functional foods has grown exponentially, driven by an increasing consumer concern for health and nutrition. Among these foods, berries have gained relevance due to their high content of bioactive compounds, mainly antioxidants such as polyphenols, flavonoids, and anthocyanins, which have been widely associated with health benefits, including protection against oxidative stress and chronic diseases [1]. The growing demand for these fruits has increased their global production, but various environmental factors threaten the sustainability of this cultivation [2]. Plants, including berries, are exposed to multiple environmental and biological stresses that can affect their growth, yield, and nutritional quality. In this framework, environmental stresses represent one of the most significant challenges to global agricultural productivity, as adverse conditions such as drought, extreme temperatures (heat and low), and salinity can alter essential physiological and biochemical processes, reducing crop yields. In parallel, biological stressors such as pathogens and herbivores also pose significant threats, often triggering complex defense mechanisms and altering the plant's metabolic profile.

Furthermore, biological stresses also represent a significant challenge to producing bioactive compounds in berries, particularly those used in functional foods [3]. Insects, fungal pathogens, and other microorganisms can interfere with the plant's ability to produce secondary metabolites, including antioxidants, flavonoids, and polyphenols, which are essential for their health-promoting properties. These stresses can trigger defense mechanisms, but excessive biological pressure may reduce the synthesis and accumulation of these valuable compounds, ultimately impacting the nutritional and therapeutic potential of the crop for food and nutraceutical applications [4]. In particular, berries stand out for their ability to enhance the immune response, a property that has earned them recognition as 'superfoods' [5].

In this context, Chile stands out for its climatic and geographical diversity, which supports a wide range of both cultivated and wild berry species [6]. Among these, native species such as *Aristotelia chilensis* (maqui), *Ugni molinae* (murtilla), *Berberis microphylla* (calafate), *Berberis darwinii* (michay), and *Fragaria chiloensis* (wild strawberries) have attracted increasing attention due to their exceptional antioxidant content and their remarkable ability to thrive under extreme environmental conditions. All of these species are wild natives that have recently entered an incipient process of domestication, making them especially relevant for understanding both natural adaptive traits and the potential for crop development under stress-prone environments [7]. Despite their promising potential, current knowledge regarding the antioxidant properties of these native berries remains limited. However, the growing demand for plant-based products and functional ingredients has fueled scientific and commercial interest in berries, particularly those rich in antioxidants [8,9]. These fruits are recognized for their high nutritional and biological value, largely attributable to their notable concentrations of essential nutrients and bioactive compounds, which also contribute to their excellent bioavailability and bioactivity [10]. Within this framework, Chilean native berries have evolved exceptional traits through long-term exposure to harsh environmental conditions, resulting in distinctive resilience and metabolic adaptations [11]. This evolutionary background, combined with their high antioxidant content, underpins their growing reputation not only as nutritionally dense foods but also as promising candidates for health-promoting applications [12–14].

Climate change has led to heat and drought becoming the most prevalent stresses in the regions where both commercial and native berries are cultivated [15]. Despite the increasing threat posed by these environmental and biological stressors, there is still a notable lack of studies addressing how such conditions impact the metabolic profiles of native berry species. Investigating how these native species respond and adapt to these challenges is crucial, as it could offer valuable insights into their resilience and their capacity to endure future climate change scenarios. These stressors have a direct effect on the nutritional composition, functional properties, and overall quality of berry fruits, attributes that are increasingly appreciated by both the food and nutraceutical industries [16]. Thus, this review focused on the most relevant literature of the last decade, addressing a critical knowledge gap by analyzing how environmental and biological stresses influence the biosynthesis of bioactive compounds in berries and their nutritional quality, with special emphasis on native Chilean species. By examining the interplay between stress conditions and metabolic responses in fruit-bearing plants, this review article highlights key biochemical mechanisms, identifies major bioactive compounds affected, and evaluates the nutritional, functional, and nutraceutical implications for food and health-related applications. This integrative approach aims to support food scientists, agronomists, and postharvest technologists in making and handling informed decisions regarding cultivar selection, cultivation strategies, processing, and formulation to maximize the health-promoting potential of native berries. Building upon this objective, the present review further distinguishes itself by its breadth and scope. Compared to previous reviews focused on specific berry species or particular stress types, this work offers a comprehensive and integrative overview of both environmental and biological stressors and their effects on the accumulation of bioactive compounds in berries. While some earlier studies emphasized either physiological

aspects or postharvest responses, this review uniquely bridges pre-harvest abiotic and biotic interactions, in vitro approaches, and postharvest treatments. Additionally, it highlights the potential of underexplored native Chilean berries, positioning them as promising models for sustainable functional food development.

To ensure a comprehensive and representative synthesis, studies included in this review were selected based on their relevance to the influence of environmental and biological stressors on secondary metabolism in berries. The selection was conducted using major scientific databases (e.g., Scopus, Web of Science, and PubMed), prioritizing peer-reviewed articles published in the last ten years. Studies were included if they addressed preharvest or in vitro stress responses, bioactive compound quantification, or physiological changes under stress in berry species. Emphasis was also given to research involving native berries and functional food potential. Ultimately, the insights provided by this review serve as a scientific foundation for the development of innovative and functional berry-based food products adapted to future environmental challenges.

2. Berries as a Source of Bioactive Compounds

2.1. Functional Roles and Phytochemical Profiles of Berry Bioactive Compounds

Berry fruits are rich in bioactive compounds, such as phenolic compounds, organic acids, tannins, anthocyanins, flavonoids, and even alkaloids with health-promoting potential, which contribute to their health benefits [17,18]. These bioactive compounds play key roles in plant defense against stresses like drought or/and salinity, pathogen microorganisms, and pests among others [19,20]. For instance, anthocyanins, a significant group of polyphenols, are abundant in conventional berries such as chokeberry (*Aronia* spp.), bilberry (*Vaccinium* spp.), honeyberry (*Lonicera caerulea*), blackcurrant (*Ribes nigrum*), grapes (*Vitis* spp.), blackberry (*Rubus* spp.), and berry cactus (*Myrtillocactus geometrizans*) [16]. These bioactive compounds offer antioxidant properties and contribute to anti-inflammatory effects and other health benefits [21]. Hence, berries are notable for their diverse profile of bioactive compounds, including phenolic acids, tannins, stilbenes, and carotenoids [22]. For instance, phenolic acids, mainly derivatives of cinnamic and benzoic acids, encompass compounds such as *p*-hydroxybenzoic acid, salicylic acid, gallic acid, ellagic acid, caffeic acid, chlorogenic acid, and neochlorogenic acid, with ellagic acid being the predominant phenolic acid in strawberries and raspberries [23,24]. Tannins are also abundant and are categorized into condensed tannins (proanthocyanidins) and hydrolysable tannins [25]. For example, chokeberry exhibits the highest concentrations of condensed tannins, whereas strawberries, raspberries (*Rubus idaeus*), and blackberries are particularly rich in hydrolysable tannins [26]. Stilbenes, such as resveratrol, are present in lower concentrations and are primarily found in grapes, bilberries, cranberries (*Vaccinium oxycoccus*), redcurrants, and strawberries [27]. Carotenoids, including lycopene, β -carotene, ζ (Zeta)-carotene, β -cryptoxanthin, lutein, 5,6-epoxylutein, trans-violaxanthin, cis-violaxanthin, and neoxanthin, are detected in relatively small quantities across various berries, with chokeberry identified as one of the richest sources, containing up to 48.6 mg/kg fresh weight (FW) [16]. In addition, the anthocyanin profiles of different berry species reveal a diversity of anthocyanins. For instance, bilberries (*V. myrtillus*) are rich in delphinidin and cyanidin derivatives, with malvidin-3-glucoside being the dominant anthocyanin [28]. Blackcurrants mainly contain delphinidin-3-rutinoside, while blackberries (*R. fruticosus*) are characterized by cyanidin-3-glucoside [29]. Blueberries (*V. corymbosum*) predominantly contain malvidin derivatives, including malvidin-3-arabinoside [30]. Chokeberries are rich in cyanidin-3-galactoside, cranberries contain peonidin-3-glucoside and cyanidin-3-glucoside, raspberries are dominated by cyanidin-3-sophoroside, and strawberries (*Fragaria x ananassa*) mainly contain pelargonidin-3-glucoside [16]. These diverse anthocyanin profiles contribute to the characteristic colors and health benefits of each berry species. Altogether, the rich and varied composition of bioactive compounds in berries underscores their relevance not only as functional foods but also as promising sources for the development of health-promoting nutraceuticals.

