

Review

# Anthocyanins: Biosynthesis, Distribution, Ecological Role, and Use of Biostimulants to Increase Their Content in Plant Foods—A Review

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**Abstract:** In the past century, plant biostimulants have been increasingly used in agriculture as innovative and sustainable practice. Plant biostimulants have been mainly investigated as potential agents able to mitigate abiotic stress. However, few information is available about their ability to influence fruit quality or change fruit phytochemical composition. In particular, very little is known about their effects on anthocyanin synthesis and accumulation. Due to the increasing demand of consumers for healthier foods with high nutraceutical values, this review tries to fill the gap between anthocyanin content and biostimulant application. Here, we elucidate the chemical structure, biosynthetic pathway, plant distribution, and physiological role of anthocyanins in plants. Moreover, we discuss the potential implications for human health derived from the consumption of foods rich in these molecules. Finally, we report on literature data concerning the changes in anthocyanin content and profile after the application of biostimulant products on the most common anthocyanin-containing foods.

**Keywords:** anthocyanidins; sustainable agriculture; fruit quality; nutraceuticals; antioxidant activity; phytochemicals; meta-analysis; bibliometric analysis



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## 1. Introduction

Over the past years, the use of chemical fertilizers as agronomic practice has strongly increased with the aim to enhance the food production and meet the global needs caused by an exponential growth of the population [1,2]. However, despite a big increment of the production that can be easily obtained after the application of chemical fertilizers, their uncontrolled use could cause different and severe problems, including global climate change, environmental pollution, and loss in the quality of the production [3]. In order to reduce these problems, the latest agronomic research lines are looking for more sustainable alternatives, which can be useful not only to limit the dependence from chemical fertilizers together to the adverse consequences caused by their application, but also to maintain or even improve the production quality [4].

In this context, plant biostimulants are actually considered a sustainable strategy to enhance crop yield under either optimal or stress conditions, since they may partially reduce chemical fertilizers [5,6]. Moreover, differently from chemical fertilizers, biostimulants are products based on natural substances often originating from food and/or industrial wastes, hence they may also strongly contribute to the circular economy aspects [7,8]. At the beginning, the effects derived from the application of biostimulants were exclusively

studied by monitoring plants under abiotic stresses, and evaluating their improvement in tolerance mechanisms [2,9–13]. Among the studied parameters, the attention was almost exclusively focused on plant physiological parameters, such as the morphological aspects, pigment content, or photosynthesis and photorespiration efficiency [14–16]. On the other hand, only a limited number of experiments were addressed to the quality of fruits produced by plants treated with biostimulants, and in particular mostly were related to the evaluation of few pomological parameters, such as size, weight, yield, and color of the produced fruits [17,18]. Consequently, the biostimulant effects on nutritional and nutraceutical attributes were and are still quite unexplored [1].

However, the consumer growing interest in healthy foods encouraged also the study of the parameters related to nutritional and nutraceutical aspects of foods derived from plant treated with biostimulants [1,19]. In particular, the current epidemiological emergency caused by SARS-CoV-2 has contributed to a change in food consumption all over the world, by increasing consumer attention not only for the origin of the raw materials, but also for the potential health benefits [19]. Moreover, the high incidence of obesity, cancer, and diabetes at global level, highlights the strong relationship between food-intake and long-term health effects [20,21], encouraging the consumption of foods rich in bioactive compounds [22]. Among them, red-black colored fruits are now receiving increasing attention due to their significant amounts of anthocyanins and anthocyanidins, compounds able to exert a wide range of biological and pharmacological properties, including antioxidant, antimicrobial, anti-inflammatory, anticancer, antidiabetic, and antiatherosclerotic activity [22]. The aims of this review are: (i) To elucidate the chemical structure, biosynthesis mechanism, plant distribution, and physiological role of anthocyanins in plants; (ii) to investigate the potential implications for human health due to consumption of foods rich in anthocyanins; (iii) to report information concerning the changes in anthocyanin content and profile following the application of biostimulant products on the most common anthocyanin-containing foods.

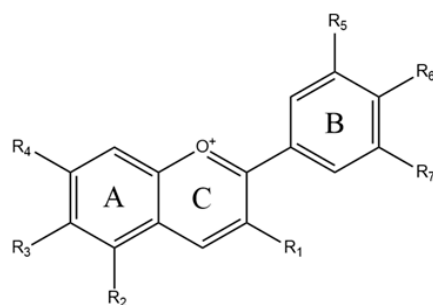
## 2. Anthocyanidins and Anthocyanins

### 2.1. Chemical Structures and Classification

Anthocyanidins are colored molecules having medium-size and belonging to the class of flavonoids [23]. Actually, 25 different anthocyanidins are known (Figure 1), that differ from each other for the presence of hydroxyl (–OH) and methoxy (–OCH<sub>3</sub>) groups bound at the scaffold core (Figure 1) [24]. Consequently, anthocyanidins are grouped into 3-hydroxyanthocyanidins, 3-deoxyanthocyanidins, and O-methylated anthocyanidins. Cyanidin (Cy), Delphinidin (Dp), Pelargonidin (Pg), three among the non-methylated anthocyanidins, are the most common in nature. In particular, it was estimated that 50% of plants producing anthocyanidins have Cy, 12% have Dp, and 10% have Pg [25,26]. Peonidin (Pn), Malvidin (Mv), and Petunidin (Pt), belonging to the methylated anthocyanidins, can be also easily found in plants [25,26].

In most of the cases, anthocyanidins are bounded with sugar moieties, forming the corresponding anthocyanins. Glycosylation is achieved enzymatically following the adding of the sugar portion at the 3rd and/or 5th position (R<sub>1</sub> and/or R<sub>2</sub> subsistent of the chemical structure displayed in Figure 1 of the scaffold [27,28]. As a consequence of the glycosylation, anthocyanins have an increased water solubility and stability with respect to the related anthocyanidins [28]. Despite the most common glycosylation process involves the condensation of monosaccharides such as glucose, galactose, rhamnose, arabinose, rutinose and xylose, also disaccharides and trisaccharides may be attached in some cases [23]. Finally, anthocyanins may be also often acylated with organic acids such as p-coumaric, caffeic, and ferulic acids via ester bonds usually to the 3-position of the sugar moiety [23,27]. Consequently, to date more than 500 different anthocyanins that differ not only for the glycosylation pattern of the scaffold, but also for the presence and position of aliphatic or aromatic carboxylates are reported. In spite of their great structure variability, the anthocyanins most distributed in plants are those originated by Cy, Dp,

and Pg. They are present in 80% of the leaves, 69% of the fruits, and 50% of the colored flowers [19,25,26,29,30]. On the other hand, anthocyanins formed by Pt, Mv, and Pn, are limitedly distributed [19,25,26,29–31].



