Review Article

Response of Bioactive Phytochemicals in Vegetables and Fruits to Environmental Factors

Abstract

This review focused on the influence of environmental systems and/or factors including high tunnel, UV and visible lights, fertilization, and irrigation on bioactive compounds in vegetables and fruits. Most studies reported that high tunnel reduced chicoric acid and luteolin in vegetables including lettuce and pac choi, and fruits including raspberry and tomato versus open field although a few studies demonstrated that high tunnel did not significantly impact on the bioactive compounds. Light including UV such as photosynthetically active radiation (PAR), UV-A, and UV-B, and visible light especially red and blue light, significantly stimulated biosynthesis of anthocyanins, flavonoids, and phenolics, and promoted their contents in vegetables such as onion and spinach, and fruits for example blueberry and strawberry. The effect of fertilization including nitrogen, phosphorus, and potassium on bioactive phytochemicals (carotenoids, flavonoids, polyphenols) in vegetables (broccoli, kale) or fruits (tomato) varied among the cultivars. Water deficit usually increased anthocyanins, flavonoids, and phenolic acids in vegetables such as lettuce and red beet, and fruits including grape and pomegranate. Taken together, the bioactive compounds in vegetables and fruits in response to environmental factors were species and varieties dependent. The negative effect of environmental factors on bioactive compounds in vegetables and fruits can be overcome by selecting appropriate cultivars, while the positive effect can be further manipulated in horticultural production for potential consumer's health benefits.

Key words: Phenolics carotenoids, high tunnel, light, fertilization, irrigation, lettuce, tomato.

1. Introduction

Vegetables and fruits are fundamental in human diets because they provide high nutritional values including macronutrients such as carbohydrate, protein, fiber and micronutrients such as minerals, and non-nutrients phytochemicals. Phytochemicals are biologically active compounds biosynthesized in plants, including polyketides, phenolics, terpenoids, alkaloids, sulfur-containing compounds, and nitrogen-containing compounds. Epidemiological studies suggested that dietary intake of vegetables and fruits rich in phytochemicals is associated with reducing risk of chronic diseases such as cardiovascular disease, inflammation, obesity, diabetes, and cancer [1, 2]. Thus, vegetables or fruits enriched with bioactive compounds are beneficial to human health. Phenolics in vegetables or fruits can function as antioxidants to protect against the overproduction of reactive oxygen species (ROS) which resulted in aging related chronic diseases in human body [3]. Besides, antioxidant polyphenols showed anti-cancer effects *in vitro* such as modulated initiation of carcinogenesis by protecting against DNA mutation, inhibited cell proliferation, induced apoptosis, and down-regulated the expression of cancer-related genes [4].

Horticultural production aims to produce vegetables and fruits with increased yield and improved overall quality. The overall quality of vegetables and fruits include phytochemical quantity because of associated health benefits for chronic disease prevention. It is well known that bioactive compound profile in vegetables and fruits is determined by genotypic factors, but the biosynthesis activities and the bioactive compound contents are strongly influenced by environmental systems and/or factors such as cultivation, light, postharvest condition, fertilization, and irrigation, etc. [5]. High tunnel cultivation, for example, is commonly used in the Midwest region of the U.S. to extend growing season and increase crop yields. Previously, extensive studies have been focused on the effect of high tunnel on the yield, biomass, starch, amino acids, protein, and vitamins of vegetables and fruits [6-11]. The impact of light on yield, total carbon, nitrogen, fiber, and minerals of vegetables and fruits has also been studied [12-15]. Utilization of various fertilizers has been reported to improve vegetable yield and quality [16, 17]. To date, some studies observed the influence of the aforementioned environmental systems and/or factors such as high tunnel, light, fertilization, and irrigation on the bioactive compounds in vegetables and fruits; however, to our best knowledge, comprehensive review is more limited yet. Therefore, this review will focus on the recent effects of high tunnel, light including UV light and visible light, fertilization, and irrigation on bioactive phytochemicals in vegetables and fruits. The underlying mechanisms involved in different environmental systems and/or factors will also be further discussed. This review will be beneficial to horticultural researches that want to produce vegetables or fruits with improved quantity of bioactive compounds to reach the protective amounts for potential consumers' healthy benefits.

2. Bioactive compounds in vegetables and fruits

Polyphenols and terpenoids are the most common bioactive compounds in vegetables and fruits. Terpenoids are the largest group of secondary metabolites, while approximately one-third of dietary polyphenols are phenolic acids [18].

Phenolics are biosynthesized through the 'shikimic pathway' or 'phenylpropanoid pathway' starting from precursor pheylpropanoid. Phenylpropanoids originate from cinnamic acid formed from phenylalanine via the enzyme phenylalanine ammonia-lyase (PAL) [19]. This enzyme is the branch point enzyme between primary and secondary metabolites [19]. Through a series of enzymes, the cinnamic acid will turn into other phenolic acids and flavonoids. Chemically, simple phenol contains one phenol ring with one hydroxyl group, while phenolic compounds consist of more than one phenol ring with more than one hydroxyl group, which are further classified into simple phenol, phenolic acid, flavonoid, tannin, stilbene, lignan, etc. [20, 21]. Phenolic acids contain two subgroups including hydroxybenzoic acids (e.g., gallic acid, vanillic acid, and syringe acid) and hydroxycinnamic acids (e.g., caffeic acid and ferulic acid). Tannins are high molecular compounds composed of hydrolysable tannins and condensed tannins (proanthocyanidins) [20]. Stilbenes are usually glycosylated with sugars in vegetables or fruits. Flavonoids are the largest subgroup in phenolic compounds. So far, more than 4000 flavonoids were identified [20]. The flavonoid skeleton consists of fifteen carbons with two aromatic rings linked by a three-carbon bridge. It is a C6-C3-C6 configuration as shown in Figure 1. Substitutions through oxygenation, alkylation, glycosylation, and/or acylation to ring A or B create subgroups of flavonoids including flavanone, flavone, isoflavone, and flavonols [22].

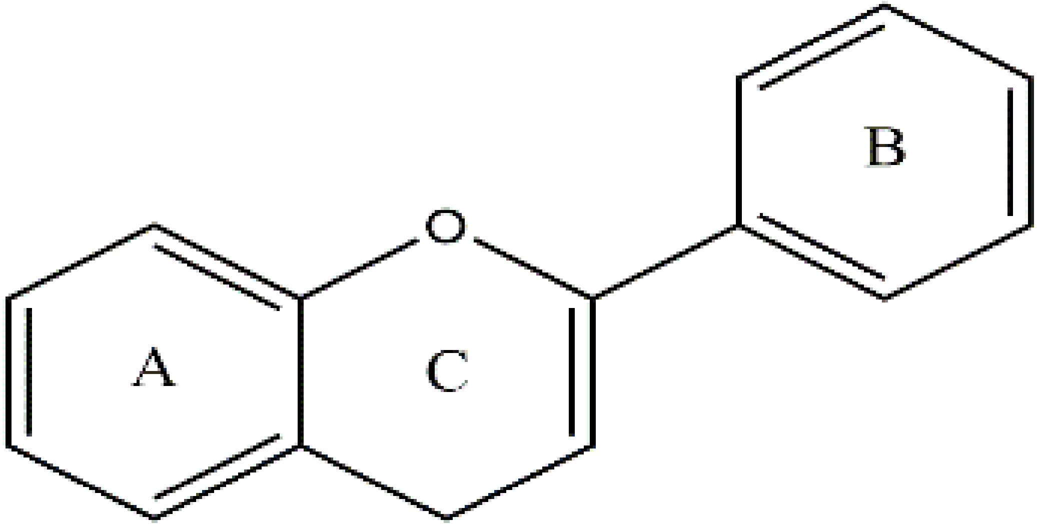

Figure 1. Flavonoid skeleton.