2.2. Native Berries from Chile as a Source of Bioactive Compounds

Chile is home to a remarkable diversity of berry fruits, some of which have gained significant economic importance. One notable example is the blueberry industry, which has positioned the country as the leading global exporter [31]. In contrast, the cultivation of native berries has seen less development, and scientific knowledge regarding their nutritional value and potential health benefits remains limited [7]. In recent years, however, there has been a growing interest in native berries, driven by the discovery of their high concentrations of bioactive compounds [16,32]. These substances are known for promoting health and have led to the exploration of native berries as promising sources of functional foods [33]. Several native Chilean berries, such as *A. chilensis*, *F. chiloensis*, *U. molinae*, *B. darwinii* and *B. microphylla* (Figure 1), stand out for their rich content of antioxidant

and health-promoting compounds [34]. These are primarily phenolic compounds, including flavonoids, phenolic acids, tannins, and other well-known natural antioxidants [35]. The wide range of bioactive compounds found in these berries has been associated with numerous health benefits [3,36]. Studies have shown their potential to help prevent chronic diseases such as cancer, type II diabetes, neurodegenerative conditions, and osteoporosis [12,37]. These native species, such as murtilla or Chilean guava, maqui or Chilean blackberry, calafate or Magellan barberry, michay or Darwin's barberry, and wild strawberry or Chilean strawberry, not only share a common geographic origin in the southern regions of Chile but also have long-standing traditional uses and increasing commercial relevance [18,38–43]. For instance, murtilla, a plant from the Myrtaceae family, produces small red berries with a pleasant aroma and flavor, which are processed into products such as jams and liqueurs [44]. This deciduous shrub grows wild from the Maule Region ($-35^{\circ}30'0.00''$ S $-71^{\circ}30'0.00''$ W) to Chiloé Island ($42^{\circ}35'52.11''$ S $73^{\circ}57'32.82''$ W), including the Juan Fernández archipelago ($33^{\circ}38'40.02''$ S $78^{\circ}49'34.41''$ W) [45]. In addition, the fruit of murtilla is rich in bioactive compounds with notable health-promoting properties [46]. For example, key compounds identified in the fruit include anthocyanins, mainly cyanidin and peonidin glucosides, with concentrations reaching approximately $1\text{ }\mu\text{mol/g}$ of dry weight [47]. The fruit also contains flavonols, particularly quercetin derivatives such as quercetin-3-glucoside and quercetin-3-glucuronide [48]. Additionally, gallic acid has been identified as a prominent phenolic compound, contributing to the fruit's antioxidant properties [49]. These bioactive compounds are primarily responsible for the antioxidant, anti-inflammatory, and potential disease-preventing effects of murtilla, making it a valuable source of natural antioxidants [50]. Additionally, studies conducted by Chacón-Fuentes et al. [41] reported for the first time the presence of isoflavonoids in *murtilla*, compounds that, due to their phytoestrogenic activity, are used in the pharmaceutical industry.

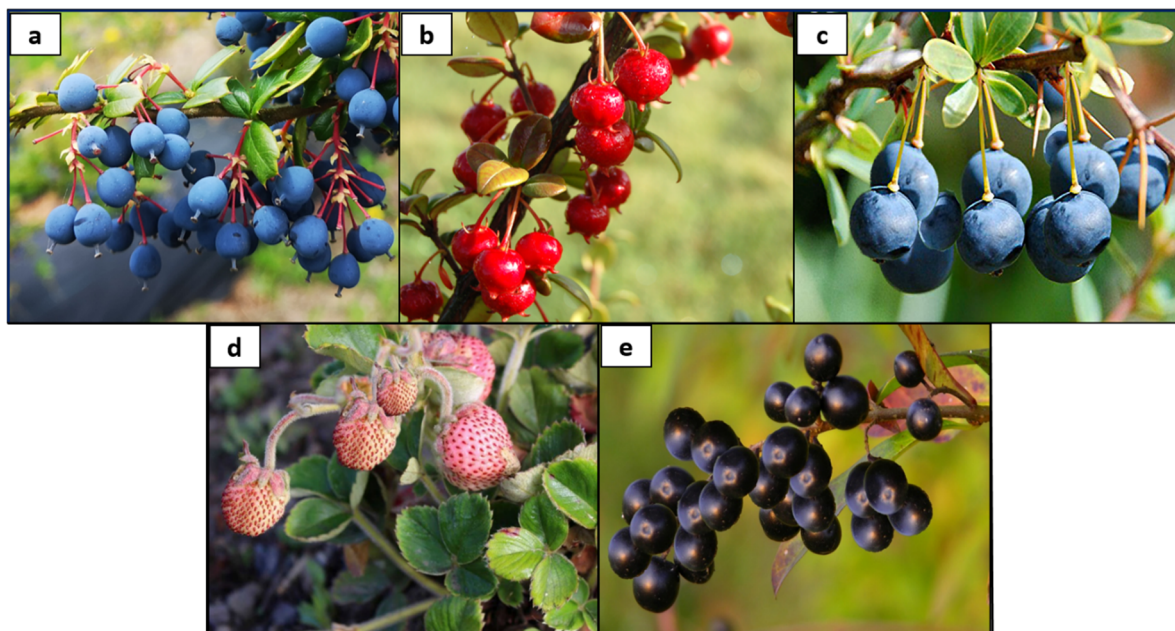


Figure 1. Photographs of the ripe fruit of different native Chilean berries. (a) Berries of michay (*Berberis darwinii*), (b) Fruits of murtilla (*Ugni molinae*), (c) Fruits of calafate (*Berberis microphylla*), (d) Fruits of white strawberry (*Fragaria chiloensis* ssp. *patagonica*), and (e) Fruits of maqui (*Aristotelia chilensis*).

On the other hand, Maqui, an evergreen shrub from the Elaeocarpaceae family, is known for its black to purple berries, which are used in both gastronomy and folk medicine [51]. Maqui is found from the Limarí Province ($30^{\circ}49'17.17''$ S $70^{\circ}59'13.59''$ W) to the Aysén Region ($46^{\circ}08'36.47''$ S $74^{\circ}12'46.04''$ W) in Chile [52]. The fruit of maqui is renowned for its rich composition of bioactive compounds, particularly anthocyanins, which are the primary contributors to its antioxidant properties [53]. The fruit contains high levels of delphinidin derivatives, such as delphinidin-3-glucoside, with concentrations of anthocyanins reaching up to $2.5\text{ }\mu\text{mol/g}$ of dry weight [54]. In addition to anthocyanins, maqui fruits are rich in phenolic compounds, including flavonoids like quercetin and kaempferol, as well as ellagic acid [53]. These compounds are associated with strong antioxidant and anti-inflammatory effects [13]. Moreover, maqui berries are also known to contain significant levels of phenolic acids, such as caffeic and ferulic acids, which further contribute to their health-promoting potential [52].