Name	Abbreviations	Substitution pattern						
		R1	R2	R3	R4	R5	R6	R7
Apigeninidin	Ap	H	OH	H	OH	H	OH	H
Arrabidin	Ab	H	H	OH	OH	H	OH	OMe
Aurantininidin	Au	OH	OH	OH	OH	H	OH	H
Capensinidin	Cp	OH	OMe	H	OH	OMe	OH	OMe
Carajurin	Cj	H	H	OH	OH	H	Ome	OMe
<b>Cyanidin</b>	<b>Cy</b>	<b>OH</b>	<b>OH</b>	<b>H</b>	<b>OH</b>	<b>OH</b>	<b>OH</b>	<b>H</b>
<b>Delphinidin</b>	<b>Dp</b>	<b>OH</b>	<b>OH</b>	<b>H</b>	<b>OH</b>	<b>OH</b>	<b>OH</b>	<b>OH</b>
Europinidin	Eu	OH	OMe	H	OH	OMe	OH	OH
Hirsutidin	Hs	OH	OH	H	OMe	OMe	OH	OMe
30-HydroxyAb	3'OHAb	H	H	OH	OH	OH	OH	OMe
6-HydroxyCy	6OHCy	OH	OH	OH	OH	OH	OH	OH
6-HydroxyDp	6OHDp	OH	OH	OH	OH	OH	OH	OH
6-HydroxyPg	6OHPg	OH	OH	OH	OH	H	OH	H
Luteolin	Lt	H	OH	H	OH	OH	OH	H
<b>Malvidin</b>	<b>Mv</b>	<b>OH</b>	<b>OH</b>	<b>H</b>	<b>OH</b>	<b>OMe</b>	<b>OH</b>	<b>OMe</b>
5-MethylCy	5-MCy	OH	OMe	H	OH	OH	OH	H
<b>Pelargonidin</b>	<b>Pg</b>	<b>OH</b>	<b>OH</b>	<b>H</b>	<b>OH</b>	<b>H</b>	<b>OH</b>	<b>H</b>
<b>Peonidin</b>	<b>Pn</b>	<b>OH</b>	<b>OH</b>	<b>H</b>	<b>OH</b>	<b>OMe</b>	<b>OH</b>	<b>H</b>
<b>Petunidin</b>	<b>Pt</b>	<b>OH</b>	<b>OH</b>	<b>H</b>	<b>OH</b>	<b>OMe</b>	<b>OH</b>	<b>OH</b>
Pulchellidin	Pl	OH	OMe	H	OH	OH	OH	OH
Riccionidin-A	RiA	OH	H	OH	OH	H	OH	H
Rosinidin	Rs	OH	OH	H	OMe	OMe	OH	H
Tricetinidin	Tr	H	OH	H	OH	OH	OH	OH
Rosinidin	Rs	OH	OH	H	OMe	OMe	OH	H
Tricetinidin	Tr	H	OH	H	OH	OH	OH	OH

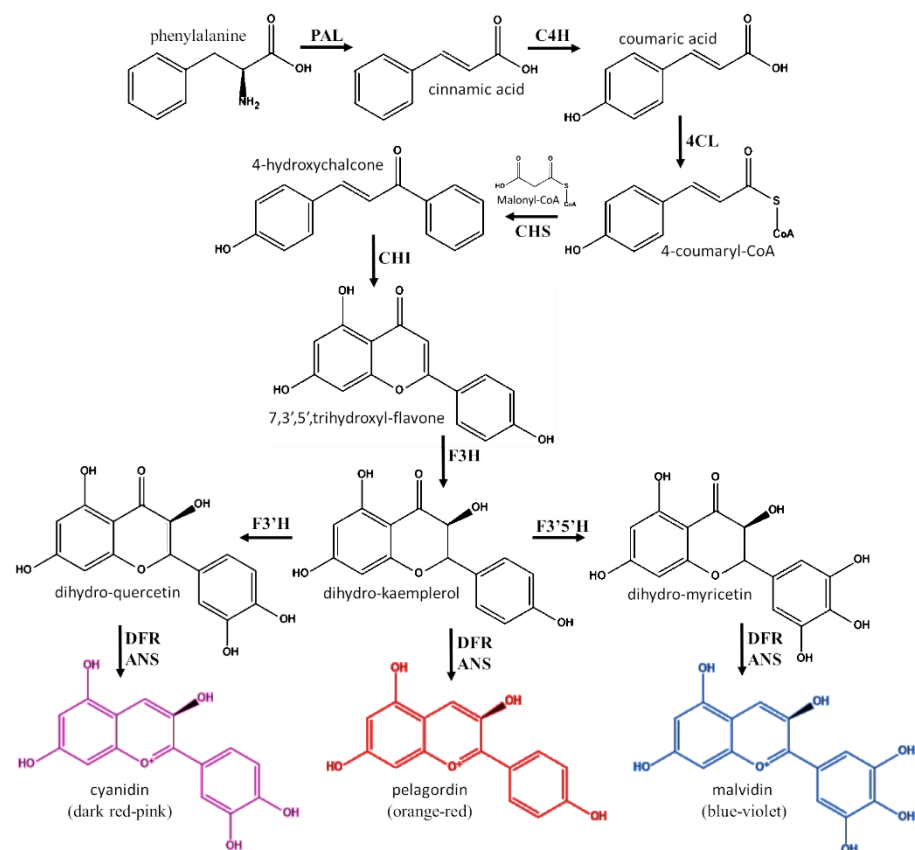
**Figure 1.** Chemical scaffold of anthocyanin compounds and their relative substituents. In the table, the most common anthocyanidins are reported in bold.

The conjugated bonds in the chemical scaffold are one of the responsible factors for the light absorption at about 500 nm [27,32]. However, also the type of substituents present in the benzyl ring, local pH, state of aggregation and complexation with other inorganic and organic molecules may contribute to color variation. In particular, it has been observed that anthocyanins may display almost the chromatic scale [27,32,33].

## 2.2. Biosynthesis

Anthocyanidins and anthocyanins are almost exclusively produced by plants, in a branch of the phenylpropanoid pathway that is also involved in the biosynthesis of other flavonoids [34,35] (Figure 2). The enzymes involved in biosynthesis of anthocyanidins are localized in the endoplasmic reticulum, organized into a multi-enzyme complex named flavonoid metabolon [34,35]. The precursor for the synthesis of all flavonoids is the phenylalanine. This amino acid marks the branch point of primary and secondary metabolism from which the phenyl-propanoid pathway can lead to the

synthesis of all phenolic compounds [34]. As first step of the pathway, phenylalanine is converted by phenylalanine ammonia-lyase (PAL) in cinnamic acid, which is then further transformed into coumaric acid by the action of cinnamic acid 4-hydroxylase (C4H). Following the activation catalyzed by the 4-coumarate-CoA ligase (4CL), 4-coumaryl-CoA reacts with three molecules of malonyl-CoA in a reaction catalyzed by chalcone synthase (CHS). This reaction allows the formation of 4-hydroxychalcone (ex. naringenin chalcone) and it marks the start of the flavonoid biosynthetic pathway. The 4-hydroxychalcone is transformed into the respective 7,3',5',trihydroxyl-flavone (ex. naringenin) by the action of chalcone isomerase (CHI). Afterwards, flavanone 3-hydroxylase (F3H) oxidizes 7,3',5',trihydroxyl-flavone into flavonol-form (ex. dihydrokaempferol). Then, dihydrokaempferol is transformed into dihydromyricetin or dihydroquercetin by the action of flavonoid 3'-hydroxylase (F3'H) or flavonoid 3',5'-hydroxylase (F3'5'H), respectively. In order to convert the three hydroflavonols into anthocyanidins, the combined action of dihydroflavonol-4-reductase (DFR) and anthocyanidin synthase (ANS) is required. The first enzyme yields to the formation of the leucoanthocyanidins, meanwhile the second one catalyzes the 2-oxoglutaratedependent oxidation of each leucoanthocyanidin into 2-flavan-3,4-diol. These latter compounds spontaneously evolve to the respective anthocyanidins [36,37].