As a typical terpenoid, carotenoids are composed of either oxygenated or non-oxygenated hydrocarbons containing over 40 carbons including double carbon bond systems [23].

Carotenoids contain two subgroups, including carotenes which lack oxygen functions (e.g., β-carotene and lycopene) and xanthophylls which contain oxygen functions (e.g., lutein and zeaxanthin) [24]. The possible biosynthesis pathways of both phenolics and carotenoids in plants are shown in Figure 2.

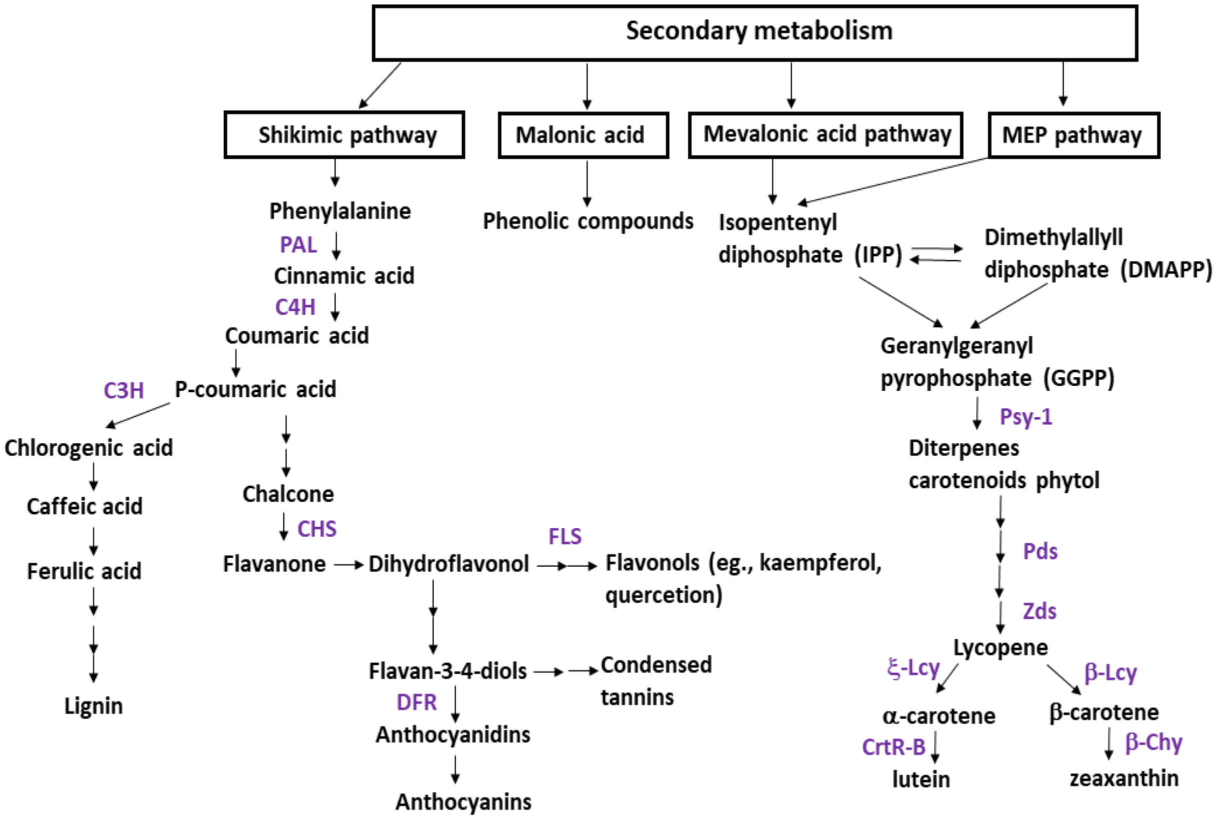

Figure 2. Bioactive compound biosynthesis [19, 94]. PAL: phenylalanine ammonia lyase. C4H: cinnamate-4-hydroxylase. C3H: p-coumaroyl ester 3-hydroxylase. CHS: chalcone synthase. FLS: flavonol synthase. DFR: dihydrfalvonol reductase. Psy-1: phytoene synthase. Pds: phytoene desaturase. Zds: ξ-carotene desaturase. ξ-Lcy: lycopene ξ-cylase. CrtR-B: α-β-hydroxylase. β-Lcy: lycopene β-cylase. β-Chy: β-carotene hydroxylase.

3. Influence of environmental systems and/or factors on bioactive compounds in vegetables and fruits

a. High tunnel cultivation

Conventionally, vegetables and fruits are grown in the open field. However, plant yield is affected by the natural environment fluctuations. Unheated plastic films covered on the tunnel, known as high tunnel, have been developed as a protective measure to protect against weather fluctuations. High tunnel, also known as high hoops or hoop houses, is constructed to be passively heated and ventilated, and so far has been widely applied in Asia, mid-west America, and western Oregon and Washington. High tunnel cultivation has many advantages such as protecting vegetables or fruits against weather fluctuations, extending growing season, and physically reducing pest infection [25]. By covering with plastics, the temperature and humidity in the high tunnel can be relatively stable in contrast to the open field. Thus the microclimate in the high tunnel favors crops physiological processes such as germination, flowering, pollination, and ripening, especially in early spring or late fall [26]. However, it is important to note that the temperature in high tunnel could be high around noon, so careful monitoring is needed. The main disadvantage of high tunnel is that most high tunnels are stationary and immovable as well as the negative impact on micronutrient values including phytochemical contents.

So far, several plastic materials have been commonly covered on the high tunnel including greenhouse-grade polyethylene (PE), polycarbonate (PC), and polypropylene (PP) either with single layer or double layers [11]. Films used for the covers range from 80-220 μm thick and up to 20 m wide [27]. The definition, structure, main design, historical and global use, microclimate change of high tunnel, and the economic profitability of high tunnel have been widely discussed [11, 26, 28]. To date, high-value and warm-season crops are primarily selected to grow in the high tunnel such as green bean, tomato, pepper, squash, cucumber, zucchini, strawberry, cut flowers, etc. [26]. However, previous studies showed reduction of phenolics in lettuce grown in the high tunnel [5, 29, 30,]. In our recent study, we have confirmed that the high tunnel cultivation resulted in reduced phenolic contents in ‘Two Star’ lettuce and decreased carotenoid contents in ‘Celebrity’ tomato in contrast to those grown on the open field [31]. It was interesting that the high tunnel cultivation did not affect the phenolic contents in ‘New Red Fire’ lettuce and carotenoid content in ‘Mountain Fresh’ tomato [31]. Therefore, the change of bioactive compounds in vegetables and fruits grown in high tunnel seems species- and varieties-dependent. A summary of recent studies related to bioactive compounds in vegetables or fruits grown in high tunnel versus open field cultivation is listed in Table 1.