Calafate, native to the Aysén and Magallanes ($53^{\circ}21'9.91''$ S $71^{\circ}33'17.2''$ W) regions, is a perennial plant from the Berberidaceae family, whose blue-black fruits are essential for producing jams and juices [55,56]. Several

polyphenols have been identified in calafate, highlighting its potential as a source of health-promoting compounds. Among the most important polyphenols reported are caffeic acid and quercetin, with concentrations of $11.345 \pm 77 \mu\text{g/g}$ and $1.093 \pm 25 \mu\text{g/g}$ of fresh weight, respectively [57]. Other phenolic compounds, such as gallic acid, chlorogenic acid, caffeic acid, p-coumaric acid, ferulic acid, rutin, myricetin, and kaempferol, are also present, with concentrations varying depending on the harvesting region [12]. For instance, in Mañihuales (Aysén Region, Chile), anthocyanin content was recorded at 0.64 mg of cyanidin/g of dry fruit [58]. These compounds play a crucial role in protecting against lipid oxidation, benefiting both food quality and human health [1]. In addition, the antioxidant activity of calafate is significant, with values of 475 and 375 μmoles of Trolox equivalents/g of fresh weight, as measured by the DPPH and ABTS methods, respectively [59].

Similarly, michay, also from the Berberidaceae family, has fruits that change color during ripening, from green to black, and are used in cooking as well as in medicinal treatments for their anti-inflammatory properties [18]. Michay is native to the temperate forests of southern South America, from Ñuble ($36^{\circ}37'59.37''$ S $71^{\circ}56'18.54''$ W) to Aysén in Chile, and in the mountainous areas of Argentine Patagonia ($44^{\circ}59'24.25''$ S $70^{\circ}40'24.35''$ W) [60]. Phytochemical analyses have identified several bioactive compounds in this species, notably benzyloquinoline alkaloids such as berberine and palmatine, which are present in root extracts [18,60]. These alkaloids have demonstrated antibacterial properties, particularly against *Staphylococcus aureus* and *Staphylococcus epidermidis* [61]. Additionally, alkaloidal extracts from the stem bark have shown potent acetylcholinesterase inhibition, suggesting potential applications in Alzheimer's disease therapy [62]. Furthermore, studies indicate that extracts from *Berberis* can modulate innate immune responses in murine phagocytes, affecting adhesion, phagocytic activity, and NF- κ B translocation, which are crucial in inflammatory processes [63].

Finally, the wild strawberry, found in two varieties, white and red, is recognized for its volatile compounds and use in food and is distributed along the southern latitudes of the country [11]. The white variety produces larger berries and is found between latitudes 35° S and 39° S, while the red variety, with smaller berries, is distributed between latitudes 35° S and 45° S [43]. These species are not only fundamental to local food but also represent a shared cultural and natural heritage in southern Chile. Phytochemical analysis has revealed that the fruit contains ellagic acid-based hydrolysable tannins, which are known for their antioxidant properties [64]. Additionally, procyanidins, a type of condensed tannin, contribute to its strong antioxidant capacity [25]. Flavonoid glycosides, particularly derivatives of quercetin and kaempferol, have also been identified in *F. chilensis*, providing various health-promoting effects [12].

3. Environmental Stressors and Their Role in Boosting Bioactive Compounds in Berries

Environmental stresses, such as temperature extremes, drought and salinity, are emerging as major challenges for global crop productivity, increasingly threatening food security [65]. These stresses induce secondary metabolic pathways, which are often not fully activated under ideal conditions, so a shorter cycle with stress can yield products with higher nutraceutical value [66]. Before harvest, the accumulation of phytochemicals in berries can be stimulated through the use of environmental stresses [67]. For example, it has been shown that exposure to higher light intensity or less frequent irrigation can increase the content of beneficial compounds such as vitamin C in plants [68–70]. Some of the most widely studied environmental stresses include UV radiation, salinity, drought and/or cold damage [71]. During these stress conditions, plants activate complex signaling cascades that modulate gene expression related to secondary metabolite biosynthesis. Key pathways such as the phenylpropanoid and flavonoid biosynthetic routes are upregulated, leading to enhanced production of antioxidants like flavonoids, anthocyanins, and phenolic acids. Additionally, environmental treatments can influence enzyme activities, such as phenylalanine ammonia-lyase (PAL) and chalcone synthase (CHS), which serve as crucial regulators in these pathways. This biochemical modulation allows plants to adapt and defend themselves against oxidative damage induced by stressors, thereby increasing the nutraceutical content of the fruits.

These environmental stimuli challenge plant development and activate sophisticated defense mechanisms, including the production of specialized metabolites (Table 1). A schematic representation of these stress-induced responses in berries is presented in Figure 2. The following section describes the main stresses affecting the bioactive compounds' accumulation in plants.

Table 1. Classification of metabolites by chemical family, representative compounds, stressor agent inducing their biosynthesis, associated plant species, magnitude of relative increase, and potential applications in the food industry.

Family of Metabolites	Compounds	Stressor Agent	Plant	Increase Value	Food Application
Anthocyanin	Delphinidin 3-glucoside [72–74]	Drought stress [73] and salinity [74]	<i>Vaccinium corymbosum</i>	8.45× [72]	It is an anthocyanin pigment used as a natural colorant in food and beverages, providing red to purple hues. It also offers antioxidant benefits, making it suitable for functional foods [75].
Anthocyanin	Delphinidin-3-O-glucoside chloride [72,76]	Drought stress and salinity [76]	<i>Vaccinium corymbosum</i>	7.74× [72]	This compound serves as a natural colorant and antioxidant in food products, enhancing visual appeal and nutritional value [75].
Flavonols	Quercetin-3-O-glucosyl-6'-acetate [72,77]	Drought stress [72,77] and salinity [77]	<i>Vaccinium corymbosum</i>	Up-regulated [72]	This flavonol glycoside exhibits antioxidant properties [78].
Flavonols	Guaijaverin [72]	Drought stress [72,79]	<i>Vaccinium corymbosum</i>	Up-regulated [72]	Its direct application in the food industry is not well-documented, but it may contribute to the preservation of food products.
Flavonols	Avicularin [72]	Drought stress [72,79]	<i>Vaccinium corymbosum</i>	Up-regulated [72]	It may serve as a functional ingredient due to its bioactive properties [80].
Flavonols	Isoquercitrin [72,79,81]	Drought stress [81] and salinity [79]	<i>Vaccinium corymbosum</i>	Up-regulated [72]	An antioxidant in various food products. Its enzymatically modified form (EMIQ) is approved as a food additive in Japan and the USA, enhancing the stability of flavors and colors in beverages, dairy products, and baked goods [78].
Flavanone	5,7-dimethoxyflavanone [72]	Drought stress [72,79]	<i>Vaccinium corymbosum</i>	Up-regulated [72]	Specific applications in the food industry are not well-established, but it may be explored for its bioactive properties.
Flavanone	Hesperidin [72]	Drought stress [72,81]	<i>Vaccinium corymbosum</i>	Up-regulated [72]	Hesperidin is widely used in the food industry as a natural preservative, flavoring agent, and functional ingredient. It inhibits spoilage microorganisms, extends shelf life, improves texture in baked and dairy products, and enhances flavor and color with its natural citrus profile. Its strong antioxidant properties also make it a valuable addition to functional foods and beverages [82].
Flavone	Eupatilin [72]	Drought stress [72]	<i>Vaccinium corymbosum</i>	Up-regulated [72]	Its application in the food industry is not well-documented, but it may have potential as a functional ingredient.
Flavone	Demethylnobiletin [72,79,83]	Drought stress [72], salinity [79] and phytohormones [83]	<i>Vaccinium corymbosum</i>	Up-regulated [72]	While specific food industry applications are limited, it may be considered for inclusion in functional foods and beverages [82].

GLVs: Green leaves volatiles.

Table 1. Cont.