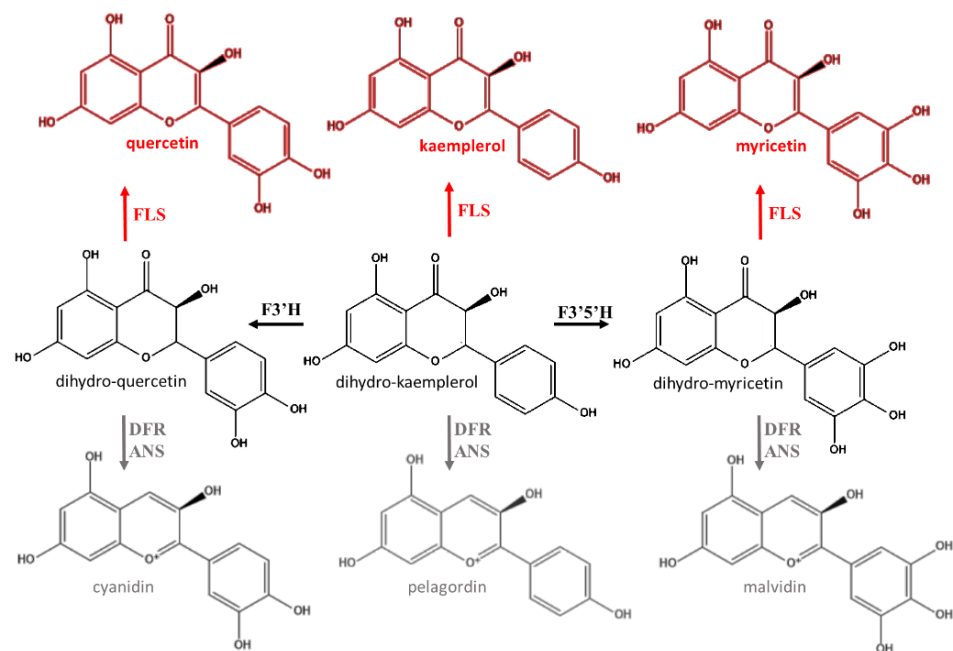
**Figure 2.** Biochemical pathway for the synthesis of anthocyanidins. PAL: phenylalanine ammonia-lyase; C4H: cinnamic acid 4-hydroxylase; 4CL: 4-coumarate-CoA ligase; CHS: chalcone synthase; CHI: chalcone isomerase; F3H: flavanone 3-hydroxylase; F3'H: flavonoid 3'-hydroxylase; F3'5'H: flavonoid 3',5'-hydroxylase; DFR: dihydroflavonol reductase; ANS: anthocyanidin synthase (ANS).

After their synthesis, anthocyanins are transported to the plant vacuole through vesicle trafficking pathway that may involve, or not, Golgi apparatus [38]. In vacuole, anthocyanidins are converted into the more stable form by the action of UDP-glucose flavonoid 3-O-glucosyltransferase (UF3GT) or UDP-glucose flavonoid 5-O-glucosyltransferase (UF5GT). These two enzymes add a sugar moiety respectively at the 3rd and/or 5th position ( $R_1$

and/or R<sub>2</sub> subsistent of the chemical structure displayed in Figure 1 of the chemical scaffold [27,28,36]. Finally, the glucoside form of anthocyanidins may be further modified in many species by glycosylation, methylation, acylation, or condensation with other organic molecules [36,37].

### 2.3. Role in Plants

Anthocyanins are one of the major groups of natural pigments and they are responsible for colors of many leaves, flowers, and fruits [39]. In the past the physiological role of anthocyanins in plants was exclusively ascribed to improve the reproductive success by facilitating communication between plants and pollinators or seed-dispersers [40]. On the other hand, in order to justify the occurrence of anthocyanins also in plant districts different from flowers and fruits, it was mistakenly assumed that they could be an incidental consequence of the flavonoid pathway [41]. Indeed, the intermediate compounds dihydrokaempferol, dihydromyricetin, and dihydroquercetin may alternatively be oxidized into respective flavon-3-ols by flavonol synthase (FLS) as well as used for the production of anthocyanins (Figure 3) [27,29]. However, it was shown that some parts of the plants devoid of immediate signaling function contained a considerable amount of these flavonoids [27,42,43]. On the other hand, anthocyanins have specific histological localization, and their accumulation patterns do not match those of other pigments [27,44].



**Figure 3.** Alternative biochemical pathway to anthocyanin synthesis. FLS: flavonoid synthase; F3'H: flavonoid 3'-hydroxylase; F3'5'H: flavonoid 3',5'-hydroxylase; DFR: dihydroflavonol reductase; ANS: anthocyanidin synthase (ANS).

For these reasons, recently, anthocyanin role in plants was questioned. To date, it is well-known that these molecules are involved in several defensive processes, including the screen role against UV-B [45–49] and plant protection against high light intensities [46,49,50]. However, light stresses are not the only abiotic stress in which anthocyanins seem to play a key role. Indeed, thanks to their high antioxidant capacity, these flavonoids are involved in all those responses that contrast oxidative stress induced by heat conditions [51,52] and water and nutrient deficit [51,53,54]. Moreover, anthocyanins are also involved in response to biotic stresses, such as mechanical damage due to herbivore attack [55–57], insect infestation or fungal infection [58–60]. Table 1 reports the main abiotic and biotic stress conditions in which variations of the total content of anthocyanins were observed.

**Table 1.** Documented plant responses to abiotic and biotic stresses that involves anthocyanins.

Condition	Specie	References	
Abiotic Stress	Heat Stress	<i>Ipomoea batatas</i>	[43,61,62]
		<i>Daucus carota</i>	[63]
		<i>Rosa hybrida</i>	[64]
		<i>Solanum melongena</i>	[65–68]
		<i>Saccharum officinarum</i>	[69,70]
		<i>Camellia sinensis</i>	[71]
		<i>Sorghum vulgare</i>	[72]
		<i>Vitis vinifera</i>	[73]
		<i>Oryza glaberrima</i>	[74]
		<i>Actinidia deliciosa</i>	[75]
	<i>Arabidopsis thaliana</i>	[76]	
	<i>Quercus suber</i>	[77]	
Abiotic Stress	Light Stress	<i>Solanum melongena</i>	[78–80]
		<i>Phalaenopsis aphrodite</i>	[81]
		<i>Silene littorea</i>	[45]
		<i>Arabidopsis thaliana</i>	[47,82–85]
		<i>Chrysanthemum morifolium</i>	[86]
		<i>Begonia semperflorens</i>	[87]
		<i>Brassica campestris</i>	[88]
		<i>Perilla frutescens</i>	[89,90]
		<i>Lonicera japonica</i>	[91]
		<i>Actinidia deliciosa</i>	[75]
	<i>Malus domestica</i>	[50,92]	
Abiotic Stress	Water Stress	<i>Camellia sinensis</i>	[93]
		<i>Vitis vinifera</i>	[51,94]
		<i>Hibiscus sabdariffa</i>	[95]
		<i>Malus domestica</i>	[96]
		<i>Fragaria ananassa</i>	[97]
		<i>Ocimum basilicum</i>	[54]
		<i>Sorghum vulgare</i>	[98]
		<i>Oryza sativa</i>	[99]
		<i>Punica granatum</i>	[53]
		Abiotic Stress	Salt Stress
<i>Nicotiana tabaccum</i>	[103]		
<i>Hibiscus rosasinensis</i>	[104]		
<i>Fragaria chiloensis</i>	[105]		
<i>Oryza sativa</i>	[106]		
<i>Solanum tuberosum</i>	[107]		
Biotic Stress	Insect Attack	<i>Arabidopsis thaliana</i>	[55–57,108]
		<i>Gossypium arboreum</i>	[109]
		<i>Solanum tuberosum</i>	[110]
		<i>Sorghum halepense</i>	[111]
		<i>Fragaria ananassa</i>	[112]
		<i>Vaccinium myrtillus</i>	[113]
Biotic Stress	Fungi Attack	<i>Arabidopsis thaliana</i>	[60,114,115]
		<i>Oryza sativa</i>	[99,106]
		<i>Fragaria ananassa</i>	[59,116,117]

