Chapter 8

Flavonoid Accumulation Behavior in Response to the Abiotic Stress: Can a Uniform Mechanism Be Illustrated for All Plants?

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Abstract

This review concentrates on two aspects of how total flavonoid content and individual flavonoid compounds change with the perception of environmental stress and the subsequent changes in those metabolites after post-harvest conditions are of the main points of the study. Hereby, along with this study, the flavonoid synthesis or their accumulation with their importance in plants and then in humans is briefly described. According to the literature cited herein, it seems that a universal mechanism concerned with flavonoid accumulation in response to the abiotic stress factors cannot be illustrated. Flavonoid accumulation exhibits different reactions to the different stressors. Flavonoid accumulation behavior not only varies depending on the developmental stage, species and even cultivars of the same species but also post-harvest processes.

Keywords: total flavonoid, abiotic stress, post-harvest processes

1. Introduction

Phenolic compounds are secondary metabolites derived from pentose phosphate, shikimate and phenylpropanoid pathways in plants [1], and a wide range of functions including participation in the regulation of growth and developmental processes and interactions with biotic and abiotic environmental stimuli have been attributed to the those phytochemicals [2]. Of those compounds, flavonoids comprise the large and common group of plant phenolics with more than 5000 different described flavonoids in six major subclasses, including flavones, flavonols, flavanones, flavanols, anthocyanidins and isoflavones [3].

Carbon skeleton of flavonoids occurs from combining of two phenyl ring and a propane chain. Rings of 2-phenyl benzopyran consisting 15 carbons are referred as A, B and C-rings [4] (**Figure 1**). Flavonoids structure's diversity can be classified according to do both major classification and oxidation level [5]. Additionally type, number and binding positions of substitutions binding to aromatic rings cause flavonoids structure's diversity [6].

Since plants are open systems and do not exist in a vacuum, they are continuously interacted with their biotic and non-biotic surroundings. In order to explore what kind of mechanisms underlining the defense against changing environmental conditions and other physiological and biochemical processes for the plant are still great concern of the researchers. Like all living and non-living things in the universe, with each step upwards in the life span, novel properties concerned with quality and quantities of the flavonoid content depending on the environmental, ontogenetic, annual and diurnal variations, which are not present at the current stage of the plant may emerge but it is worthy to underline that these effects are species dependent. The post-harvest practices such as "from wild to domestication," "from fields to shelves" and "from shelves to pharmacy" are also great interest of the consumers for the sustainable healthier life conditions. Hence, universal and uniform mechanisms with respect to the production, accumulation or secretion of the flavonoid have not been proposed yet (**Figure 2**). Two aspects of flavonoid content and their individual compounds can be discussed. One is the content which is directly dependent on plant species itself and with its responses against abiotic stress conditions. This can be simplified as "plant health." The later one is about the changes, which are related to the human consumption. This second aspect can be also simplified as "human health."

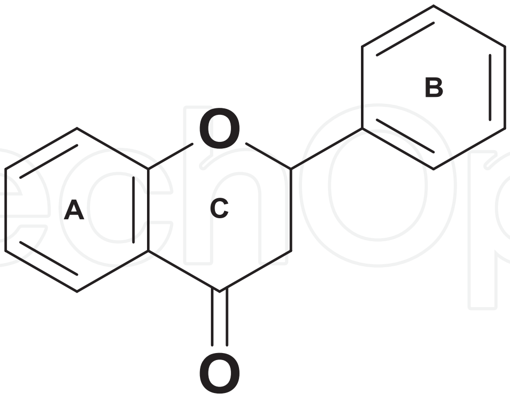

Figure 1. The basic structure of flavonoids.