Family of Metabolites	Compounds	Stressor Agent	Plant	Increase Value	Food Application
GLVs	3-hexanone [84]	Herbivory damage (aphids) [84]	<i>Ugni molinae</i>	9.2× [84]	Flavoring agent in various food products, providing sweet and fruity notes [85].
GLVs	3-hexanol [84]	Herbivory damage (aphids) [84]	<i>Ugni molinae</i>	5.5× [84]	It is used as a flavoring agent in baked goods, non-alcoholic beverages, ice cream, and hard candies, providing wine and spice notes [85].
GLVs	2,4-Dimethyl acetophenone [84]	Herbivory damage (aphids) [84]	<i>Ugni molinae</i>	4.6× [84]	Flavoring agent in various food categories, including meat products, dairy, and processed vegetables, providing a floral profile [85].
Terpenes	Pinene [84]	Herbivory damage (aphids) [84]	Murtilla (<i>Ugni molinae</i>)	7.6× [84]	Natural preservative in bakery products [86].
Terpenes	Sabinene [84]	Herbivory damage (aphids) [84]	Murtilla (<i>Ugni molinae</i>)	26.0× [84]	It is used in the food industry to provide fresh and spicy notes to products such as beverages, confectionery, and processed foods-[86].
Terpenes	β-myrcene [84]	Herbivory damage (aphids) [84]	Murtilla (<i>Ugni molinae</i>)	11.0× [84]	It's a monoterpene with a herbaceous and balsamic aroma, used as a flavoring additive in the production of foods and beverages [86].
Terpenes	1,8 cineole [84]	Herbivory damage (aphids) [84]	Murtilla (<i>Ugni molinae</i>)	38.2× [84]	It is used in the food industry for its refreshing aroma and antimicrobial properties [86].
Terpenes	Limonene [84]	Herbivory damage (aphids) [84]	Murtilla (<i>Ugni molinae</i>)	17.4× [84]	Natural preservative in sauces and dressings [86].
Terpenes	Andrographidin B [72]	Drought stress [72] and phytohormones [84]	<i>Vaccinium corymbosum</i>	Up-regulated [72]	It may contribute to the development of natural preservatives or food supplements, though its use in food processing and formulation is still under investigation [86].

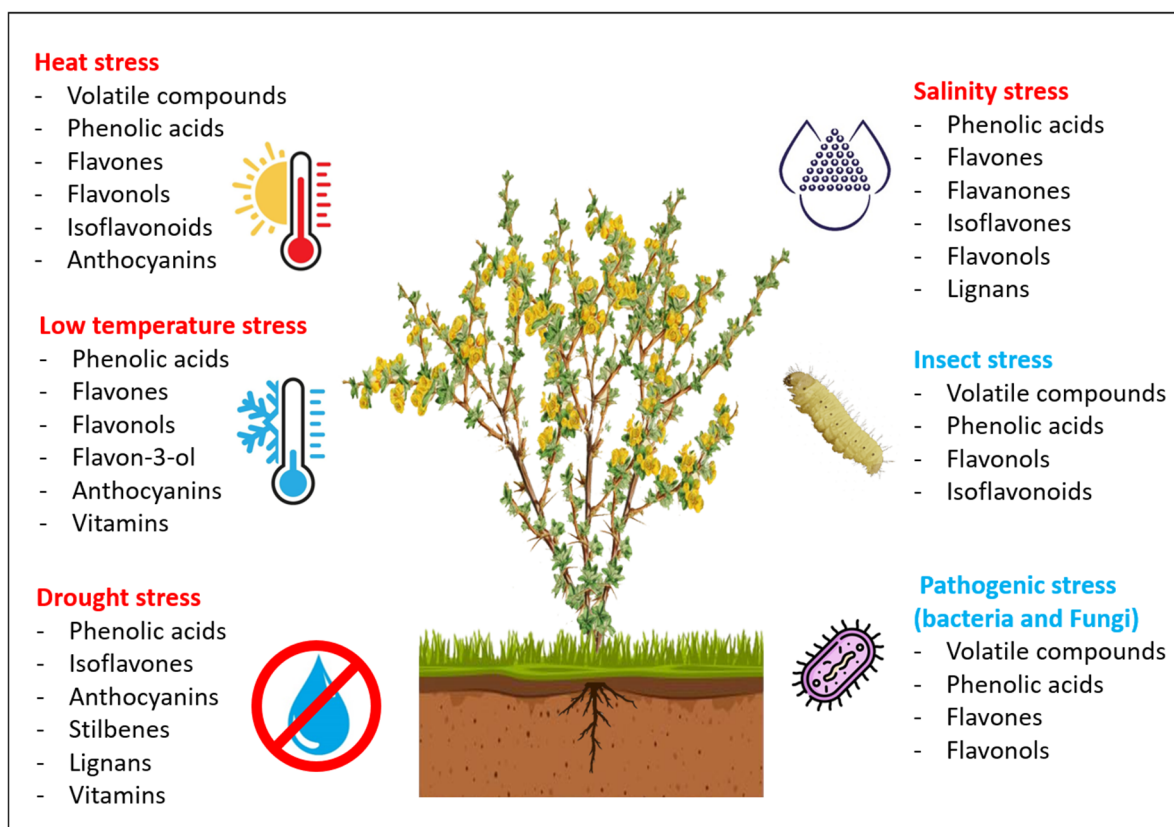


Figure 2. Schematic representation of stress-induced bioactive compound production in native berries. This diagram highlights the native berry plant's response to environmental cues. Abiotic (red) and Biotic (blue) stressors trigger the synthesis of specialized metabolites in the plant, modulating phytochemical profiles and contributing to both plant resilience and the nutraceutical value of the fruits.

3.1. Drought and Heat Stresses: Effect on Physiology and Bioactive Compound Accumulation in Berries

Drought and heat stress (generally associated with uncontrolled environmental conditions) are among the most detrimental environmental stresses, especially for plants grown in arid and semi-arid regions [87]. Water scarcity affects over 40% of the world's arable land, disrupting the physiological functions of plants, reducing photosynthetic efficiency, and accelerating senescence [88]. In berries, which are highly sensitive to water availability and temperature, the consequences of drought and heat stress are significant [89]. Drought causes dehydration and stunted growth, while elevated temperatures disrupt the biosynthesis of key bioactive compounds, especially antioxidants [70]. These stress conditions negatively affect the nutritional and functional qualities of berries, particularly the levels of polyphenols, flavonoids, and anthocyanins, which are closely associated with health benefits such as protection against oxidative stress [1]. Consequently, a reduction in the production of these compounds under environmental stress can significantly compromise the overall quality and health-promoting potential of berry crops [90]. While it is well established that severe or prolonged environmental stresses can negatively impact plant physiology and diminish antioxidant capacity, mounting evidence suggests that controlled or moderate stress conditions may, in contrast, act as a trigger for the enhanced synthesis of antioxidant compounds. This hormetic response not only reflects the plant's adaptive mechanisms but also underscores the potential of stress-induced metabolic shifts to boost the nutritional and functional value of plant-derived foods.

Therefore, while environmental stressors such as drought and heat often negatively impact the phytochemical content of berries, certain conditions can stimulate the accumulation of bioactive compounds, enhancing their antioxidant properties [91]. For instance, in blueberries, exposure to UV-B radiation has been shown to significantly increase anthocyanin levels. Specifically, anthocyanin content increased 2.9-, 4.2-, 5.1-, and 9.0-fold after 6, 12, 24, and 48 h of UV-B treatment, respectively, indicating that such stress can promote the accumulation of flavonoid compounds [92]. Similarly, in strawberries, drought stress has been associated with increased anthocyanin and total phenolic contents [93]. Studies have demonstrated that water deficit conditions can lead to a 36–56% increase in anthocyanin accumulation, depending on the harvest time, suggesting that such stress can enhance the fruit's antioxidant capacity [93]. These findings highlight that, under specific stress conditions, berries

may bolster their production of health-promoting phytochemicals, potentially improving their nutritional and functional qualities [94]. Water deficit often leads to oxidative stress through the accumulation of reactive oxygen species (ROS), due to disrupted cellular homeostasis and membrane damage. In response, plants frequently enhance the synthesis of antioxidant compounds, such as polyphenols and flavonoids to neutralize ROS and stabilize cell structures [95].