Beyond the involvement of anthocyanins to contrast the oxidative stress conditions related to abiotic and biotic menaces, anthocyanins seem to be also able to contribute to the physiological processes during non-stress conditions, such as the elevation of leaf temperature [91,118]; transport of nutrients and monosaccharides [119–121]; and regulation of osmotic balance [51,105]. Table 2 reports the main plant physiological pathways in which anthocyanins are involved.

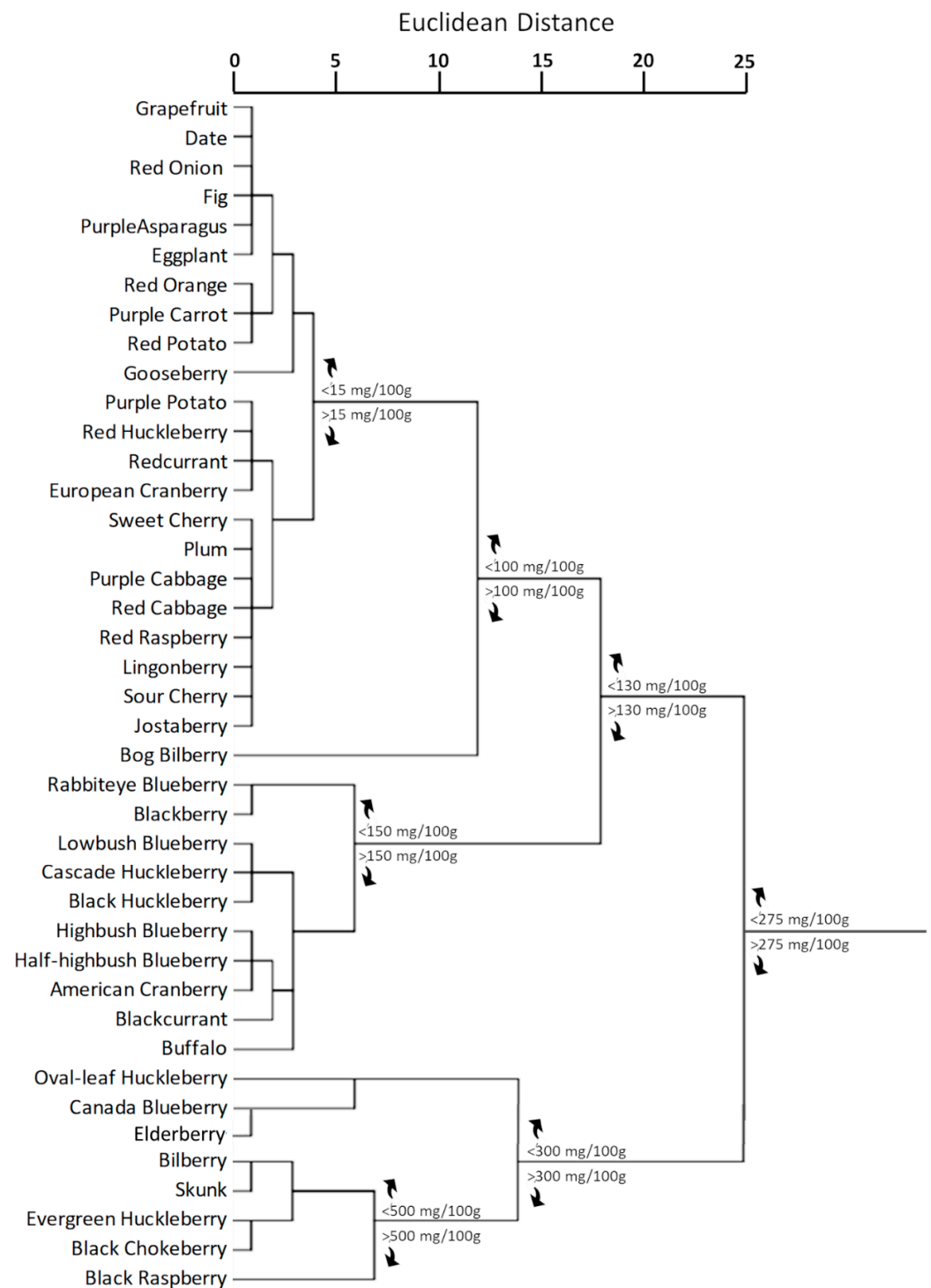


**Table 2.** Documented plant physiological processes in which anthocyanins are involved.

Plant Physiological Role	Specie	References
Elevation of Leaf Temperature	Several species	[121–126]
	<i>Lactuca sativa</i>	[127]
	<i>Arabidopsis thaliana</i>	[128,129]
	<i>Galax urceolata</i>	[130]
Senescence	Several species	[131–134]
	<i>Populus euramericana</i>	[135]
	<i>Arabidopsis thaliana</i>	[136,137]
	<i>Brassica oleracea</i>	[138]
	<i>Actinidia deliciosa</i>	[139]
	<i>Torenia fournieri</i>	[140]
Transportation of Monosaccharides	Several Species	[119–121]
	<i>Zea mays</i>	[141,142]
	<i>Vitis vinifera</i>	[143–145]
Regulation of Osmotic Balance	Several species	[125,146,147]
	<i>Xerophyta viscosa</i>	[148]
	<i>Vitis vinifera</i>	[149–151]
	<i>Fragaria ananassa</i>	[152]
	<i>Populus deltoides</i>	[153]
	<i>Arabidopsis thaliana</i>	[76,129]
	<i>Craterostigma wilmsii</i>	[148]
Camouflage	Several Species	[123,154–160]
	<i>Theobroma cacao</i>	[121]
	<i>Mangifera indica</i>	[121]
Enhancing of Light Absorption	Several Species	[126,155,161–163]
	<i>Theobroma cacao</i>	[121]
	<i>Zea mays</i>	[164]
	<i>Mangifera indica</i>	[121]

#### 2.4. Distribution in Edible Sources and Contribution in Human Diet

Fruits and vegetables are the only edible sources from which it is possible assuming anthocyanin compounds [26,165]. Although among the fruits the anthocyanin content is very variable, generally the level of anthocyanins in fruits is much higher than in vegetables [166]. The lowest anthocyanin content per 100 g of fresh weight was recorded for grapefruit [167,168], date [169], and fig [170], meanwhile some berries, such as cranberry [19], chokeberry [171], huckleberry [172], blueberry [173], raspberry [174,175], and bilberry [176,177] shows the highest one. Concerning vegetables, the most reach in anthocyanidins and anthocyanins are red cabbage [178–180], purple cabbage [181], and purple potato [61,182]. However, total anthocyanin content in fruits and vegetables considerably varies among the different genera and cultivars, and it is strongly affected by different light, temperature, and agronomic factors [183]. Figure 4 shows the cluster distribution of anthocyanins in plant kingdom according to the anthocyanin content reported in Phenol-Explorer Online Database [184–186]. For this analysis, Euclidean distances were calculated by using the average linkage method.