1.1. Abiotic stress challenges regarding with quantity versus quality: two sides of the coin

As sessile organisms, plants are often exposed to various environmental stress factors. Hence, plants must regulate their growth and development in response to ever-changing

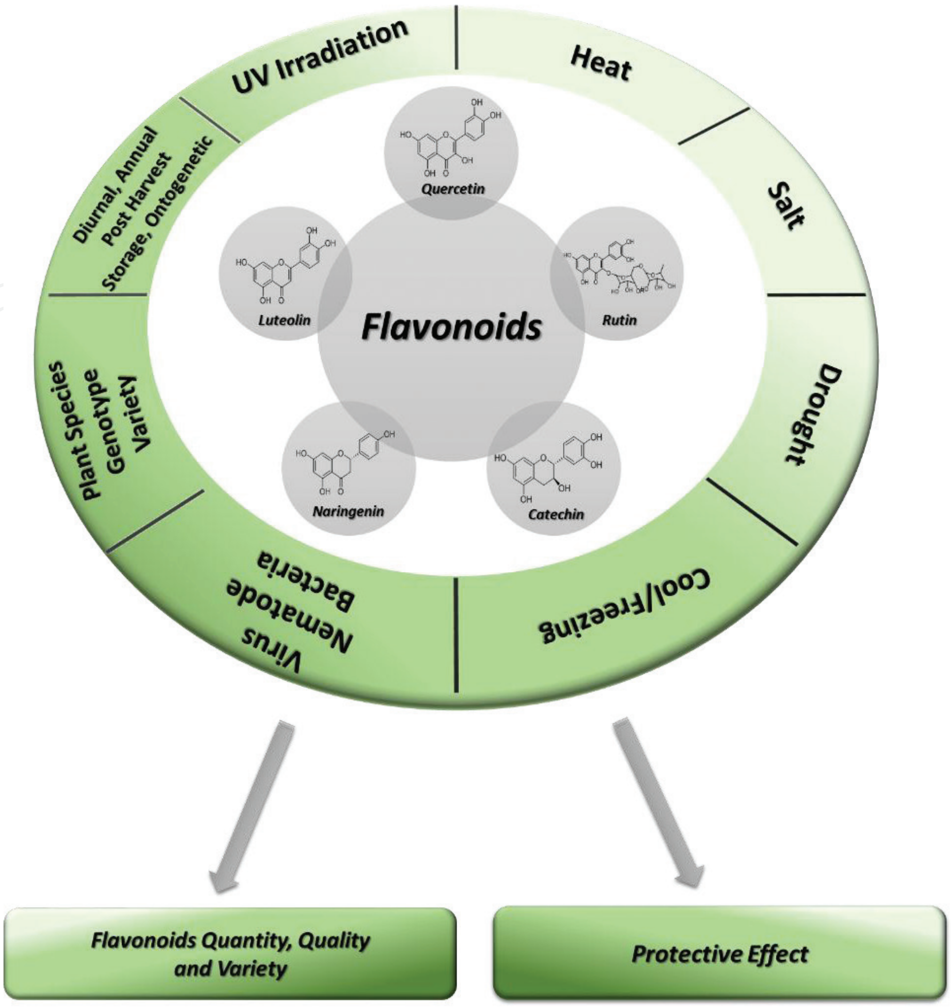

Figure 2. Biotic and abiotic factors affecting flavonoid content and composition in plants.

environmental conditions and their stimuli. Once plants cannot tolerate or overcome the unfavorable environmental conditions, plant growth and development are likely adversely influenced and subsequently significant loss of crop yields [7, 8]. Along with the stress conditions, plant behavior may change with respect to the secondary metabolite synthesis, production, secretion and storage when subjected to the abiotic stress factors [9]. Some secondary metabolite synthesis, enzyme activities and soluble substance accumulation were positively influenced by abiotic stress conditions. These are considered as consequences of plant adaptive strategies concerned with establishment of some changes allowing to the plant to sustain its life under ever-changing conditions.

Many results concerned with total flavonoid and their individual compounds in response to the different stressors. For total flavonoid content, increases were determined [2, 10–14, 16, 17, 19, 20] whereas decreases were found [15, 18, 21] under different stress conditions.

Based on the literature review, we cannot deduce and explain the flavonoid accumulation or their compound profile using one simple sentence. The stress effect is compound specific. A uniform mechanism for compound profile variation cannot be illustrated [22]. Furthermore, the flavonoid accumulation is likely dependent stress factors, frequency, duration and timing.

1.2. Is it adaptive strategy to sacrifice the primary metabolites through increases in secondary metabolite production against stress conditions or high efficiency use of secondary metabolite biosynthesis pathway?