Table 1. Bioactive compounds in vegetables and fruits grown in high tunnel versus open field.

Vegetables or fruits	Plastics	Bioactive compounds	Reference
Lettuce (‘Red Sails’, ‘Kallura’)	Single layer PE	Reduced phenolic contents in both varieties	30
Lettuce (‘Barone’, ‘Red Sails’)	Luminance PE	Reduced phenolic contents in both varieties	5
Lettuce (‘Two Star’, ‘New Red Fire’), tomato (‘Celebrity’, ‘Mountain Fresh’)	Single UV clear PE	Reduced phenolic contents in ‘Two Star’ lettuce but not in ‘New Red Fire’. Reduced carotenoid contents in ‘Celebrity’, but not in ‘Mountain	31
Pac choi, red leaf lettuce, romaine lettuce, spinach	Single layer PE	Reduced phenolic contents in all species	29
Raspberry (‘Glen Ample’, ‘Glen Dee’, ‘Maurin Makea’)	PE	No significant difference	34

The microclimate in the high tunnel is complicated because many factors are changed in contrast to the open field, including air temperature around the plants, humidity, insect, and light. considering UV-A, UV-B and PAR are essential to phenolics or carotenoids biosynthesis in vegetables or fruits due to stimulating the PAL enzyme activity [5, 19]. However, studies reported that UV light especially UV-B and UV-A radiation ranged from 250-400 nm were absorbed by PE films, thus resulting in less UV light to the vegetables or fruits grown in the high tunnel [32, 33]. Similarly, our previous study showed that PE films reduced 46% UV-B, 33% UV-A, and 17% PAR inside the tunnel compared to the open field [31]. Therefore, receiving less UV-B light in the high tunnel lowers the activity of PAL enzyme in vegetables or fruits, which results in lower accumulation of bioactive compounds. However, not all vegetables or fruits showed such decreasing trend of bioactive compounds. Except for our recent study [31], Palonen et al (2017) demonstrated that high tunnel did not significantly affect the bioactive compound contents in three varieties of raspberry [34]. Hence, the effect of high tunnel cultivation on bioactive compounds in vegetables or fruits may be cultivar- and variety-dependent.

The main purpose of utilizing high tunnel is to extend growing season and increase yields for food sustainability. In terms of bioactive compounds in vegetables and fruits grown in the high tunnel, the negative effect on bioactive compound accumulation might be overcome by selecting various varieties. In addition to the results shown in Table 1, more studies may be warranted by expanding current lettuce, tomato, and pepper to other high-value and warm-season crops such as squash, cucumber, zucchini, strawberry, and cut flowers and by understanding the underlying mechanisms focusing on the key genes or enzymes involved in the phenolic or carotenoid biosynthesis as illustrated in Figure 2.

b. Light spectra

Light is an important abiotic factor influencing bioactive compound biosynthesis in vegetables and fruits [35, 36]. Secondary metabolites especially phenolics and their derivatives are responsive to UV light to accumulate in epidermal cells for reducing UV penetration in deeper cell tissues [37, 38]. It is reported that phenolics in plants absorbed UV-B wavelength from 280-320 nm and worked as ROS scavengers to protect against UV-B radiation which is considered as a self-defensive mechanism to protect against UV exposure [39]. Verdaguer et al. (2017) demonstrated that UV-A light improved the leaf chlorophyll content and photosynthetic activity in plants [40]. UV-B light stimulated phenolics, alkaloids and terpenoids biosynthesis in plants [41-43]. The studies related to the effects of UV light on bioactive compound accumulation in vegetables and fruits are summarized in Table 2. The influence of UV light on bioactive compounds in vegetables and fruits seems variable among cultivars and varieties.

Table 2. Effect of UV or PAR light on bioactive compounds in vegetables and fruits.

Vegetables or fruits	Light	Bioactive compounds	Reference
Blueberry, lettuce ('Lollo Rosso' and 'Lollo Biondo'), strawberry, and raspberry	UV	UV increased phenolics and anthocyanins in 'Lollo Rosso', raspberry, and blueberry, but did not alter phenolic and anthocyanin contents in 'Lollo Biondo'	66
Coleus aromaticus	UV-B	Increased carotenoid, anthocyanin, and flavonoid compounds	67
Lemon catmint, lemon balm, and sage	UV-B, PAR	UV-B and PAR increased polyphenol contents sage, UV-B and PAR increased phenolic acid contents in lemon catmint and lemon balm	68
Tomato ('Oregon Spring' and 'Red Sun')	UVA + UVB	UV light increased phenolic and carotenoid contents in both varieties	25

Prunella vulgaris	UV-B	UV-B light increased total flavonoid, rosmarinic acid, caffeic acid content	69

It has been reported that UV radiation favored the flavonoid biosynthesis in leafy tissues [44]. UV-A and UV-B also stimulated the a key gene Chalcone synthase (CHS) for flavonoid biosynthesis pathway, resulting in accumulation of flavonols such as quercetin and kaempferol [45, 46]. Thus, UV-A and UV-B elevated flavonoid contents in vegetable and fruits. Agati et al (2013) demonstrated that PAR favored the flavonoids accumulation especially the quercetin in the crop [47].

In addition to UV light, visible light is another critical factor for vegetables and fruits growth. It is well known that blue light plays an important role in chloroplast development, chlorophyll formation and stomata opening, while red light is crucial to plant growth such as stem elongation, leaf expansion, and photosynthesis [48]. Blue light has been demonstrated in simulating the transcription of cryptochrome *CRY*1 gene that is responsible for anthocyanin biosynthesis in *Arabidopsis thaliana* [49]. Extensive studies have been focused on the effect of visible light spectra on the growth and development of vegetables and fruits [48, 50, 51], but some studies showed the effect of visible light especially red and blue light on bioactive phytochemicals in vegetables and fruits (Table 3).

Table 3. Effect of visible light on bioactive compounds in vegetables and fruits.

Vegetables or fruits	Light spectra	Bioactive compounds	Reference
Chinese cabbage	Blue, green, red, red:blue (6:1), yellow	Blue, green, red, and yellow all reduced carotenoid contents, but red:blue (6:1) did not alter carotenoids	70
Chinese kale sprouts	Red	Enhanced total phenolics	71

Chili pepper (‘*Capsicum annuum*’, ‘Cheonyang’)	Blue, red	Blue+red increased carotenoid contents in both varieties. Blue improved capsaicinoid content in both varieties	48
Green oak lettuce	Blue, far red, green, red, and yellow	Blue and red increased carotenoid contents in lettuce, but far red, green and yellow reduced carotenoids	72
Lettuce (‘Hongyeomjeokchukmyeon’ and ‘Aram’)	Blue and red	Red 53: blue 47, red 58: blue 42 increased anthocyanins in both varieties	73
Lettuce ‘Red Cross’	Blue, green and red	Blue light increased phenolic and carotenoid contents, but green and red light did not	74
Lettuce (‘Outredgeous’)	Blue, green, far red, and red	Red, red+green+blue, red+blue increased anthocyanin contents. Far red reduced anthocyanin contents	75
Lettuce (‘Lollo Rossa’) and basil (‘genovese gigante’)	Blue	Increased phenolics in lettuce. No effect of blue light on phenolics in basil	76
Lettuce (‘Grizzly’)	Blue, red, red:blue (7:3), white	red:blue (7:3) increased carotenoid contents. No effect of blue, red and white on carotenoids	77
Mustard (‘yellow mustard’), spinach (‘Geant d’hiver’), rocket (‘Rucola’), dil (‘Mammouth’), parsley (‘Plain Leavd’), green onion (‘White Lisbon’)	Red	Red increased antioxidant capacity in dill and parsley, but did not alter antioxidant capacity in mustard, spinach, rocket, and green onion	78