**Figure 4.** Cluster distribution of anthocyanins in plant kingdom based on the total anthocyanin content according to Phenol-Explorer Database [184–186]. Euclidean distances were calculated with average linkage method. Statistical analysis and graphical representation were made using SPSS v. 24 software. The cluster was generated by using SPSS ver.24 statistical software.

In the recent years, some flowers were proposed as alternative edible sources of phytochemicals. In order to be included in human diet, flowers have to be non-toxic and innocuous [187,188]. Indeed, flowers may contain toxic substances, including hemagglutinins, oxalic acid, cyanogenic glycosides, or alkaloids and cause severe damage to the consumers [187]. However, many flowers can be considered safe, and therefore can be consumed as food. Although flowers are little known as edible sources, they have been



used for over 500 years in Europe and China as herbal medicine [189]. Actually, they are mainly used for enhancing the aesthetic value of foods, as evidenced by the increasing number of edible flower cookbooks, culinary magazine articles, and dedicated television segments [190,191]. Despite edible flowers are still considered a niche product, they are gaining attention due to their exotic aroma and textures, delicate flavor, attractive color and phytochemical composition [192]. In particular, edible flowers are a potential source of several bioactive compounds, including anthocyanins [191–193]. Among them, begonia (*Begonia tuberhybride*), tagete (*Tagetes patula*), mini rose (*Rosa chinensis*), mini daisy (*Bellis annua*), litoria (*Clitoria ternatea*), cosmos (*Cosmos sulphureus*), and cravine (*Dianthus chinensis*) are the most known and commercialized [192].

Apart from their origins and physiological roles in plants, anthocyanidins and anthocyanins seem to play important roles in human health and well-being [19,27,177]. Indeed, their intake through the consumption of foods rich in these flavonoid compounds seems to be linked to an improvement of the redox balance thanks to their high scavenging and reducing activities [19,183,194]. On the other hand, interesting properties, such as antitumor, antiatherogenic, antiviral, and anti-inflammatory effects, decrease of capillary permeability and fragility, inhibition of platelet aggregation and immune stimulation were reported [195]. The positive effects ascribed to the consumption of fruits and vegetables rich in anthocyanidins and anthocyanins are not limited to the gastro-intestinal tract. Indeed, anthocyanins resisting to gastric digestion may be absorbed in the stomach via bilitranslocase-mediated mechanism [196–199], or in the intestine through a mechanism involving the sodium–glucose co-transporter as suggested for other flavonoids [197–201].

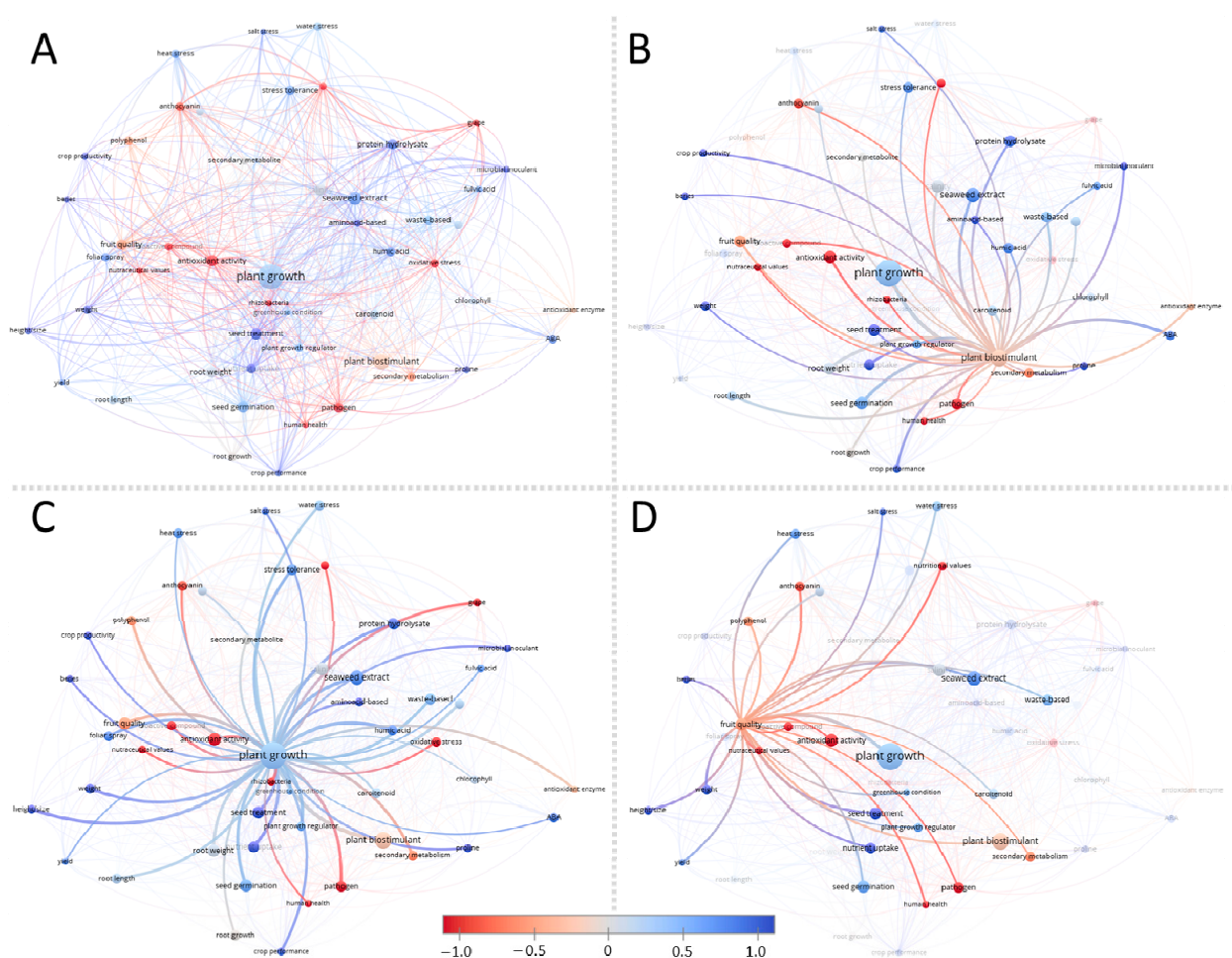
### 3. Plant Biostimulants

Biostimulants are products used in agriculture aimed to promote plant growth without being nutrients, soil improvers, or pesticides [1,9,13,202,203]. In particular, biostimulants are distinguished from agrochemicals because they only influence the vigor of plants and have no direct action against pests or diseases. Rather, they uniquely facilitate the uptake of existing and applied nutrients [204], resistance to abiotic stress such as salinity [6,11,100,205,206], temperature [2,13,207–211], or drought [208,212–216], following in an improvement of the final production also in adverse environmental conditions [1].