As previously mentioned, pentose phosphate, shikimate and phenylpropanoid pathways are of the three pathways in plants, which are responsible for biosynthesis of phenolic compounds [1]. Shikimic acid is a key intermediate in the synthesis of both aromatic amino acids and phenylpropanoids, and oxidative pentose phosphate pathway is of the precursors for the biosynthesis of aromatic amino acids, lignin and flavonoids [23]. Regulation and expression of the genes on the pathways have been well elucidated, but the pathway compartmentation is not yet known [24]. Some of the synthesis-associated genes and enzymes involved in phenolics biosynthesis were characterized in Arabidopsis (*Arabidopsis thaliana*), maize (*Zea mays*) and petunia (*Petunia hybrid*). Also *Fragaria* spp. has been studied for their genes and enzymes ([25–30]; cited by [24]). In order to determine which pathway is preferred for biosynthesis secondary metabolites under abiotic stress factors, the expression of protein or enzymes associated with synthesis of secondary metabolites in the pathways should be determined and then compared with the control group-not stressed group. Determination of the long or short distance metabolic pathways or high or low energy cost pathways in response to the stress is also great concern to understand plant behavior and signaling.

Stressors bring about quantitative and qualitative changes in plant metabolites. Of those, in general, biosynthesis of proteins in the plant leaves is suppressed, triggering the changes at gene expression levels and subsequently the synthesis of new proteins. For the lipid content and composition, the disturbances concerned with fatty acid composition, especially changes in fatty acid carbon chains. The variations in the lipid composition influence membrane lipids and transport functions of membranes. Furthermore, accumulation of the compatible solutes is of the responses against drought, high temperature or high salinity, maintaining the osmotic adjustment and turgor regulation [31].

Plant secondary metabolites have been considered or often referred to as metabolites which are not fundamentals for sustainability of basic plant life processes. However, the crucial and wide range roles of secondary metabolites have been understood. The accumulation of phenylpropanoids increased in response to the environmental stress including pathogen attack, UV-radiation, high light, nutrient deficiency etc. According to Bryant et al. [32] hypothesis, an exchange occurs between carbon and biomass production or formation of defensive secondary metabolites, proposing that secondary metabolites are involved in protective processes of plants in response to stressors. For example, phenyl amide formation and accumulation of anthocyanin and polyamines have been reported as a response to the environmental stresses [33, 34].

1.3. Over accumulation of flavonoid versus reactive oxygen species? Non-enzymatic antioxidant system but any relations with the enzymatic antioxidant system (SOD, CAT, APX)?

Flavonoids are secondary metabolites synthesized by general phenylpropanoid pathway in plants [35]. They have been considered as a secondary (non-enzymatic) reactive oxygen species scavenging system in plants and humans [36]. Flavonoids exhibit direct scavenging of reactive oxygen species [36] one of the ways scavenging reactive oxygen species, flavonoids can easily donate hydrogen atom. Thus, while reactive oxygen species are inactivated by flavonoids, flavonoids return to phenoxyl radical [37]. Flavonoids phenoxyl radical can react with other free radicals and then acquiring a stable quinone structure [38]. The other way of scavenging reactive oxygen species, flavonoids return to phenoxyl radical by donating hydrogen atom at the first step. At the second step, phenoxyl radical scavenge other high reactive radical (R•) by radical-radical termination. Flavonoid phenoxyl radical is highly stabile radical due to presence of a resonance structure redistributed the unpaired electron on the aromatic core [39] **(Figure 3)**.

1.4. The possible protective defense roles of flavonoids in response to UV light have been documented in many studies but what happens if the flavonoid and other pigments cannot completely block the sunlight transmission?

UV light from sunlight is primarily required to perform photosynthesis as basic function and developmental process such as de-etiolation, phototropism and flowering of the plants [40, 41]. But interestingly, the UV light causes damage to DNA, protein and cell membranes of the plants, because, as sessile organisms, plants are more exposed to the UV-light. Subsequently, normal growth and development of plants are retarded [41]. Short-wavelength UV light is grouped into three categories. Of those, UV-A (315–400 nm) directly reaches the earth's surface, and UV-B (280–315 nm) and UV-C (100–280 nm) are blocked by the ozone layer. However, a small quantity of UV-B reaches the earth's surface because of ozone layer depletion and subsequently causes DNA damages [42].