It seems that impact of visible light especially the blue and red light on carotenoids in vegetables and fruits varies among the cultivars and the underlying mechanisms are mostly unknown. When manipulation of visible light via specific light spectra is recognized as a promising solution for phytochemical biosynthesis, more studies appear to be warranted to confirm the effect and discover the underlying mechanisms.

c. Fertilization

Fertilizers including nitrogen (N), phosphorus (P), and potassium (K) are beneficial to crop yield and quality [52]. Nitrogen is an important nutrient for plant growth and development, especially for protein synthesis [52, 53]. Potassium is important involved in numerous biochemical and physiological processes and photosynthesis in plants [54]. For example, fertilizers including nitrogen, phosphorus and potassium have been reported to increase rice yield from 19 to 41% and rapeseed yield from 61 to 76% [55]. Recently, there is a growing interest to study the effect of fertilization including N, P, and K on bioactive compounds in vegetables or fruits, which is summarized in Table 4.

Table 4. Effect of fertilization on bioactive compounds in vegetables and fruits.

Vegetables or fruits	Fertilizers	Bioactive compounds	Reference
Broccoli	N (0, 15, 30, 50 kg/ha). N (30, 60, 90, 150 kg/ha) +S (50, 100 kg/ha)	N over 30 kg/ha reduced glucoraphanin and flavonols in broccoli, but not on progoitrin. S supply did not alter glucosinolates or flavonols in broccoli	79
Kale	N treatment (6, 13, 26, 52, 105 mg/L) at constant 1NH$_4^+$: 3NO$_3^-$. NH$_4^+$: NO$_3$ ratio (100%, 75:25%, 50%:50%, 25%: 75%, 0:100%)	Increased N rate improved carotenoids in kale. Increased NO$_3^-$ improved the carotenoids in kale	80
Lettuce (‘Mutigreen 1’, ‘Mutigreen 3’, and ‘Multired 4’)	N supply	60-120 mg/L N increased phenolic contents ‘Mutigreen 3’, 120 mg/L increased phenolic contents ‘Mutigreen 1’. ‘Multired 4’ is less responsive to N supply	12
Lettuce (‘Romana’)	No nitrogen fertilization, no phosphorus fertilization	No nitrogen fertilization resulted in increased polyphenol contents. No effect of P deficiency in polyphenols	81
Lettuce	N supply	Increased carotenoids in lettuce	82

Mustard ('Xuelihong', 'Zhujie')	N (10 and 25 mM), S (0.5, 1, and 2 mM)	Increased N resulted in total phenolics in both varieties, increased S improved total phenolics in both varieties	52
Onion	N supply: dominant ammonium (NH_4^+), dominant nitrate (NO_3^-)	Dominant nitrate (NO_3^-) increased quercetin glycosides, organosulfur compounds	83
Tomato ('BARI tomato 15')	Trichoderma-enriched biofertilizer (BioF/compost)	BioF/compost did not significantly alter carotenoid contents	84
Tomato ('Firenze', 'Rio Grande')	Organic fertilizer	Did not significantly alter carotenoid contents in both varieties	85
Tomato ('Honey Bunch')	N (0, 78, 157, 23, 314, 392 kg/ha)	Increased N rate did not significantly change carotenoids in tomato	86
Tomato ('Fla. 8153', 'Mountain Spring')	K (0, 23, 46, 93, 186, and 372 kg/ha)	Increased K improved lycopene contents in 'Fla. 8153', but did not improve lycopene contents in 'Mountain Spring'	87
Watercress	N (6, 56, 106 mg/L) S (8, 16 32 mg/L)	Increased N improved carotenoids in watercress. Carotenoids in watercress were not responsive to S	88

Overall, the effect of fertilizers such as N, P, and K on bioactive compounds in vegetables and fruits is variable among different cultivars. Besides the fertilization concentration, the dominant type of N-fertilizers such as ammonium or nitrate also influences the bioactive compounds in vegetables and fruits. A few researches have been conducted to study the mechanism of N to bioactive compounds in vegetables and fruits. For example, low nitrogen concentration in fertilizer stimulated flavonoid accumulation [56]. Bryant et al (1983) hypothesized that N deficiency resulted in lower N uptake, causing the reduction of plant growth and photosynthesis, further reducing the N-based secondary metabolites such as alkaloids but increasing the C-based secondary metabolites such as flavonoids [57]. However, to date, there is no deep study regarding the mechanisms of P and K on bioactive compounds in vegetables and fruits. Hence, more studies are needed to discover the influence and the underlying mechanisms of P and K on the alteration of bioactive compounds in vegetables and fruits.

d. Irrigation

Water accounts for more than 80% of growing tissues in crops and regulates the physiological processes such as growth, exocytosis, hormone signaling, metabolism, nutrient collection, etc. [58]. However, in arid or semi-arid areas, drought, deficit irrigation or water scarcity are the most common environmental stresses which influence the production of vegetables and fruits, especially the secondary metabolites [59-61]. Hence, this phenomenon generates the research interests of water stress on bioactive compounds in vegetables or fruits. The impact of irrigation on bioactive compounds in vegetables and fruits is summarized in Table 5.

Table 5. Effect of irrigation on bioactive compounds in vegetables and fruits.

Vegetables or fruits	Irrigation	Bioactive compounds	Reference
Berry (‘Cabernet Sauvignon’) and grape (‘Chardonay’)	Water deficit	Increased anthocyanins, in ‘Cabernet Sauvignon’. Increased carotenoids and aromatic volatiles in ‘Chardonay’	62
Grapevine leaves (‘Touriga Nacional’)	Regulated deficit irrigation (RDI), RDI60, RDI40, RDI20, providing 60, 40, and 20% of reference evapotranspiration	Increased irrigation reduced total phenols, hydroxycinnamic acids, and flavonols	89

Lettuce ('Lollo Bionda', 'Vera')	Deficit irrigation, three management allowable depletion levels (MAD) at 25%, 50%, and 75%	In both varieties, 50% MAD increased phenolics acids, 75% MAD increased flavonoids	90
Lettuce	Irrigation at 100%, 85%, and 70% of evaporated water	Decreased irrigation improved total phenolics in lettuce	91
Red beet	Water: 100%, 50%, and 30%	Decreased water irrigation increased the total phenolics.	92
Pomegranate	Sustained defitic irrigation (SDI: 32% of reference evaporatranspiration)	32% SDI increased total phenolics and betalains	93

It has been demonstrated that water deficit stress induced a series of key enzymes which were involved in the 'phenolpropanoid pathway' in plants including PAL, C4H, 4CL, CHS, and flavanone-3-hydroxylase (F3H) [62]. Therefore, phenolic acids and flavonoids were accumulated in vegetables and fruits. So far, most studies showed that water deficit generally favored the biosynthesis of bioactive compounds in vegetables and fruits, but not all. For example, Mena et al (2012) observed that deficit irrigation at 12% and 43% reduced the total phenolics and total anthocyanins in pomegranate in contrast to the control group which irrigated with 75% [63]. Besides, the effect of deficit irrigation during different growing seasons should be taken into consideration. Pék et al (2013) reported that total phenolics in broccoli were significantly enhanced by the non-irrigated method in the spring, but not in the autumn, indicating that the growing season might also affect the bioactive compounds in the vegetables [64].

