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Review Article

Seasonal Variations in Dietary Flavonoid Content of Edible Plants

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Abbreviations

CE Catechin equivalent
dw Dry weight
fw Fresh weight
QE Quercitin equivalent
RE Rutin equivalent
ROS Reactive oxygen species
SAW Summer-autumn-winter
SS Spring-summer
UV Ultraviolet

Abstract

Flavonoids are ubiquitous compounds commonly found in vegetables, fruits and other plant foods. Although not considered nutrients per se, consumption of various flavonoids is associated with established health benefits. Their biosynthesis, and therefore concentrations, are influenced by genetic, geographic and environmental conditions. Flavonoid content in foods can be seasonal, potentially influencing their total intake and biovailability. In view of the potential role of flavonoids in human health, studies published over an 11-year period (2009 to 2020) investigating links between flavonoid content and season in edible and medicinal plants, were examined. The limited studies to date focus on a small range of plant species. Within this, there is consistent evidence that flavonoid content varies according to season, particularly in relation to plant genotype and environmental conditions such as temperature, geographic location, light conditions/UV radiation and drought/water stress. Seven studies detected highest total flavonoid content at the end of winter and lowest in mid-autumn. From the included studies, rutin was the most commonly studied flavonoid, showing its highest levels in both spring and winter. These findings suggest studies on flavonoid intake should include seasonal considerations. Further studies on seasonal variations of common dietary flavonoids are warranted to enable such studies.

Keywords: Flavonoids, availability, seasonal variability, environment

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INTRODUCTION

Flavonoids are non-nutrient components found in fruits and vegetables, and are integral to plant physiology (1, 2). Once consumed, these compounds can also influence human health by protecting vitamins, enzymes and fats from oxidation and consequently reducing their degradation and losses(1, 2). Many of the beneficial health effects of flavonoids are attributed to antioxidant properties such as scavenging of free radicals, prevention of lipid peroxidation and chelating metal ions (1, 3). The quantities required for such effects require consistent intakes over prolonged periods of time as their bioavailability and absorption is relatively limited. It is important to note that several disease processes can be exacerbated when there is a critical surplus of reactive oxygen species (ROS) exceeding antioxidant defences(4), particularly over an extended period. Flavones, catechins and components of the flavonoid classes: quercetin, myricetin and rutin (found in fruits, nuts, vegetables, cereals, tea and wine) are particularly effective *in vitro* at minimising potential damage due to excessive accumulation of ROS(2, 5). Flavonoids may also assist prevention of neurodegenerative diseases such as Alzheimer's and Parkinson's

disease(2) and intake of flavonoid-rich fruit (i.e. blueberries) may affect various measures of cognition(6). Further, various anti-inflammatory(7), anti-microbial and hepatoprotective properties(1) are associated with increased flavonoid intakes.

It is well established in plants that the functional roles of flavonoids are predominately affected by interactions with the environment(1). Plant fertility, growth and development are influenced by flavonoids which act as visual attractants for pollinators, as photoreceptors, and provide protection against pathogens and environmental stresses such as solar ultraviolet (UV)-B radiation, drought, water stress and photooxidative damage (2, 8). The content and composition of flavonoids vary in response to various stressors, influenced by genetics and environmental conditions such as geographical location, presence of pests or pathogens and seasonality (9-11).

Flavonoid bioactivity can vary according to the specific time of the year (8, 9), thus implying a link between seasonal factors, peak availability and potential health implications. Several seasonal studies have investigated environmental influences on flavonoid availability and their variability in a defined range of plant varieties, focussing on plants used for medicinal purposes (3, 10, 12-16). However, studies investigating seasonal availability of flavonoids in plants commonly consumed as foods are still relatively scarce. The accumulating evidence of flavonoid consumption influencing human health has relied on annualised consumption estimates. Given emerging evidence that flavonoid content is influenced by environmental conditions this review investigates research to date on the seasonal availability of various flavonoids to provide context to population studies on flavonoid-health associations.

METHODS

Literature search strategy

The search frame for this review was for published, peer-reviewed articles from January 2009 through August 2020 using key terms *"flavonoids", "polyphenols", "seasonal"* and *"variation"* in the Medline (PubMed) electronic database. Two hundred and forty articles were found through this search strategy in which titles were firstly screened for relevance to biochemical compounds and seasonality in plants (Figure 1).