#### 3.1. Bibliometric Analysis

According to PubMed database, 1680 scientific papers related to biostimulant research were published from 1958, indicating an increasing interest for this sustainable agronomic practice. However, despite products working as biostimulants are used as alternative agronomic practice since more than 20 years, only recently biostimulants are deeply under investigation. Indeed, more than 50% of the 1680 papers (856) concerning biostimulants have been published in the last 5 years. Moreover, the title, abstract, and the keywords of the papers published in the last 5 years were used for bibliometric analysis aimed to find the co-occurrence of terms using VOSviewer 1.6.15 [217,218]. In order to avoid redundancies, only the words that were repeated at least five times in the text were used for this analysis; typographical errors were removed and similar terms were standardized to a single form. Consequently, 50 terms were selected, and clustered according to the association strength (from  $-1$  to  $+1$ ). Finally, a visual cluster analysis (Figure 5, Panel A) was generated, where 6 clusters and 585 links were identified and integrated into a network pathway.

Focusing on the term “plant biostimulant” (Figure 5, Panel B) we found a strong correlation with the different typologies of formulations currently present on the market. Although, biostimulants are formulated with a great variety of ingredients, they are generally classified into algal-based, protein hydrolysate, aminoacid-based, humic acid, fulvic acid, food and industrial waste-based, and microbial inoculant [219].



**Figure 5.** Visual cluster analysis generated using papers published during the last 5 years and related to biostimulant products. The plot was generated by using VOSviewer software (ver. 1.6.15) [217,218]. Panel (A) reports the general plot; Panel (B) highlights the connections between the terms “Plant Biostimulant” and other terms; panel (C) highlights the connections between the terms “Plant Growth” and other terms; panel (D) highlights the connections between the terms “Fruit Quality” and other terms. For each panel, the bubble map visualizes the 50 most frequent terms that appeared in the papers published in the last 5 years ( $n = 856$ ). Bubble size indicates the frequency of occurrence of the words; the color indicates the association strength (from  $-1$  to  $+1$ ); the lines between bubbles represent the linkage among terms.

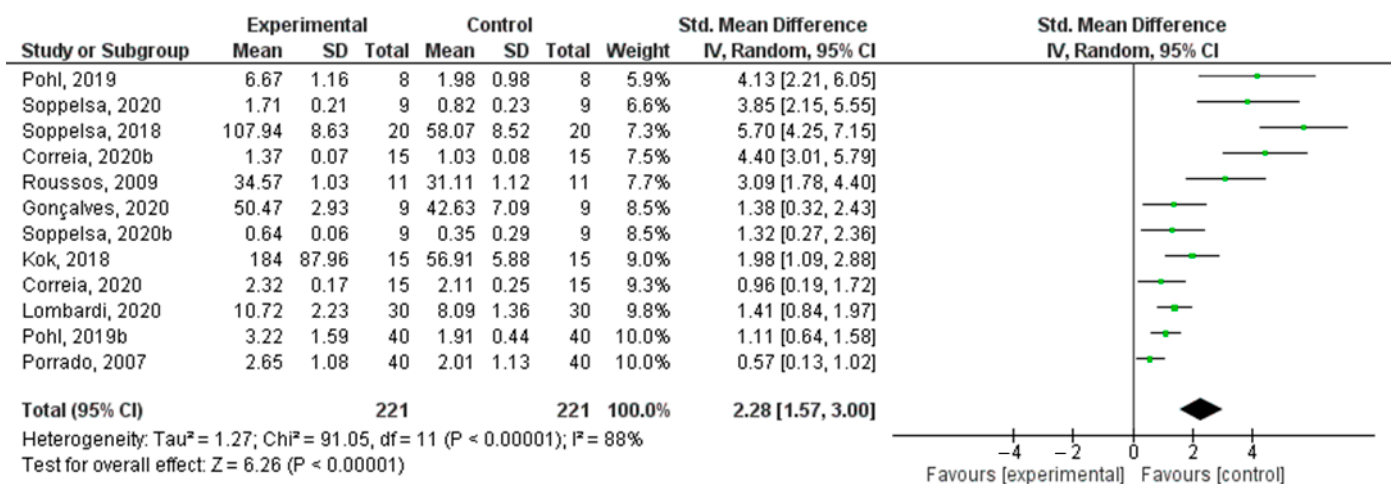
Meanwhile “plant growth” were the words most used in the 865 articles (Figure 5, panel C), “fruit quality” and “human health” resulted to be the least commons. This result should not be surprising, since researches always focused on the potential effects derived from the application of the biostimulant products on agronomical (“plant weight,” “plant height,” “crop productivity,” “crop performance”) and plant physiological (“chlorophyll,” “proline,” “abscisic acid,” “secondary metabolism”) parameters. In particular, these parameters were almost exclusively investigated in stress conditions, such as “heat stress,” “water deficit,” and “salt stress.”

Finally, our analysis revealed that only few researches dealt with the quality of fruits produced by plants treated with biostimulant. This is also confirmed by the publication of only 20 papers in the last 5 years regarding the evaluation of the fruit quality after the treatment with biostimulants. In particular, as it is showed in Figure 5, Panel D, only some attributes related to fruit quality were deeply investigated, such as those pomological (“weight” and “size”) and those related to production (“yield”) parameters. On the other hand, the potential effects of the biostimulant application on fruit quality, in term of both nutritional and nutraceutical attributes, and on “human health” were poorly studied [1]. In the following sections, we report what has currently been published regarding the effect

of biostimulants on fruit quality, with special attention to anthocyanin and anthocyanidin content.