In terms of a positive effect of promotion of water deficit on bioactive compounds, however, deficit irrigation usually reduces the crop yield, biomass, production, and quality. The strategies of water deficit stress on accumulated bioactive compounds in vegetables and fruits should be considered carefully.

The impact of the aforementioned environmental factors on bioactive compounds was highlighted in lettuce as an example in Figure 3.

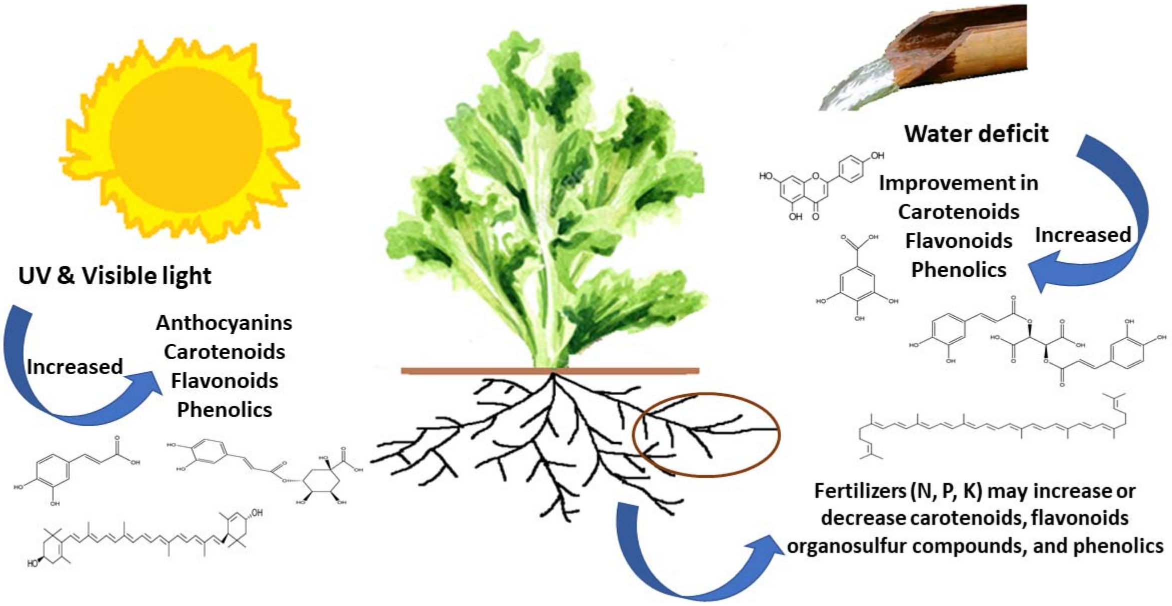

Figure 3. Responses of bioactive compounds in lettuce to light, fertilization, and irrigation.

4. Conclusion

In conclusion, this review summarized and discussed the major high impact environmental systems and/or factors affecting bioactive compounds yield and quality in vegetables and fruits. These main environmental systems and/or factors include high tunnel, UV and visible light, fertilization, and irrigation. Although the response of bioactive compound accumulation in vegetables and fruits to high tunnel, light, fertilization and water deficit stress varies among cultivars, less biosynthesis of bioactive compounds in responsive to high tunnel versus open field but more bioactive compound biosynthesis in response to UV light and visible red and blue light as well as water deficit stress are generally observed in most studies. The effect of nitrogen, phosphorus, and potassium fertilization on bioactive compounds in vegetables or fruits seems variable. More studies to confirm the influence and the underlying mechanisms by focusing on the key genes and biosynthesis enzymes or even using transgenic technology to enhancing phytochemical biosynthesis as we previously reported [21, 65] appear to be warranted. Overall, a negative effect of environmental factors on the bioactive compounds in vegetables and fruits may be overcome by selecting various cultivars, while a positive effect of environmental factors on bioactive compound accumulation in vegetables and fruits can be further manipulated in horticultural production for potential consumer's health benefits.

ACKNOWLEDGEMENT

This study was supported in part by a USDA Cooperative Project KS511-1001903 from the Agricultural Experiment Station, Kansas State University (Contribution #19-259-J from the Kansas Agricultural Experiment Station).

COMPETING INTERESTS

Authors have declared that no competing interests exist.

Reference

1. Liu RH. Dietary Bioactive Compounds and Their Health Implications: Dietary bioactive compounds and health…. Journal of Food Science. 2013;78:18–25. https://doi.org/10.1111/1750-3841.12101
2. Birt DF, Hendrich S, Wang W. Dietary agents in cancer prevention: flavonoids and isoflavonoids. Pharmacology & Therapeutics. 2001;90:157–177. https://doi.org/10.1016/S0163-7258(01)00137-1
3. Garcia-Salas P, Morales-Soto A, Segura-Carretero A, Fernández-Gutiérrez A. Phenolic-

Compound-Extraction Systems for Fruit and Vegetable Samples. Molecules. 2010;15:8813–8826. https://doi.org/10.3390/molecules15128813