3.2. Salinity Stress: Effect on Physiology and Phytochemical Production in Berries

Soil salinity, affecting around 20% of irrigated land, disrupts plant growth by altering ion balance, reducing nutrient uptake, and causing toxic sodium buildup, which severely impacts berries by affecting growth and antioxidant production [96]. Similarly, waterlogging, caused by excess water, leads to oxygen deprivation in the roots, disrupting nutrient absorption and increasing disease susceptibility [97]. Prolonged flooding significantly reduces berry yields and alters metabolic pathways involved in secondary metabolite synthesis, including antioxidants [98]. Understanding the combined effects under various stresses is essential for developing varieties that can maintain both yield and nutritional quality in changing environmental conditions. For example, in commercially cultivated berries such as strawberries, moderate salt stress (40 and 80 mmol/L NaCl) increased antioxidant capacity, as well as levels of ascorbic acid, anthocyanins, and superoxide dismutase activity [99]. Additionally, a reduction in nitrogen supply under saline conditions enhanced antioxidant capacity and increased flavan-3-ols, anthocyanins, and total phenols in strawberries [100].

These findings highlight the complex yet potentially beneficial role of salinity and water-related stresses in modulating antioxidant pathways in berries. Rather than being solely detrimental, carefully managed stress conditions may enhance the nutritional and functional value of berries. This underscores the importance of adopting integrated breeding and agronomic strategies aimed at optimizing stress tolerance while simultaneously enhancing the production of health-promoting phytochemicals.

3.3. Low Temperature Stresses: Impact on Bioactive Compounds in Berries

Low temperature stresses (commonly ranging from 0 °C to 10 °C) are significant challenges for plants in temperate and high-altitude regions, where such conditions can restrict growth, alter membrane fluidity, and reduce enzymatic activity, ultimately leading to irreversible damage and reduced productivity [101,102]. Nevertheless, berries, including native species like maqui (*Aristotelia chilensis*), have developed cold tolerance mechanisms that allow them to survive frost and maintain antioxidant production under such stress [103]. In contrast, conventional berries (e.g., blueberries, raspberries, strawberries) often struggle to retain their bioactive properties when exposed to cold stress [104]. For instance, low temperature exposure, particularly in the range of 2–8 °C, has been shown to significantly affect growth and bioactive compound profiles in strawberries and blueberries [94]. In strawberries, cold stress can lead to increased antioxidant enzyme activity, although catalase activity may decrease under prolonged exposure to low temperatures [105]. In blueberries, moderate cold stress (approximately 4–10 °C) has been associated with an accumulation of antioxidants, particularly phenolic compounds, suggesting a potential adaptive response to low temperatures via enzymatic pathways [95]. This is particularly interesting because the increase in bioactive compounds can be assessed not only through their direct quantification, but also by analyzing the expression and activity of related enzymes. In this sense, enzymes serve as key indicators of the synthesis or accumulation of these compounds under various stress conditions, including salinity and drought. Under drought conditions, the strawberry cultivar ‘Fortuna’ showed a 2.77-fold and a 2.23-fold increase in catalase and peroxidase activity, respectively, as reported by Perin et al. [106]. Under saline stress, ‘Fortuna’ also exhibited a 2.55-fold increase in catalase activity and a 1.20-fold increase in peroxidase activity. Similarly, the ‘Festival’ cultivar under saline stress showed a 2.51-fold increase in catalase activity and a 1.07-fold increase in peroxidase activity. These findings suggest that both drought and salinity can enhance antioxidant enzyme activities in strawberries, particularly catalase. Research on the effects of low temperature stress on native Chilean berries remains limited; however, available evidence from other fruit species suggests that exposure to cold conditions (typically below 8 °C) could significantly influence the synthesis of bioactive compounds and the antioxidant activity of these fruits. Such stress may alter metabolic pathways, potentially enhancing or reducing the accumulation of health-promoting secondary metabolites. Consequently, further investigation is needed to clarify how cold stress impacts these native berries and to inform the development of targeted cultivation and postharvest practices that preserve or improve their nutritional and functional properties.

4. Impact of Biological Stresses on Bioactive Compound Synthesis in Berries: Insights into Herbivory and Microbial Interactions

Biological stresses, resulting from interactions with living organisms such as herbivores and microorganisms, play a crucial role in shaping the production of bioactive compounds in plants [107]. Berries, as well as native berries, have evolved under diverse and often harsh environmental conditions [108]. They are frequently exposed to such biological pressures and have developed intricate biochemical mechanisms to cope with them [109]. These defense responses involve activating secondary metabolic pathways that produce compounds such as flavonoids, phenolics, tannins, and volatile organic compounds (VOCs), contributing to plant protection and fruit quality [110].

Among the various forms of biological stresses, insect herbivory is considered as a potent trigger for plant defense activation and can significantly influence the metabolic profile of berries [111]. Upon insect attack, plants activate a range of defense responses that include the de novo synthesis of secondary metabolites such as phenolic compounds, VOCs, and alkaloids [112]. These bioactive compounds function in plant defense by deterring herbivores or attracting natural enemies of the attacking insect [113]. Importantly, many of these stress-induced compounds also possess strong antioxidant, antimicrobial, and anti-inflammatory properties, which are highly valued from a human nutritional perspective [114]. As such, moderate levels of herbivory may inadvertently enhance the nutritional and functional quality of berries by elevating their content of bioactive phytochemicals, including flavonoids and other polyphenols, which are known to confer health benefits [115].

However, while herbivory has received significant attention, the effects of microbial pathogens on the metabolic profiles of native berries remain largely unexplored. Despite growing interest in the modulation of secondary metabolites by biological stresses, there is still a significant gap in our understanding of how infections by fungi and bacteria influence these pathways, particularly regarding native berries. Most available studies have focused on the antimicrobial properties of berries extracts in vitro rather than investigating how infections trigger the accumulation of defense-related compounds in plants [116,117]. For instance, although flavonoids, tannins, lignans, and anthocyanins are known to exhibit antimicrobial activity through mechanisms such as membrane disruption and inhibition of microbial adhesion, their inducible biosynthesis in response to active infections remains poorly studied under natural conditions.

4.1. Herbivory and Microbial Influences on VOC Emissions in Native Berries: Implications from Defense to Fruit Quality

Volatile organic compounds are key elements of native berries' chemical defense strategies. Herbivory damage has been reported to induce the release of volatile organic compounds. For example, in *U. molinae*, herbivory damage significantly induces the release of VOCs [118]. Murtilla subjected to herbivore feeding exhibited the highest emission rates, reaching up to $439.3 \pm 20.0 \mu\text{g}/\text{cm}^2/\text{day}$, compared to control plants without feeding, which peaked at $112.8 \pm 17.4 \mu\text{g}/\text{cm}^2/\text{day}$. Compounds such as 2-hexanone, α -pinene, 1,8-cineole, β -myrcene, and trans-caryophyllene were more abundant in murtilla, particularly under herbivore stress [18,30,38,40,104,118]. In addition, most emitted compounds fall into two major categories: green leaf volatiles, including alcohols, ketones, and esters, and terpenes (monoterpenes and sesquiterpenes) [119].