### 3.2. Plant Biostimulant Treatment Affecting the Quality of Edible Fruits and Vegetables

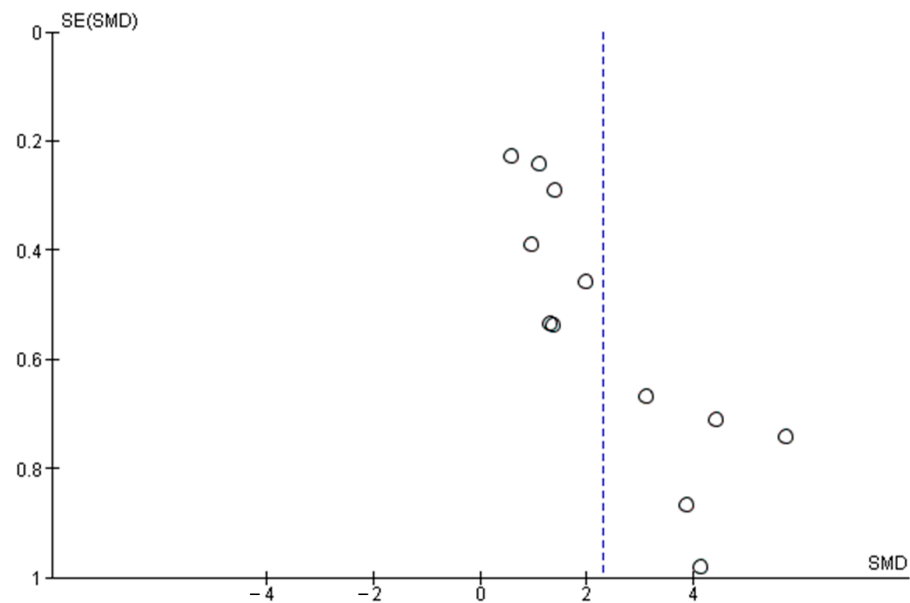
Among the different parameters evaluated for fruit quality, color is one of the major factors in creating a positive image of the fruit for the consumers, and consequently it has a great effect on sales [1]. As previously mentioned, the red-violet color in several fruits is due to the presence of anthocyanins and anthocyanidins, and their estimation is then an aspect belonging to the fruit quality [220,221]. Here, we report a forest plot in which randomized-controlled studies comparing the effect derived from the application of biostimulants on total anthocyanin content against control group (water only treated) are displayed (Figure 6). Inclusion criteria were: (i) Studies had to report a quantitative analysis of anthocyanin content; (ii) among the experimental conditions, unstressed plants had to be used as controls; (iii) the number of biological replicates evaluated during the trials had to be clearly expressed; (iv) no restrictions regarding publication dates were imposed; (v) the studies were eligible exclusively if they were published in English; (vi) studies had to be published in peer reviewed scientific journals. Outcome measures included both the evaluation of the total anthocyanin content via spectrophotometric and chromatographic methodologies. Consequently, data from 12 publications were identified and included in the meta-analysis (Figure 6).



**Figure 6.** Forest plot for the effects of biostimulant application on anthocyanin content of the analyzed studies [15,222–230], plotted according to the standard mean difference. The weight of each study is represented by the size of the green box. The forest plot displays a horizontal line that indicates the lower and upper limits of the 95% confidence interval (CI) of the effect reported for each study. The vertical line represents the no-effect, and if it crosses the horizontal lines it indicates the non-significance of the data reported in the respective study. The black diamond at the bottom represents the average effect size. Heterogeneity was assessed using  $I^2$  statistical test, that represents the amount of total variation that could be attributed to heterogeneity. The figure was generated by Review Manager Software, ver. 5.4.1.

Analyzing the forest plot, there was evidence of heterogeneity ( $I^2 = 88\%$ ,  $p > 0.0001$ ) but no evidence of publication bias was detected after the examination of funnel plot (Figure 7). This is the first study to systematically review the effect derived from the biostimulant application and the increasing of anthocyanin content in fruits produced from biostimulant-treated plants. Our meta-analysis showed strong evidence of association between biostimulants and the increasing of anthocyanin compounds. These findings are in line with previous works that have found a relationship between the biostimulant application and the general improvement of polyphenolic compounds in fruits harvested from plants treated with different biostimulants [231,232], supporting the notion that these products may promote the fruit quality affecting the content of these pigments. In the

following sections, we analyze in detail the works in which quantitative and qualitative variations of anthocyanin compounds have been recorded.



**Figure 7.** Funnel plot showing symmetrical distribution of studies indicating absence of publication bias in studies measuring the anthocyanin content in plants treated with the biostimulants. The figure was generated by Review Manager Software, ver. 5.4.1.

### 3.2.1. Apple (*Malus domestica*)

Apples are the most common fruits consumed all over the world, and they are a very rich source of antioxidant bioactive compounds, including polyphenols. The coloration of red apple skin derives from the presence of anthocyanins in the fruit epicarp, especially glycosylated Cy, such as cyanidin-3-O-glycosides and cyanidin-3-O-galactosides [233].

In a recent work, Soppelsa et al. evaluated the effects derived by the application of ten different typologies of biostimulants on apple quality [223]. They conducted the experiments during two consecutive seasons using biostimulants based on humic acids (HA), seaweed extracts (SWE), protein hydrolysates (PH), amino acids (AAB), vitamins (VTB), chitosan (CHTB), or containing silicon (SLB). The parameters related to fruit quality included pomological, physiochemical, nutritional, and nutraceutical attributes. At the end of the experimentation, they showed how the application of the biostimulants did not affect the tree productivity as well as physiochemical parameters of the fruits, such as flesh firmness (FF), total soluble solids (TSS), and total acidity (TA). On the other hand, one of the major effects of the biostimulant application was the significant change in skin apple coloration. However, the observed effect was detected only in apples treated with SWE, PH, and VTB. Their results were also supported by the evaluation of the total anthocyanidin content (TAC), showing that apples treated with these biostimulants presented an anthocyanin concentration double than the respective untreated fruits. Consequently, when authors evaluated the total polyphenol content (TPC) and antioxidant activity via ABTS assay, they found higher values for the apples treated with the mentioned biostimulants. Authors, according to previously published data [234], hypothesized that the boosted final red coloration might be linked to the modulation of plant endogenous growth regulators (such as cytokinins and abscisic acid). These events led to an enhancement of anthocyanin biosynthesis and accumulation in the skin during ripening.

In a more recent work the effect derived from the application of  $\text{CaCl}_2$  alone or in combination with SWE or with a commercial biostimulant formulation enriched in silicon and zinc was evaluated [224]. Also in this case, SWE application did not affect the final yield, meanwhile the treatment was able to affect the coloration of the fruit skin enhancing the anthocyanin production. In addition, an effect on the accumulation of Ca, Zn, and Mn



in the apple skin was observed after the application of both typologies of biostimulants. In addition, the authors suggested that the accumulation of these minerals in the skin, along with the increase of phenolic compounds during fruit ripening and storage, may represent the principal explanations of the reduced fruit susceptibility to post-harvest disorders.

### 3.2.2. Eggplant (*Solanum melongena*)

Among the vegetables, eggplants are one of the edible sources having very high amount of anthocyanins stored mainly in the skin. In particular, the skin showed to be rich in the rutinoside forms of Mv, Cy, and Pn [235]. However, the effect of biostimulant products on eggplants is actually less studied.

Pohl et al. studied the effects resulting from the application of SWE biostimulant derived from *Ascophyllum nodosum* [222] on six different eggplant cultivars (Cristal, Epic, Flavine, Gascona, and Onyx, WA 6020). In this work, they showed that all the plants treated with SWE set higher number of fruits of smaller diameter, resulting in a significant increment of total and marketable yield. Concerning the nutraceutical properties, the authors highlighted how the effect could be significantly different among cultivars. In particular, they reported that some cultivars (Cristal, Epic and WA 6020) recorded a more significant increase of TAC after the application of the biostimulant.

Sabatino et al. who inoculated *Rhizophagus irregularis* mycorrhiza on eggplant rootstocks, showed how FF was positively affected, in addition to several nutritional values, such as P, Fe, and protein content. From a nutraceutical point of view, also higher values of ascorbic acid, TPC, TAC, chlorogenic acid and glycoalkaloids were observed [236].