4. Zhang Y-J, Gan R-Y, Li S, et al. Antioxidant Phytochemicals for the Prevention and Treatment of Chronic Diseases. Molecules. 2015;20:21138–21156. https://doi.org/10.3390/molecules201219753
5. Oh M-M, Carey EE, Rajashekar CB. Antioxidant phytochemicals in lettuce grown in high tunnels and open field. Horticulture, Environment, and Biotechnology. 2011;52:133–139. https://doi.org/10.1007/s13580-011-0200-y
6. Gimenez C, Otto R., Castilla N. Productivity of leaf and root vegetable crops under direct cover. Scientia Horticulturae. 2002;94:1–11. https://doi.org/10.1016/S0304-4238(01)00356-9
7. Both AJ, Reiss E, Sudal JF, et al. Evaluation of a Manual Energy Curtain for Tomato Production in High Tunnels. HortTechnology. 2007;467–472. https://doi.org/10.21273/HORTTECH.17.4.467
8. de Villiers DS, Wien HC, Reid JE, Albright LD. Energy Use and Yields in Tomato Production: Field, High Tunnel, and Greenhouse Compared for the Northern Tire of the USA. Acta Horticulturae. 2011;373–380. https://doi.org/10.17660/ActaHortic.2011.893.34
9. Powell M, Gundersen B, Cowan J, et al. The Effect of Open-Ended High Tunnels in Western Washington on Late Blight and Physiological Leaf Roll Among Five Tomato Cultivars. Plant Disease. 2014;98:1639–1647. https://doi.org/10.1094/PDIS-12-13-1261-RE
10. Marshall K, Erich S, Hutton M, et al. Nitrogen Availability from Compost in High Tunnel Tomato Production. Compost Science & Utilization. 2016;24:147–158. https://doi.org/10.1080/1065657X.2015.1102663
11. Janke RR, Altamimi ME, Khan M. The Use of High Tunnels to Produce Fruit and Vegetable Crops in North America. Agricultural Sciences. 2017;08:692–715. https://doi.org/10.4236/as.2017.87052
12. Mampholo BM, Maboko MM, Soundy P, Sivakumar D. Variety-specific responses of lettuce grown in a gravel-film technique closed hydroponic system to N supply on yield, morphology, phytochemicals, mineral content and safety. Journal of Integrative Agriculture. 2018;17:2447–2457. https://doi.org/10.1016/S2095-3119(18)62007-6
13. Mashabela MN, Selahle KM, Soundy P, et al. Bioactive Compounds and Fruit Quality of Green Sweet Pepper Grown under Different Colored Shade Netting during Postharvest Storage: Photo-selective netting and pepper quality…. Journal of Food Science. 2015;80:H2612–H2618. https://doi.org/10.1111/1750-3841.13103
14. Mudau AR, Soundy P, Mudau FN. Response of Baby Spinach (Spinacia oleracea L.) to Photoselective Nettings on Growth and Postharvest Quality. HortScience. 2017;52:719–724. https://doi.org/10.21273/HORTSCI11875-17
15. Ntsoane LLM, Soundy P, Jifon J, Sivakumar D. Variety-specific responses of lettuce grown under the different-coloured shade nets on phytochemical quality after postharvest storage. The Journal of Horticultural Science and Biotechnology. 2016;91:520–528. https://doi.org/10.1080/14620316.2016.1178080
16. Stagnari F, Galieni A, Pisante M. Drought stress effects on crop quality. In: Ahmad P (ed) Water Stress and Crop Plants. John Wiley & Sons, Ltd, Chichester, UK. 2016;375–392
17. Zikalala BO, Nkomo M, Araya H, et al. Nutritional quality of baby spinach (***Spinacia***

oleracea L.) as affected by nitrogen, phosphorus and potassium fertilisation. South African Journal of Plant and Soil. 2017;34:79–86.

18. Robbins RJ. Phenolic Acids in Foods: An Overview of Analytical Methodology. Journal of Agricultural and Food Chemistry. 2013;51:2866–2887. https://doi.org/10.1021/jf026182t
19. Dixon RA, Paiva NL. Stress-induced phenylpropanoid metabolism. The plant cell. 1995;7:1085
20. Ignat I, Volf I, Popa VI. A critical review of methods for characterisation of polyphenolic compounds in fruits and vegetables. Food Chemistry. 2011;126:1821–1835. https://doi.org/10.1016/j.foodchem.2010.12.026
21. Ayella AK, Trick HN, Wang W. Enhancing lignan biosynthesis by over-expressing pinoresinol lariciresinol reductase in transgenic wheat. Molecular Nutrition & Food Research. 2007;51:1518–1526. https://doi.org/10.1002/mnfr.200700233
22. Balasundram N, Sundram K, Samman S. Phenolic compounds in plants and agri-industrial by-products: Antioxidant activity, occurrence, and potential uses. Food Chemistry. 2006;99:191–203. https://doi.org/10.1016/j.foodchem.2005.07.042
23. Abuajah CI, Ogbonna AC, Osuji CM. Functional components and medicinal properties of food: a review. Journal of Food Science and Technology. 2015;52:2522–2529. https://doi.org/10.1007/s13197-014-1396-5
24. Johnson EJ. The role of carotenoids in human health. Nutrition in clinical care. 2002;5:56–65
25. Luthria DL, Mukhopadhyay S, Krizek DT. Content of total phenolics and phenolic acids in tomato (Lycopersicon esculentum Mill.) fruits as influenced by cultivar and solar UV radiation. Journal of Food Composition and Analysis. 2006;19:771–777. https://doi.org/10.1016/j.jfca.2006.04.005
26. Jett LW. High Tunnels. In: A Guide to the Manufacture, Performance, and Potential of Plastics in Agriculture. Elsevier. 2017;107–116
27. Espí E, Salmerón A, Fontecha A, et al. PLastic Films for Agricultural Applications. Journal of Plastic Film & Sheeting. 2006;22:85–102. https://doi.org/10.1177/8756087906064220
28. Galinato SP, Miles CA. Economic Profitability of Growing Lettuce and Tomato in Western Washington under High Tunnel and Open-field Production Systems. HortTechnology. 2013;453–461. https://doi.org/10.21273/HORTTECH.23.4.453
29. Zhao X, Iwamoto T, Carey EE. Antioxidant capacity of leafy vegetables as affected by high tunnel environment, fertilisation and growth stage. Journal of the Science of Food and Agriculture. 2007;87:2692–2699. https://doi.org/10.1002/jsfa.3032
30. Zhao X, Carey EE, Young JE, et al. Influences of organic fertilization, high tunnel environment, and postharvest storage on phenolic compounds in lettuce. HortScience 2007;42:71–76
31. Woolley A, Sumpter S, Lee M, et al. Accumulation of Mineral Nutrients and Phytochemicals in Lettuce and Tomato Grown in High Tunnel and Open Field. American Journal of Plant Sciences. 2009;10:125–138. https://doi.org/10.4236/ajps.2019.101011
32. Vox G, Schettini E. Effects of agrochemicals, ultra violet stabilisers and solar radiation on the radiometric properties of greenhouse films. Journal of Agricultural Engineering 2013;44:11. https://doi.org/10.4081/jae.2013.e11
33. Kamweru PK, Ndiritu FG, Kinyanjui T, et al. UV Absorption and dynamic mechanical

analysis of polyethylene films. International Journal of physical Science. 2015;9:545-555.

34. Palonen P, Pinomaa A, Tommila T. The influence of high tunnel on yield and berry quality in three floricane raspberry cultivars. Scientia Horticulturae. 2017;214:180–186. https://doi.org/10.1016/j.scienta.2016.11.049

35. Gruda N. Impact of environmental factors on product quality of greenhouse vegetables for fresh consumption. Critical Reviews in Plant Sciences. 2005;24: 227-247.

36. García-Macías P, Ordidge M, Vysini E, et al. Changes in the Flavonoid and Phenolic Acid Contents and Antioxidant Activity of Red Leaf Lettuce (Lollo Rosso) Due to Cultivation under Plastic Films Varying in Ultraviolet Transparency. Journal of Agricultural and Food Chemistry. 2007;55:10168–10172. https://doi.org/10.1021/jf071570m

37. Frohnmeyer H. Ultraviolet-B Radiation-Mediated Responses in Plants. Balancing Damage and Protection. PLANT PHYSIOLOGY. 2003;133:1420–1428. https://doi.org/10.1104/pp.103.030049

38. do Nascimento NC, Menguer PK, Sperotto RA, et al. Early Changes in Gene Expression Induced by Acute UV Exposure in Leaves of Psychotria brachyceras, a Bioactive Alkaloid Accumulating Plant. Molecular Biotechnology. 2013;54:79–91. https://doi.org/10.1007/s12033-012-9546-3

39. Hahlbrock K, Scheel D Physiology and Molecular Biology of Phenylpropanoid Metabolism. 23

40. Verdaguer D, Jansen MAK, Llorens L, et al. UV-A radiation effects on higher plants: Exploring the known unknown. Plant Science. 2017;255:72–81. https://doi.org/10.1016/j.plantsci.2016.11.014

41. Johnson CB, Kirby J, Naxakis G, Pearson S. Substantial UV-B-mediated induction of essential oils in sweet basil (Ocimum basilicum L.). Phytochemistry. 1999;51:507–510. https://doi.org/10.1016/S0031-9422(98)00767-5

412. Gerhardt KE, Lampi MA, Greenberg BM. The effects of far□red light on plant growth and flavonoid accumulation in Brassica napus in the presence of ultraviolet B radiation. Photochemistry and Photobiology. 2008;84:1445-1454.