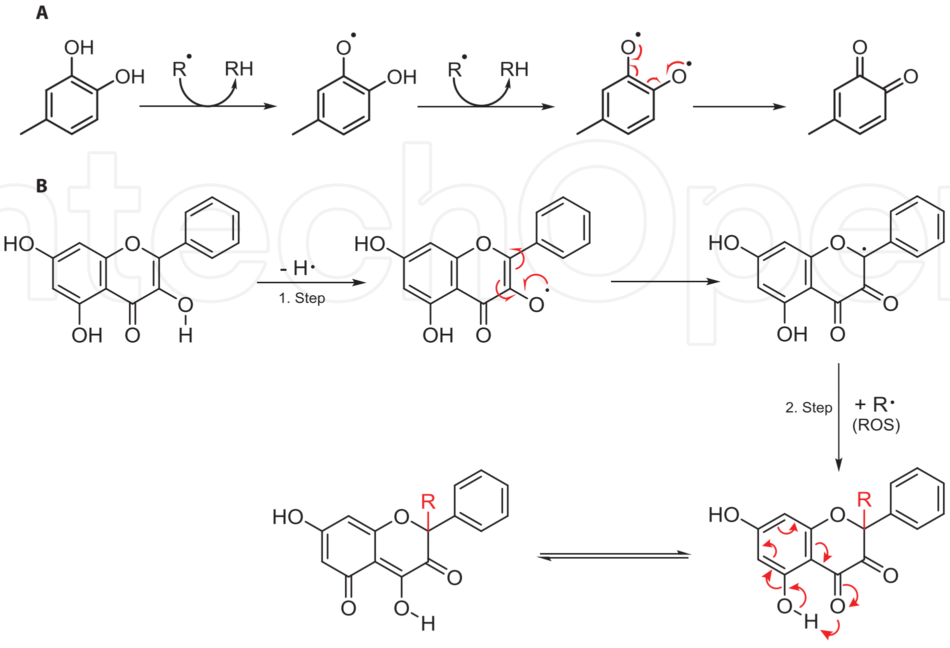

Figure 3. Scavenging of ROS by flavonoids, reproduced from Pietta [38] (A) and reproduced from Amic [39] (B).

UV-B has highest energy of UV light that reaches the earth surface [43]. Although the high level of UV-B causes damage to biomolecules, low level of UV-B regulates morphology, development, phycology and biochemical compositions [44]. While long wavelengths UV light-induced regulation is provided with photoreceptors including phototropins, neochromes, phytochromes, rhodopsins and cryptochromes [45] (**Figure 5**), UV-B-induced regulation is provided with UV RESISTANCE LOCUS 8 (UVR8) receptor protein [46]. UVR8 directly absorbs UV-B radiation and induces the transcription of flavonoids biosynthesis genes by orchestrating UV protective gene expression responses [47].

Flavonoids are synthesized with phenylpropanoid pathway in plant and the pathway includes enzymes such as phenylalanine ammonia lyase (PAL), 4-coumaroyl: CoA ligase (4CL), Chalcone Synthase (CHS), Chalcone Isomerase (CHI), Flavone Synthase (FS) and Dihydroflavonol-4-Reductase (DFRA) [48]. CHS is key enzymes for flavonoid biosynthesis pathway. CHS catalysis condensation reaction of Coumaroyl CoA and Malonyl CoA.

Upregulation of CHS genes transcription in response to the several stressors was reported to induce flavonoid biosynthesis [49]. UVR8 protein interacts with the WD40-repeat domain of COP1 after perception of UV-B light that is one of the stressors [50]. Consequently, UVR8-COP1 complex leads to activation of HY5 gene expression [47]. HY5 proteins as a transcription factor play an enhancing role for UV-B induced-CHS gene expression during seedling development by binding to a conserved G-box sequence [51, 52]. Thus, flavonoids that accumulate in upper epidermis layer specially absorb a large amount of 280–340 nm wavelengths [53]. Thus, the flavonoids accumulated in upper epidermis layer protect the internal tissues of leaves and stems against UV-B. Since the synthesis of kaempferol is deficient in chalcone flavone isomerase mutant tt4 *A. thaliana*, the plant exhibits high sensitivity to UV light [54]. Along with the absorption of UV light with chromophore group of flavonoids, flavonoids may undergo a transformation. While flavonoids with aromatic chromophore absorb light in the 250 nm region of UV spectra, flavonoids contain carbonyl that are conjugated with the aromatic ring chromophore absorb light in the 350 nm region of UV spectra. The transformation of flavonoids after of UV light absorption in vitro conditions is illustrated in **Figure 4** [55].