Furthermore, both pathogenic and beneficial microbial interactions can also influence VOC emissions. For example, in *R. idaeus*, specific bacterial genera were associated with the production of distinct VOC classes: *Gluconobacter* with acids and alcohols, *Rosenbergiella* with monoterpenes and ketones, and *Methylobacterium* and *Sphingomonas* with aldehydes [120]. These interactions suggest a complex and dynamic interplay between plant microbiota and the volatile profile, which may affect defense, fruit quality, and aroma. Based on the scientific evidence reviewed and discussed, the alterations in volatile organic compound (VOC) profiles induced by pathogen attacks are still poorly characterized in native berry species, despite their ecological and agronomic relevance. This represents an important gap in our current understanding of their defense mechanisms and metabolic responses. While commercial berries have received some attention, mainly regarding treatments to enhance postharvest resistance, the impact of active infections on VOC emissions in native species is still an open research area.

4.2. Biological Stress Responses in Modulation of Antioxidants and Volatiles in Berries

Antioxidant compounds such as flavonoids, phenolic acids, tannins, anthocyanins, and lignins are essential for plant health and environmental adaptation, human nutrition, and fruit quality [121]. In berries, as in other plants, these compounds help maintain cellular redox balance and play critical roles in constitutive and inducible defense mechanisms [122]. In native species such as *U. molinae*, domestication efforts focused on improving fruit yield and size have led to a reduction in the concentration of key polyphenols like rutin, quercetin, and kaempferol in

cultivated ecotypes compared to their wild relatives [38]. For instance, controlled common garden studies reported decreases of up to 21.9% in myricetin and 9.7% in quercetin in first-generation domesticated plants. These reductions were associated with increased insect populations and herbivory damage, reinforcing the role of antioxidant compounds in ecological defense [118]. Moreover, four flavonols and two isoflavonoids have been identified in its leaves, with quercetin and rutin reaching concentrations of 89.8 and 75.2 mg/g, respectively [40]. These molecules contribute to plant resilience under biological stresses and enhance the fruit's nutraceutical value.

On the other hand, antioxidant compounds in conventional berries, such as strawberries also respond dynamically to biological stimuli. Strawberry fruit, like many others, can activate resistance and enhance antioxidant capacity through the induction of enzymes like peroxidase (POD), catalase (CAT), superoxide dismutase (SOD), and ascorbate peroxidase (APX), along with the synthesis of phenolic antioxidants [123]. The accumulation of phenolic compounds activates flavonoid biosynthesis and enhances resistance to the fungus [124]. In complement, blueberries are highly susceptible to postharvest decay due to *Botrytis* and *Alternaria* spp., and the activity of key antioxidant enzymes (SOD, CAT, POD, APX), and the levels of polyphenols, flavonoids, and anthocyanins, improving resistance to *A. tenuissima* [125].

Volatile organic compounds and antioxidant compounds represent two distinct yet interconnected arms of the plant's defense system against biological stress [126–128]. Similar stimuli, such as herbivory or pathogenic infection, activate both metabolic pathways. Notably, moderate biological stresses may enhance the accumulation of compounds with recognized nutraceutical value [96].

Future research should unravel the regulatory crosstalk between VOC, antioxidant production, herbivory, and pathogen interactions. It should also show how these compounds can be optimized to reinforce these defense traits and manage disease resistance while preserving or enhancing fruit quality.

5. Environmental Stresses Management for the Accumulation of Bioactive Compounds Pre- and Postharvest

In recent years, several studies have reported that the agronomic management of environmental factors through controlled stress can positively affect the accumulation of bioactive compounds [96]. It is widely known that understanding the environmental factors and growing conditions that positively influence bioactive accumulation allows for the development of agronomic practices aimed at enhancing the nutritional quality of berries [95]. For example, blueberry plants have been shown to respond to pre- and post-harvest UV exposure by increasing flavonoid accumulation and antioxidant capacity [129]. UV exposure enhances flavonol accumulation early in fruit development and boosts anthocyanin and proanthocyanidin contents. Blueberries grown under greenhouse conditions and exposed to UV-B radiation showed accelerated fruit maturation, increased sugar accumulation, and up to a 167% rise in anthocyanin content in mature fruits [130]. Furthermore, cultivar-dependent responses in blueberry leaves indicated that UV-B-resistant cultivars accumulate antioxidants more rapidly and to higher levels than sensitive ones. While UV-C exposure is primarily used for sterilization, it also improves antioxidant properties [131]. Similarly, in strawberries, controlled water stress (Ir50) combined with Absciscic Acid treatment significantly enhanced fruit quality. This interaction led to the highest levels of total anthocyanins, malic, ellagic, and caffeic acids, as well as chlorogenic antioxidant activity, suggesting improved phenolic biosynthesis, sweetness, and overall quality [132]. According to Çeliktöpus et al. [133], applying a 50% deficit irrigation level led to a significant increase in quality-related compounds. Total phenolic content increased by 27% and total antioxidant content by 7%, compared to full irrigation [133]. Beyond UV light and water stress, other abiotic stresses like salinity, water deficit, and low temperatures can also trigger antioxidant accumulation in blueberries [95]. Furthermore, postharvest controlled environmental stress treatments, such as physical damage, high or low temperatures, altered atmospheric gas composition, UV light, or phytohormone applications, also influence plant tissues, with cold chain management reducing postharvest losses [134]. For instance, anthocyanin levels in strawberries increased by 154% after being submerged in hot water at 45 °C for 5 min, following a 12-day period [135]. In addition, a study by Flores and del Castillo [136] found that pre-harvest methyl jasmonate (MJ) treatment significantly increased myricetin, ellagic acid, and quercetin in 'Glen Lyon' red raspberries. Ellagic acid and quercetin increased in all three varieties studied (Glen Lyon, 'Glen Ample, and Tumaleen) even at lower MJ concentrations. Post-harvest MJ treatment did not significantly increase the levels of these compounds, but it helped maintain them during storage by preventing their natural decline. Thus, pre-harvest MJ is effective for boosting bioactive compounds, while post-harvest MJ aids in their preservation during storage.

6. Future Perspectives on Production of Biocompounds and Emerging Technologies in Berries

In the future, food production will require more efficient and sustainable methods that do not depend on large land areas. Additionally, advancing the use of emerging technologies will be key to enabling the efficient concentration of bioactive compounds with improved functional properties. The following section outlines future perspectives on food production through in vitro cultivation and the application of emerging technologies:

6.1. In Vitro Production of Bioactive Compounds Under Stress

In vitro plant cultivation represents a key biotechnological strategy for the sustainable and standardized production of high-value bioactive compounds, particularly in the food and pharmaceutical industries [137,138]. By enabling the growth of plant cells, tissues, or organs under controlled conditions, independent of environmental variables such as climate or seasonality, this approach ensures continuous production of secondary metabolites with functional properties [139–141].

Compared to naturally grown plants, in vitro techniques often yield higher concentrations of bioactive compounds and more consistent product quality [142]. Additionally, these systems allow for applying chemical elicitors and precisely regulated abiotic stress conditions, including variations in water availability, light, temperature, and atmospheric gases, to enhance metabolite synthesis [143] (Figure 3). Successful implementation depends on the careful standardization of factors such as plant tissue type (e.g., leaves, roots, hairy roots), culture media, and hormonal treatments, in order to ensure both reproducibility and scalability. The following sections outline various strategies used to induce abiotic stress under in vitro conditions.