43. Velikova VB. Isoprene as a tool for plant protection against abiotic stresses. Journal of Plant Interactions. 2008;3:1–15. https://doi.org/10.1080/17429140701858327

44. Wade HK, Bibikova TN, Valentine WJ, Jenkins GI. Interactions within a network of phytochrome, cryptochrome and UV-B phototransduction pathways regulate chalcone synthase gene expression in Arabidopsis leaf tissue: Chalcone synthase photoregulation. The Plant Journal. 2002;25:675–685. https://doi.org/10.1046/j.1365-313x.2001.01001.x

45. Chappell J, Hahlbrock K. Transcription of plant defence genes in response to UV light or fungal elicitor. Nature. 1984;311:76–78. https://doi.org/10.1038/311076a0

46. Jenkins GI. Structure and function of the UV-B photoreceptor UVR8. Current Opinion in Structural Biology. 2014;29:52–57. https://doi.org/10.1016/j.sbi.2014.09.004

47. Agati G, Brunetti C, Di Ferdinando M, et al. Functional roles of flavonoids in photoprotection: New evidence, lessons from the past. Plant Physiology and Biochemistry. 2013;72:35–45. https://doi.org/10.1016/j.plaphy.2013.03.014

48. Gangadhar BH, Mishra RK, Pandian G, Park SW. Comparative Study of Color, Pungency, and Biochemical Composition in Chili Pepper (Capsicum annuum) Under Different Light-emitting Diode Treatments. HortScience. 2012;47:1729–1735. https://doi.org/10.21273/HORTSCI.47.12.1729

49. Wu G, Spalding EP. Separate functions for nuclear and cytoplasmic cryptochrome 1 during photomorphogenesis of Arabidopsis seedlings. Proceedings of the National Academy of Sciences. 2007;104:18813–18818. https://doi.org/10.1073/pnas.0705082104
50. Piovene C, Orsini F, Bosi S, et al. Optimal red:blue ratio in led lighting for nutraceutical indoor horticulture. Scientia Horticulturae. 2015;193:202–208. https://doi.org/10.1016/j.scienta.2015.07.015
51. Tinyane PP, Sivakumar D, Soundy P. Influence of photo-selective netting on fruit quality parameters and bioactive compounds in selected tomato cultivars. Scientia Horticulturae. 2013;161:340–349. https://doi.org/10.1016/j.scienta.2013.06.024
52. Li J, Zhu Z, Gerendás J. Effects of Nitrogen and Sulfur on Total Phenolics and Antioxidant Activity in Two Genotypes of Leaf Mustard. Journal of Plant Nutrition. 2008;31:1642–1655. https://doi.org/10.1080/01904160802244860
53. Barker AV, Pilbeam DJ. Handbook of plant nutrition. CRC press. 2015.
54. Cakmak I. The role of potassium in alleviating detrimental effects of abiotic stresses in plants. Journal of Plant Nutrition and Soil Science. 2005;168:521–530. https://doi.org/10.1002/jpln.200420485
55. Yousaf M, Li J, Lu J, et al. Effects of fertilization on crop production and nutrient-supplying capacity under rice-oilseed rape rotation system. Scientific Reports. 2005. https://doi.org/10.1038/s41598-017-01412-0
35. Bongue-Bartelsman M, Phillips DA. Nitrogen stress regulates gene expression of enzymes in the flavonoid biosynthesis pathway of tomato [anthocyane]. *Plant Physiology and* Biochemistry. 1995;33: 539-546.
57. Bryant JP, Chapin FS, Klein DR. Carbon/Nutrient Balance of Boreal Plants in Relation to Vertebrate Herbivory. Oikos. 1983;40:357. https://doi.org/10.2307/3544308
58. González-Chavira MM, Herrera-Hernández MG, Guzmán-Maldonado H, Pons-Hernández JL. Controlled water deficit as abiotic stress factor for enhancing the phytochemical content and adding-value of crops. Scientia Horticulturae. 2018;234:354–360. https://doi.org/10.1016/j.scienta.2018.02.049
59. Gray D, Pallardy S, Garrett H, Rottinghaus G. Acute Drought Stress and Plant Age Effects on Alkamide and Phenolic Acid Content in Purple Coneflower Roots. Planta Medica. 2003;69:50–55. https://doi.org/10.1055/s-2003-37026
60. Gómez-Caravaca AM, Verardo V, Segura-Carretero A, et al. Phenolic Compounds and Saponins in Plants Grown Under Different Irrigation Regimes. In: Polyphenols in Plants. Elsevier. 2014;37–52
61. Niculcea M, Martinez-Lapuente L, Guadalupe Z, et al. Characterization of phenolic composition of Vitis vinifera L. 'Tempranillo' and 'Graciano' subjected to deficit irrigation during berry development. 2015.
62. Deluc LG, Quilici DR, Decendit A, et al.Water deficit alters differentially metabolic pathways affecting important flavor and quality traits in grape berries of Cabernet Sauvignon and Chardonnay. BMC Genomics. 2009;10: 212. https://doi.org/10.1186/1471-2164-10-212
63. Mena P, Galindo A, Collado-González J, et al. Sustained deficit irrigation affects the colour and phytochemical characteristics of pomegranate juice: Sustained deficit irrigation affects phenolics and colour of pomegranate juice. Journal of the Science of Food and Agriculture. 2013;93:1922–1927. https://doi.org/10.1002/jsfa.5991
64. Pék Z, Daood H, Nagyné M, et al. Effect of environmental conditions and water status on

the bioactive compounds of broccoli. Open Life Sciences. 2013;8:777-787. https://doi.org/10.2478/s11535-013-0172-7