It is worthy to note that the flavonoids are not unique functional UV-blocker absorbing all UV-B irradiation but the other protective roles of flavonoids cannot be ignored in spite of deficient in absorption of all UV-B irradiation since UV-B induced increase in the quantity of flavonoids has been reported, suggesting that flavonoids may exhibit functions including signal molecules, antioxidant molecules, defensive compounds, allelochemicals [56] after UV-B exposure in plant.

When the UV light cannot be completely blocked via defense system apparatus of the plants, UV light reaches to DNA, resulting in formation of cyclobutene pyrimidine dimers (CPDs) and 6-4 photoproducts (6-4PPs) on DNA [57, 58]. There are two mechanisms repairing the photoproduct that can inhibit transcription and replication and induce mutations [48]: first one is photolyases enzyme, and the other one is nucleotide excision repair mechanism [60]. CPD Photolyase gene expression is regulated by a wide spectrum of light, including far-red, red and blue light [61]. But recent studies reported that photolyase gene expression was regulated by UVR8 receptor protein and the regulation mechanism remains poorly understood [62]. In order to exhibit DNA repair activity, photolyase enzyme needs UV-A light [63] but

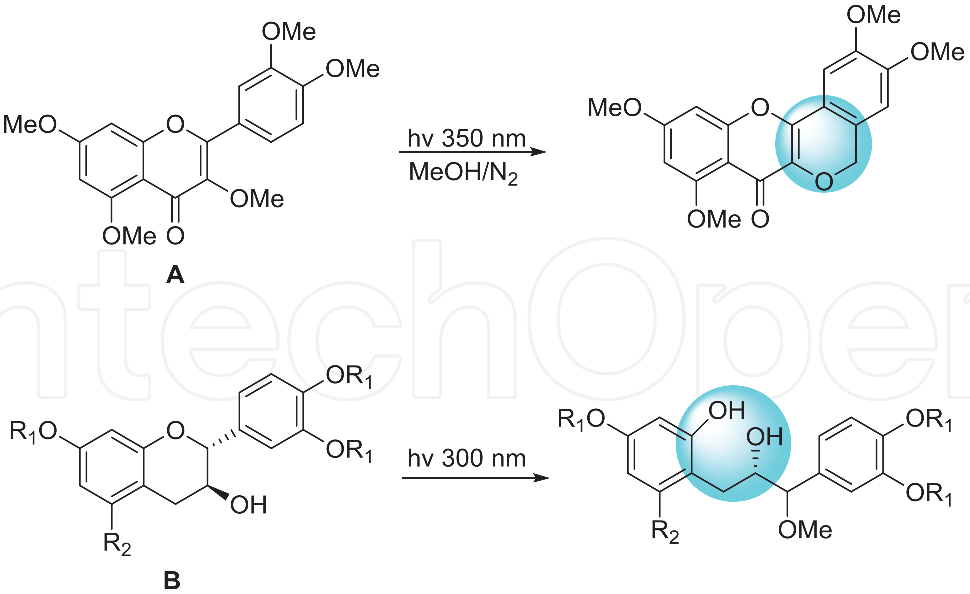

Figure 4. Photochemistry of quercetin pentamethyl ether (A) and photochemistry of flavan-3-ols (B) [55].