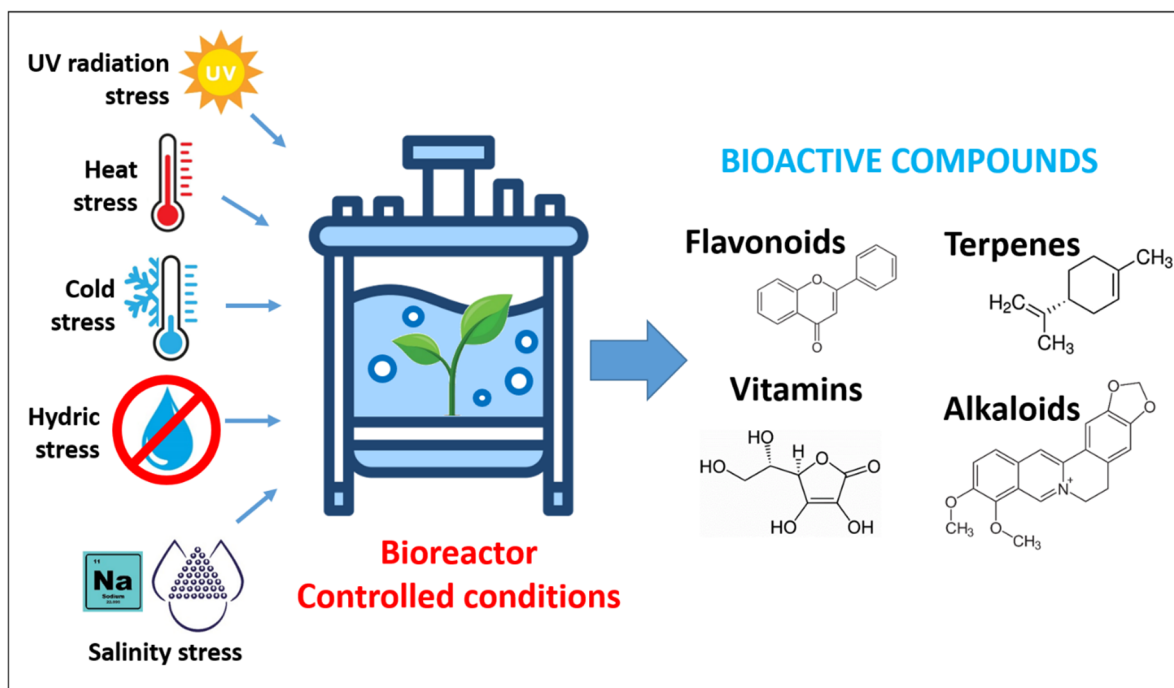


Figure 3. Schematic representation of in vitro plant responses to abiotic stress. The arrows indicate the different stresses (UV radiation, heat shock, cold, and salinity) that positively influence the induction of secondary metabolite pathways, resulting in the production of flavonoids, terpenes, alkaloids, or vitamins.

Among the strategies used to induce abiotic stress under in vitro conditions, water and salinity stress are commonly simulated using osmotic and ionic agents, such as polyethylene glycol (PEG) and salts like NaCl, Na₂SO₄, or CaCl₂, which are added to the culture medium [144]. Water stress leads to the production of ROS, inducing oxidative stress, and can increase the biosynthesis of phenolic acids and terpenes [145]. Salinity stress can similarly stimulate phenolic compound production, and the presence of specific ions, both cations (e.g., Na⁺, Ca²⁺) and anions (e.g., Cl[−], SO₄^{2−}), can modulate the synthesis of alkaloids [146]. *Scrophularia striata* Boiss, a medicinal plant native to Iran, has demonstrated a remarkable ability to respond positively to osmotic stress induced by polyethylene glycol (PEG 6000), activating antioxidant defense mechanisms and promoting the accumulation of phenolic compounds. In particular, the application of PEG 6000 (70 g/L) and high sucrose concentration (60 g/L) in a modified Murashige and Skoog (MS) medium significantly enhanced the production of phenolic compounds in *S. striata* cells. Total phenolic content increased by 1.8-fold compared to the control,

while specific flavonoids such as rutin, myricetin, and resveratrol showed substantial increases of 5.53-, 13.8-, and 10.07-fold, respectively. These results highlight the strong positive effect of osmotic stress on the accumulation of secondary metabolites in this species [147].

In addition to osmotic treatments, ultraviolet radiation represents another potent abiotic elicitor. In vitro culture enables the production of phenolic compounds such as quercetin, caffeic acid, terpenes, alkaloids, and resveratrol [148]. In addition to osmotic treatments, ultraviolet radiation represents another potent abiotic elicitor. In vitro culture enables the production of phenolic compounds such as quercetin, caffeic acid, terpenes, alkaloids, and resveratrol [148]. The application of abiotic elicitors, including UV stress, stimulates their biosynthetic pathways, enhancing accumulation with high potential for functional foods [149]. In vitro, UV stress can be applied using specific lamps emitting different UV bands [150]. For example, UV-C irradiation significantly increased the accumulation of secondary metabolites in callus cultures of the Öküzgözü grapevine, including total phenolics, flavonols, catechin, ferulic acid, trans-resveratrol, and tocopherols [151].

Atmospheric gas composition also plays an important role in modulating plant responses. Elevated CO₂ levels can enhance in vitro plant growth by boosting photosynthesis and increasing the availability of non-structural carbohydrates, which support the synthesis and accumulation of secondary metabolites. Meanwhile, ozone can elicit plant defense responses, enhancing total phenols, flavonoids, and anthocyanins [152]. A study conducted in subarctic heathlands demonstrated that enhanced UV-B radiation, alone or combined with elevated CO₂, stimulated the germination and fruit production of *Vaccinium myrtillus* and other species while also altering their polyphenol and anthocyanin profiles with potential ecological and nutritional implications. In *Empetrum hermaphroditum*, elevated CO₂ had a significant positive effect on syringetin glycosides and all five measured anthocyanins (delphinidin-3-hexoside, cyanidin-3-hexoside, petunidin-3-hexoside, malvidin-3-pentoside, and malvidin-3-hexoside) [153]. Both high and low temperatures can stimulate the production of secondary metabolites, although the outcomes differ depending on the type of stress [154]. In cell cultures of strawberry (*Fragaria ananassa* cv. Shikinari), although optimal cell growth occurred at 30 °C, the highest anthocyanin content was achieved at 20 °C. When the temperature was gradually shifted from 30 °C to 20 °C after 3 days and maintained at 20 °C until day 9, anthocyanin production on day 9 increased 1.8 times compared to cultures kept constantly at 20 °C, 3 times compared to those at 25 °C, and 4 times compared to those maintained at 30 °C. This suggests that the gradual temperature decrease and prolonged exposure to 20 °C stimulate anthocyanin biosynthesis more effectively than constant temperatures at 25 °C or 30 °C. On the other hand, extremely low temperatures (below −20 °C) can lead to severe physiological and morphological alterations, including reduced water and mineral uptake, decreased photosynthetic rates, membrane disruption, ionic imbalances, and increased ROS production, all of which compromise cellular integrity [155]. Through cold stress applied to blueberry callus and suspension cultures, bioactive phenolic compounds (gallic and chlorogenic acid) were obtained. Their concentration increased up to 1.5× in callus and 2.5× in suspension, reaching 170 and 110 mg/g of dry weight, respectively [156].

The application of controlled abiotic stressors, such as UV radiation, salinity, and chemical elicitors, under in vitro conditions is an effective biotechnological strategy to boost the production of bioactive compounds in plants. These stimuli activate specific defense pathways that enhance the synthesis of phenolics and other secondary metabolites. In vitro culture enables precise environmental control, continuous and sustainable production, and provides standardized, scalable conditions. This is particularly valuable for the food and nutraceutical industries, as it shortens production time, ensures reproducible compound levels, and facilitates the recovery of pure and active metabolites.