65. Su X, Xu J, Rhodes D, et al. Identification and quantification of anthocyanins in transgenic purple tomato. Food Chemistry. 2016;202:184–188. https://doi.org/10.1016/j.foodchem.2016.01.128
66. Ordidge M, García-Macías P, Battey NH, et al. Phenolic contents of lettuce, strawberry, raspberry, and blueberry crops cultivated under plastic films varying in ultraviolet transparency. Food Chemistry. 2010;119:1224–1227. https://doi.org/10.1016/j.foodchem.2009.08.039
67. Kumari R, Prasad MNV. Effects of UV-B Pretreatment on Essential Oil Components, Health Sensory Secondary Metabolites and Antioxidant Potential of Coleus Aromaticus. Pharmaceutical Research. 2017.
68. Manukyan A. Effects of PAR and UV□B radiation on herbal yield, bioactive compounds and their antioxidant capacity of some medicinal plants under controlled environmental conditions. Photochemistry and photobiology. 2013;89: 406-414.
69. Zhang XR, Chen YH, Guo QS, et al. Short-term UV-B radiation effects on morphology, physiological traits and accumulation of bioactive compounds in *Prunella vulgaris* L. Journal of Plant Interactions. 2017;12:348–354. https://doi.org/10.1080/17429145.2017.1365179
70. Fan X, Zang J, Xu Z, et al. Effects of different light quality on growth, chlorophyll concentration and chlorophyll biosynthesis precursors of non-heading Chinese cabbage (Brassica campestris L.). Acta Physiologiae Plantarum. 2013;35:2721–2726. https://doi.org/10.1007/s11738-013-1304-z
71. Deng M, Qian H, Chen L, et al. Influence of pre-harvest red light irradiation on main phytochemicals and antioxidant activity of Chinese kale sprouts. Food Chemistry. 2017;222:1–5. https://doi.org/10.1016/j.foodchem.2016.11.157
72. Chen X, Xue X, Guo W, et al. Growth and nutritional properties of lettuce affected by mixed irradiation of white and supplemental light provided by light-emitting diode. Scientia horticulturae. 2016;200: 111-118.
73. Baek GY, Kim MH, Kim CH, et al. The Effect of LED light combination on the anthocyanin expression of lettuce. IFAC Proceedings Volumes. 2013;46:120–123. https://doi.org/10.3182/20130327-3-JP-3017.00029
74. Li Q, Kubota C. Effects of supplemental light quality on growth and phytochemicals of baby leaf lettuce. Environmental and Experimental Botany. 2009;67:59–64. https://doi.org/10.1016/j.envexpbot.2009.06.011
75. Stutte GW, Edney S, Skerritt T. Photoregulation of bioprotectant content of red leaf lettuce with light-emitting diodes. HortScience. 2009;44:79–82
76. Taulavuori K, Pyysalo A, Taulavuori E, Julkunen-Tiitto R. Responses of phenolic acid and flavonoid synthesis to blue and blue-violet light depends on plant species. Environmental and Experimental Botany. 2018;150:183–187. https://doi.org/10.1016/j.envexpbot.2018.03.016
77. Amoozgar A, Mohammadi A, Sabzalian MR. Impact of light-emitting diode irradiation on photosynthesis, phytochemical composition and mineral element content of lettuce cv. Grizzly. Photosynthetica. 2017;55:85–95. https://doi.org/10.1007/s11099-016-0216-8
78. Bliznikas Z, Zukauskas A, Samuolienė G, et al. Effect of Supplementary Pre-Harvest LED Lighting on the Antioxidant and Nutrition Properties of Green Vegetables. Acta

Horticulturae. 2012;85–91. https://doi.org/10.17660/ActaHortic.2012.939.10
79. Jones RB, Imsic M, Franz P, et al. High nitrogen during growth reduced glucoraphanin and flavonol content in broccoli (Brassica oleracea var. italica) heads. Australian Journal of Experimental Agriculture. 2007;47:1498-1505.
80. Kopsell DA, Kopsell DE, Curran-Celentano J. Carotenoid pigments in kale are influenced by nitrogen concentration and form. Journal of the Science of Food and Agriculture. 2007;87:900–907. https://doi.org/10.1002/jsfa.2807
81. Galieni A, Di Mattia C, De Gregorio M, et al. Effects of nutrient deficiency and abiotic environmental stresses on yield, phenolic compounds and antiradical activity in lettuce (Lactuca sativa L.). Scientia Horticulturae. 2005;187:93–101. https://doi.org/10.1016/j.scienta.2015.02.036
82. Coria-Cayupán YS, Sánchez de Pinto MI, Nazareno MA. Variations in bioactive substance contents and crop yields of lettuce (Lactuca sativa L.) cultivated in soils with different fertilization treatments. Journal of Agricultural and Food Chemistry. 2009;57:10122-10129.
83. Perner H, Rohn S, Driemel G, et al. Effect of Nitrogen Species Supply and Mycorrhizal Colonization on Organosulfur and Phenolic Compounds in Onions. Journal of Agricultural and Food Chemistry. 2008;56:3538–3545. https://doi.org/10.1021/jf073337u
84. Khan MY, Haque MM, Molla AH, et al. Antioxidant compounds and minerals in tomatoes by Trichoderma -enriched biofertilizer and their relationship with the soil environments. Journal of Integrative Agriculture. 2017;16:691–703. https://doi.org/10.1016/S2095-3119(16)61350-3
85. Riahi A, Hdider C. Bioactive compounds and antioxidant activity of organically grown tomato (Solanum lycopersicum L.) cultivars as affected by fertilization. Scientia Horticulturae. 2013;151:90–96. https://doi.org/10.1016/j.scienta.2012.12.009
86. Simonne AH, Fuzere J M, Simonne E, et al. Effects of nitrogen rates on chemical composition of yellow grape tomato grown in a subtropical climate. Journal of plant nutrition. 2007;30:927-935.
87. Taber H, Perkins-Veazie P, Li S, White W, Rodermel S, Xu, Y. Enhancement of Tomato Fruit Lycopene by Potassium Is Cultivar Dependent. HortScience. 2008;43:159–165.
88. Kopsell DA, Barickman TC, Sams CE, McElroy JS. Influence of Nitrogen and Sulfur on Biomass Production and Carotenoid and Glucosinolate Concentrations in Watercress (Nasturtium officinale R. Br.). Journal of Agricultural and Food Chemistry. 2007;55:10628–10634.
89. Barreales D, Malheiro R, Pereira JA, et al. Effects of irrigation and collection period on grapevine leaf (Vitis vinifera L. var. Touriga Nacional): Evaluation of the phytochemical composition and antioxidant properties. Scientia Horticulturae. 2049;245:74–81. https://doi.org/10.1016/j.scienta.2018.09.073.
90. Malejane DN, Tinyani P, Soundy P, et al. Deficit irrigation improves phenolic content and antioxidant activity in leafy lettuce varieties. Food Science & Nutrition. 2018;6:334–341. https://doi.org/10.1002/fsn3.55991.
91. Sahin U, Kuslu Y, Kiziloglu FM, Cakmakci T. Growth, yield, water use and crop quality responses of lettuce to different irrigation quantities in a semi-arid region of high altitude. 2014;9: 195-202.
92. Stagnari F, Galieni A, Speca S, Pisante M. Water stress effects on growth, yield and quality traits of red beet. Scientia Horticulturae. 2014;165:13–22.

https://doi.org/10.1016/j.scienta.2013.10.026.

93. Peña ME, Artés-Hernández F, Aguayo E, et al. Effect of sustained deficit irrigation on physicochemical properties, bioactive compounds and postharvest life of pomegranate fruit (cv. 'Mollar de Elche'). Postharvest Biology and Technology. 2013;86:171–180. https://doi.org/10.1016/j.postharvbio.2013.06.034.

94. Enfissi EMA, Nogueira M, Bramley PM, Fraser PD. The regulation of carotenoid formation in tomato fruit. The Plant Journal. 2017;89:774–788. https://doi.org/10.1111/tpj.13428