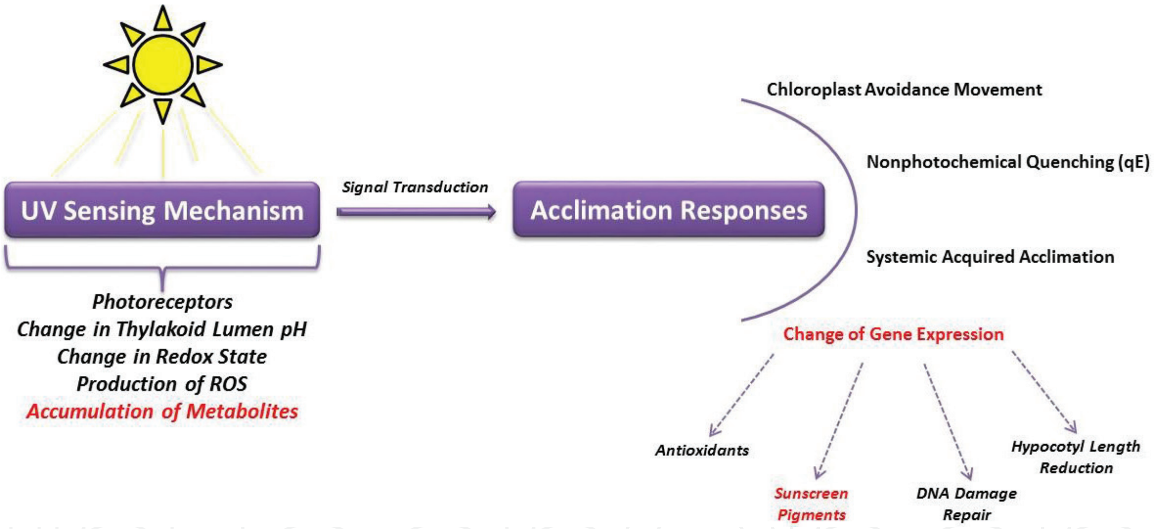

Figure 5. UV light perception, signaling and responses in Arabidopsis (scheme adapted from Li et al. [45]).

the light is not required for the activity of dark repair called nucleotide excision repair mechanism. Recently, photolyase and nucleotide excision repair mechanism in *A. thaliana* were well described [60].

1.5. The fate of the flavonoid-enriched crop plants through the food chain: terminal

Any direct and indirect biotic or abiotic stressors or their combinations at certain time or simultaneously influence the phytochemistry and subsequently the changes orchestrate the plant protection and plants' biological activities. Herewith, phytochemistry of a plant can be regarded as protective roles for plants against stressors and health-promoting properties for humans. The quality of the crop plants is a combination attributed to their composition and contents that shape the commodity value for human consumption. Since humans are, in general, considered to be at the top of the food chain, the terminal of the flavonoid-enriched/poor crop plants would be the human, resulting the health standards.

Nothing stays the same as its former form and the changes are inevitable for all living and non-living things. Therefore, numerous studies—as listed in **Table 1** but not limited in this chapter—have been performed in order to keep the stability or dynamic changes of flavonoid content and its compound. Of those studies, atmosphere conditions are of great interest for long-term storage and subsequently essential for keeping biological value of the crop. In the study reported on *Allium cepa* var. *calonicum* Backer) by [64] (see the detail in **Table 1**), the highest content after storage at conditions with gas composition of 5% CO_2 + 5% O_2 was achieved. Two major compound—quercetin 3,4′-di-O-glucoside and quercetin 4′-O-glucoside (spiraeoside)—exhibited an increase [64]. Effect of carbon dioxide-enriched atmosphere on total

Storage conditions/ cultivars/harvest times	Total flavonoid content	Plant species	Researchers
Different storage temperatures (0, 2, 4, and 6 + 2°C) + 5%, 10%, 20% or 0.03% CO_2	Total flavonoid content	*Phoenix dactylifera* L.	[54]
Storage conditions were at 50, 25, 4, and −20°C	Total flavonoid content	*Anemopsis californica*	[59]
Freeze and thermal drying	Total flavonoid content	*Oxycoccus palustris Pers.*	[60]
Stability testing at different temperatures	Flavonoid glycosides	*Calendula officinalis* and *Betula* sp.	[61]
Storage at 27°C for 9 days	Total flavonoid content	*Paluma cultivar*	[62]
Temperature and storage time	quercetin-3-rutinoside, quercetin-3-glucoside, quercetin-3-ᴅ-galactoside	*Sorbus aucuparia*	[63]
Subunit parts of the rhizome during the thermal drying process under treatment temperatures ranging from 40 to 120°C	Mangiferin, iristectorigenin A, irigenin, irilone dichotomitin	*Belamcanda. chinensis* (L.) DC.	[64]
Cultivars and storage conditions	Total flavonoids	*Pistachia vera* L.	[65]
Normal atmosphere and 0% CO_2 + 21% O_2, (2) 5% CO_2 + 5% O_2, 5% CO_2 + 2% O2, 2% CO_2 + 5% O_2, 2% CO_2 + 2% O_2	Quercetin 3,4′-di-O-glucoside, quercetin 3-O-glucoside (isoquercetin), quercetin 4′-O-glucoside (spiraeoside)	*Allium cepa* var. *calonicum* Backer	[64]
At ambient temperature (about 25 ± 2°C) in a refrigerator (4 ± 0.2°C) and sampling days 0, 2, 4, 6, 8, 10, 12, 14	Total flavonoid content	*Juglans sigillata*	[67]