6.2. Emerging Technologies for the Concentration of Bioactive Compounds in Native Berries

The application of emerging technologies has gained increasing attention as a sustainable and efficient alternative for the extraction and concentration of bioactive compounds from berries [157]. Techniques such as high hydrostatic pressure (HHP), pulsed electric fields (PEF), ultrasound-assisted extraction (UAE), microwave-assisted extraction (MAE), enzyme-assisted extraction (EAE), and membrane filtration (MF) have demonstrated significant advantages over conventional methods, including higher extraction yields, reduced use of solvents, preservation of thermolabile compounds, and improved selectivity [158–160]. For instance, in berries, rich in anthocyanins, flavonoids, and other phenolic compounds, these technologies offer promising pathways to enhance the recovery of health-promoting compounds while maintaining their bioactivity. Furthermore, their potential integration into scalable industrial processes aligns with the growing demand for clean-label functional ingredients and environmentally responsible production systems.

Among such technologies, HHP is a non-thermal technology that applies pressures between 100 and 800 MPa to disrupt cell wall structures and membranes, enhancing the release of intracellular compounds such as anthocyanins, flavonoids, and phenolic acids while preserving thermolabile molecules [161,162]. This method has shown high efficiency in bioactive compounds, significantly improving extraction yields and maintaining the chemical integrity and bioactivity of antioxidant compounds [163]. Additionally, HHP increases mass transfer rates and reduces the need for organic solvents, contributing to cleaner and more sustainable processes [164]. Pulsed Electric Fields employ short high-voltage pulses to induce electroporation, enhancing membrane permeability and facilitating the extraction of polyphenols and anthocyanins from plant tissues, with minimal thermal degradation [165–167]. PEF is particularly effective for antioxidant-rich berries that are sensitive to conventional processing conditions [168].

Ultrasound-Assisted Extraction, based on acoustic cavitation generated by ultrasound waves (20 kHz–100 MHz), disrupts plant cells and improves mass transfer, leading to greater recovery of polyphenols, flavonoids, and anthocyanins with reduced time and solvent use [169,170]. UAE also preserves thermolabile bioactives, and its tunability allows selective enhancement of specific compounds [171,172].

Microwave-Assisted Extraction uses microwave energy to generate localized heating in polar solvents and tissues, disrupting cell structures and improving the release of antioxidants, including flavonoids and phenolic acids [173]. MAE offers fast processing, high efficiency, and preservation of sensitive compounds due to volumetric heating and selective energy absorption [133,174], making it well-suited for native berries with high antioxidant value.

Enzyme-Assisted Extraction enhances the recovery of phenolic compounds by enzymatically degrading cell wall components like cellulose and pectin, facilitating a gentle and selective release of bioactives without harsh treatments [175]. EAE is adaptable to different berry species and formulations, preserving the functionality of sensitive molecules while aligning with eco-friendly processing [176].

Membrane Filtration, including micro-, ultra-, and nanofiltration, enables the selective separation and concentration of bioactives based on molecular size and interaction with membranes, preserving thermolabile compounds and avoiding solvents [177,178]. MF is energy-efficient, scalable, and integrates easily into continuous processing lines with low environmental impact [179,180].

Together, these non-thermal, green extraction technologies provide sustainable, efficient, and scalable methods for enhancing the value of native Chilean berries as high-value sources of functional ingredients rich in antioxidants, aligning with global demands for clean-label, health-promoting food products.

7. Limitations

Despite the comprehensive scope and multidisciplinary integration of this review, several limitations must be acknowledged to contextualize its findings and guide future research directions. First, although the review covers a wide range of environmental and biological stressors affecting berries, there is a significant imbalance in the available literature. Conventional berry species, such as *Fragaria* × *ananassa*, *Vaccinium* spp., and *Rubus* spp., are heavily represented, while data on native or underutilized berries, particularly those from South America, remain limited and fragmented. This disproportion restricts comparative analysis and hinders the generalization of stress responses across species. Second, a lack of methodological standardization across studies complicates direct comparisons. Differences in experimental design (e.g., type, intensity, and duration of stress applied), developmental stages of the plants, analytical platforms (e.g., LC-MS, GC-MS, spectrophotometry), and reporting metrics lead to substantial variability in results. As a consequence, trends in metabolite accumulation or stress physiology cannot always be directly contrasted or synthesized into a unified model. Further efforts are needed to harmonize protocols for stress imposition, sampling, and metabolite quantification, particularly in *in vitro* systems and pre-harvest settings. Third, the scarcity of mechanistic and genetic-level studies on stress responses in berries, especially native species, limits our understanding of the underlying regulatory networks. While some transcriptomic and proteomic data exist for commercial cultivars, very few studies delve into the gene expression pathways, epigenetic regulation, or transcription factors involved in bioactive compound biosynthesis under stress in non-model species. This hinders the possibility of identifying conserved or divergent stress response mechanisms relevant to breeding or metabolic engineering. Fourth, the translational gap between laboratory findings and real-world applications remains a critical challenge. Many reported increases in bioactive compound content or antioxidant activity are observed under controlled *in vitro* or greenhouse conditions, which may not reflect field performance under complex and dynamic environmental variables. Moreover, the stability, bioavailability, and efficacy of these compounds postharvest and after processing are not always evaluated, limiting their practical value in the development of functional foods. Fifth, most reviewed studies focus on

individual stress factors, whereas in natural and agricultural systems, multiple stressors often occur simultaneously (e.g., drought plus heat, or salinity plus pathogens). These combined or interactive effects are less studied and can yield synergistic, antagonistic, or unpredictable outcomes in plant physiology and metabolite accumulation. More holistic and ecologically realistic approaches are needed to understand how plants respond to multifactorial stress environments. Lastly, while this review integrates both physiological and biochemical responses with applied perspectives, it does not provide a systematic meta-analysis, nor does it quantify effect sizes or heterogeneity across studies. The goal was to offer a qualitative and integrative synthesis rather than statistical generalizations, which should be addressed in future reviews or dedicated meta-analytical efforts. Taken together, these limitations underline the need for more integrative, standardized, and species-diverse studies on stress-induced metabolic responses in berries, especially those with high ecological and nutritional value but limited current cultivation. Addressing these gaps will be essential for advancing both fundamental plant science and the sustainable development of functional berry-based products.

8. Conclusions

Environmental and biological stresses exert a significant influence on the biosynthesis of bioactive compounds in berries, with a particular emphasis on native Chilean species, which have evolved unique adaptive mechanisms, representing a strategic resource in the formulation of climate-smart functional foods. These stress-induced responses enhance the production of antioxidant and functional metabolites, including phenolics, flavonoids, anthocyanins, and VOCs, directly impacting the nutritional quality and potential health benefits of berry-derived foods. Understanding these complex mechanisms is not only essential for harnessing the inherent nutritional and functional potential of these native berries within current and future environmental scenarios shaped by climate change, but also for informing sustainable agricultural practices.

Furthermore, advancements in preharvest stress management techniques offer promising new avenues for the efficient production of bioactive compounds while minimizing environmental impact. In addition, the application of emerging processing technologies provides innovative strategies for effectively concentrating, preserving, and valorizing these functional compounds in berry-based food products.

To fully realize this potential and address the intertwined challenges of climate change, food security, and public health demands, future research should prioritize integrated, multidisciplinary approaches. These efforts must encompass detailed stress simulation studies under both *in vivo* and *in vitro* conditions, the optimization and scaling-up of green and efficient extraction technologies, comprehensive assessments of bioaccessibility and bioactivity of stress-modulated compounds, and the development of effective postharvest management strategies to maintain fruit quality and bioactive content. By bridging the knowledge gaps in plant physiology, metabolomics, and food science, we can unlock the full potential of native berry species as sustainable resources for health-promoting compounds and foster the development of innovative, functional foods that contribute to healthier diets and more resilient food systems.

Author Contributions

M.C.-F. and C.B.-D.: Conceptualization, Visualization, Writing—original draft preparation, Writing—review and editing, and Project administration. M.O.-N., G.A.-G., M.B.-J. and L.M.: Writing—original draft preparation and Writing—review and editing. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement

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Conflicts of Interest

The authors declare no competing financial interest.

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