### 3.2.3. Grape (*Vitis vinifera*)

Due to the economic impact of grape and its related products, the effect of biostimulant application on *Vitis vinifera* is certainly one of the most studied. In general, biostimulants were employed with the aim to promote plant growth and fruit quality, and in particular several of the published manuscripts investigated how to improve the color of skin grape because it is not only directly linked to fruit maturity, but also to the good preparation of food secondary processed foods, including wines [237].

Tommaso Frioni et al. studied the effects derived from the spray application of a SWE biostimulant containing *Ascophyllum nodosum* extracts on three different grape cultivars (Sangiovese grown under Mediterranean conditions, Pinot Noir and Cabernet Franc within a cool-climate viticulture region) [238]. The product was sprayed five times during the season at the doses described in the product label. The authors found that SWE was not able to affect leaf gas exchanges, fruit yield, berry cluster or fruit size, but positively affected the phenolic content. In particular, the authors found that anthocyanins were strongly accumulated in the skin of the fruits. Overall, they hypothesized that the biostimulant might boost anthocyanins and other polyphenols close to veraison and then later in the season, maintaining active the accumulation before harvest. This hypothesis was supported by the fact that SWE-triggering anthocyanin biosynthesis in grape skins anticipated veraison. Finally, they also described an effect dependent on the genotype, due to the recording of higher values in Sangiovese and Pinot Noir cultivars than in Cabernet Franc.

Similar results were also obtained in a more recent study, in which the effect observed after the foliar application of a similar biostimulant was evaluated on both physiological and biochemical parameters of *Vitis vinifera* (cv. Sangiovese) [239]. In this work, the authors stated the SWE-based biostimulant was able to affect the eco-physiological parameters and secondary metabolic pathways, resulting in improved grape quality. In particular, the applications of *A. nodosum* extract had significant effects on phenylpropanoid biosynthesis, both in berry skins and in leaves, influencing anthocyanin partitioning and lowering the biosynthesis of methoxylated compounds. However, in disagreement with Frioni, Palliotti et al. also observed an improvement of the leaf gas exchanges, maximum photosystem II efficiency, and grape maturity.

A very recent work studied the effect derived from the application of a natural biostimulant in the accumulation of anthocyanins in “Red Globe” grapes, by investigating the potential mechanism of action through the study of the changes in gene expression and activities of proteins involved in flavonoid pathways [221]. In particular, these authors found that after the treatment with the biostimulant all genes involved in the anthocyanin biosynthesis were up-regulated and the activities of the key enzymes related to this pathway, including PAL, CHI, UFGT, and DFR, increased.

#### 3.2.4. Cherry (*Prunus avium*)

Sweet cherry has a relevant economical value due to its commercial characteristics, nutritional value, and beneficial health effects [240]. Unfortunately, the quality of cherries is severely compromised by climatic conditions, resulting in a significant economic loss. Despite this, only limited studies have attempted to find solutions to the problem using sustainable agronomic techniques. Berta Gonçalves et al. studied the effect of salicylic acid, glycine-betaine complex, and SWE as biostimulants applied during pre-harvest period by foliar spray [225]. The effects were evaluated on the “Staccato” cultivar, and the authors found that all the treatments positively affected size, soluble solid content, pH, color, antioxidant activity, polyphenol, and vitamin C content. Among the tested biostimulants, glycine-betaine and SWE products showed the best results, in term of physiochemical, nutritional, and nutraceutical parameters. In particular, authors found that cherries treated with this biostimulant showed a higher content of neochlorogenic, p-coumaric, chlorogenic acids, cyanidin-3-O-rutinoside and cyanidin-3-O-glucoside, rutin, luteolin, and vitamin C. These results were in correlation with a higher antioxidant capacity.

Sofia Correia et al. treated Skeena sweet cherry trees by repeated foliar spray applications of a biostimulant based on Ca, gibberellic acid, abscisic acid, salicylic acid, glycine betaine, and SWE [15]. They measured the physiological and biochemical performance for two consecutive years (2015–2016) and demonstrated that the biostimulant application increased the physiological performance and water status of the trees. Among the different formulations, the spray application of SWE was shown to be the best for increasing yield and reducing cherry cracking as well as improving photosynthetic performance and leaf metabolite content. Moreover, also maturity index and anthocyanin content in cherries were strongly increased after the application of ABA-based biostimulant and SWE.

#### 3.2.5. Strawberry (*Fragaria ananassa*)

For centuries, strawberries have been consumed mainly because of their sweet taste, but the potential of this fruit is mainly related to its phytochemical composition. Indeed, strawberries are a good source of vitamin C, anthocyanins, proanthocyanidins, and other antioxidants, and its consumption is correlated to cardiovascular protection and anti-inflammatory effects [241]. The results derived from the application of biostimulant aimed to preserve, or increase, the nutritional and nutraceutical content of these fruits, were largely investigated.

For example, Guido Lingua et al. in 2013 studied the effect of arbuscular mycorrhiza colonization on the amount of anthocyanins, showing how the symbiosis could induce an increase of TAC [59]. Moreover, the authors investigated the qualitative anthocyanin profile via HPLC-MS/MS and discovered that Cy and Pg were the most varying anthocyanins. In 2020, Nadia Lombardi et al. studied the effects of treatments with three selected *Trichoderma* strains (T22, TH1, and GV41) in strawberry plants, by measuring the productivity, primary and secondary metabolites, and proteome of the formed fruits [227]. They reported that the application of the biostimulant positively affected plant growth, increased fruit yield, and favoured the selective accumulation of anthocyanins in the skin of red ripened fruits. By performing HPLC analysis, they found that not all anthocyanins were equally affected by the biostimulant application. In particular, only the glucoside and rutinoside forms of Cy or Pg were affected by the treatment. With the aim to understand the mechanism that led to a higher anthocyanin accumulation in the fruits, they performed proteomic



analysis and demonstrated that the microbial inoculants highly affected the profile of proteins associated with responses to stress/external stimuli, nutrient uptake, protein metabolism, carbon/energy metabolism, and secondary metabolism. Moreover, bioinformatic analysis revealed a concomitant modulation of different plant physiological processes following the microbial inoculation. To this purpose, they found that in treated plants there was an increased level of PAL, CHI, and other enzymes involved in anthocyanin biosynthesis, meanwhile proteins catalyzing the transformation of secondary metabolites into lignin derivatives, such as elicitor-activated genes, and isoflavone reductases were down represented.

#### 4. Conclusions

The application of plant biostimulants as agriculture practice represents a sustainable way to reduce fertilizers and other chemicals, also reducing the environmental contamination. This aspect increased the attention not only of the farmers but also of consumers, who are more confident in sustainable foods because perceived safer and healthier. As reported in this review, plant biostimulants are shown to be able to increase fruit quality parameters in plant grown both in controlled and adverse conditions. However, compared with the high number of published reports, few scientific papers were focused on fruit quality in term of nutraceutical aspects, and in particular on a punctual class of bioactive compounds, such as anthocyanins. Moreover, most part of the published papers simply reports the effects of biostimulant applications on plants, but few have investigated their potential mechanisms of action. Consequently, it is important to highlight the urgent need for further studies that should be focused on the biostimulant chemical composition and on the investigation of the biochemical and molecular pathways involved in their displayed actions.

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