Table 1. Continue

Table 1. Continued

Storage conditions/ cultivars/harvest times	Total flavonoid content	Plant species	Researchers
Different cultivars	Spiraeoside (quercetin-4′-O-β-ᴅ-glucoside), rutin and quercetin	*Allium cepa*	[70]
Different plant parts, developmental storage and storage durations (1, 2, 3 and 4 days)	Total flavonoid content	*Clinacanthus nutans* (Burm. f.)	[66]
Storage at 6, 16 and 25°C for 6 days.	Flavonol	*Fragaria ananassa* Duch.	[68]
Different temperatures 25 ± 2°C (room temperature) and 10 ± 1°C (refrigerator) at different time of intervals (1st, 5th and 10th day)	Total flavonoid content	*Brassica rapa* L.	[71]
Storage for 0–7 months at 25 and 37°C	Total flavonoid content	*Oryza sativa* (milled rice)	[72]
Light ((photosynthetically active radiation (PAR) level of 56 ± 0.5 μmol m^{-2} s^{-1} (H); 31 ± 0.2 μmol m^{-2} s(L), or in dark (D). and maturity (0–5% red, 20% red, 50% red, 80% red, 100% red)	Ellagic acid, quercetin, kaempferol and cyanidin 3-glucoside	*Rubus ideaus* L.	[69]
Storage for 7, 15 and 30 days at 4, 22 and 35°C	Catechin, epicatechin, procyanidins B1-B4 and total flavonoids	Cocoa powder	[73]
Industrially squeezed, pasteurized, concentrated and stored under refrigeration (4°C) and at room temperature (20°C)	Flavanone-7-O-glycosides, fully methoxylated flavones	*Citrus clementina* Hort. ex Tan. *C. reticulata* Blanco × *C. sinensis* Osb., *C. sinensis*	[74]
Cultivar and storage conditions	Total flavonoid content	*Malus domestica* Borkh.	[75]

Table 1. Various studies concerned with the post-harvest processes and different cultivars influence on flavonoid content.

flavonoid content changes in *Phoenix dactylifera* L. fruit in response cold storage was tested and the fruits stored under low temperature conditions (0°C) or relatively high CO_2 concentration (20% CO_2) was reported not to exhibit any chilling or CO_2 injury symptoms. Modified conditions have been reported to extend not only the date storability and then fruit quality but also magnify the maintenance of fruit quality in response to the cold temperature storage [65].

Furthermore, the influence of different plant parts, developmental storage and storage durations (1, 2, 3 and 4 days) [66], different temperature and sampling days [67], different storage days [68], Light (photosynthetically active radiation (PAR) level and maturity [69] has been examined to indicate that the there is no constant stability or dynamics of flavonoid content and its compounds in quantity and quality.

2. Conclusion

As a conclusion, since plants are open systems and do not exist in a vacuum, they are continuously interacted with their biotic and non-biotic surroundings. Based on the literatures cited in the present chapter, a universal mechanism with respect to the accumulation behavior of flavonoid cannot be illustrated even the flavonoids commonly exhibit a tendency toward increase in response to the unfavorable conditions. Up to our best research, flavonoid accumulation behavior varies depending on the developmental stage, species and even cultivars of the same species. It also exhibits different reaction to the different stressors.

Beyond physiological aspect for the plants for their survival mechanism, plants are also sources for other living organisms. The quality and then biological efficacy of the flavonoid containing crops are great issue for human beings. According to the literature cited herein, the fate of the flavonoids containing herbal products including bulbs, leaves, fruits etc is influenced by the storage temperatures, storage time, modified storage conditions, cultivars, different parts and subunit parts of the plant, light and maturity.

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