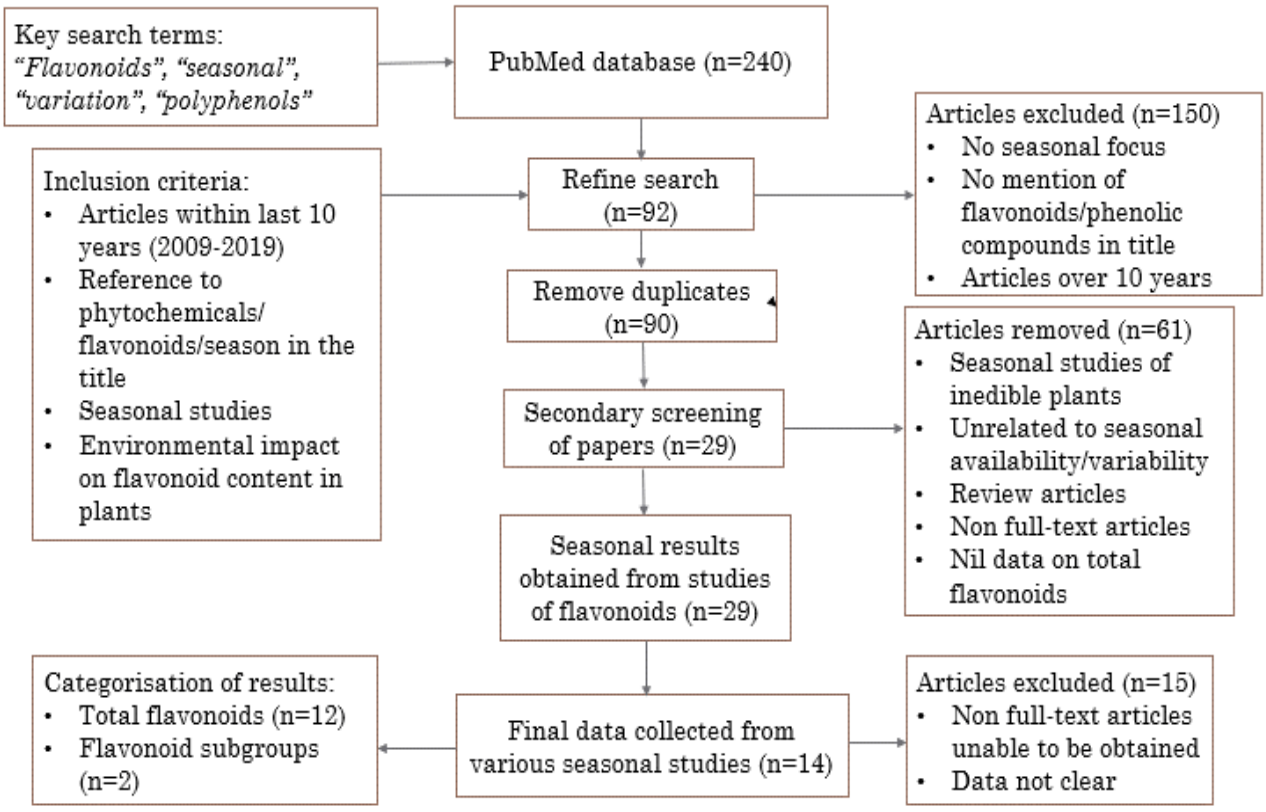

Fig. 1. Flow diagram describing the course of research undergone for the collection of included articles

Table 1: Comparison of total flavonoids in edible plant varieties showing the extent of flavonoid content variation across seasons (seasons adjusted to country of study)

Plant variety Total flavonoids	Spring	Summer	Autumn	Winter
Broccoli[a](Santos, 2017)		12.1	3.3	
Portuguese kale[a] (Santos, 2017)		12.0	8.1	
Savoy cabbage[a] (Santos, 2017)		4.1	4.1	
White cabbage[a] (Santos, 2017)		2.5	3.2	
Portuguese tronchuda cabbage[a] (Santos, 2017)		10.5	5.0	
Turnip leaves[a] (Santos, 2017)		5.5	8.7	
Turnip roots[a] (Santos, 2017)		1.6	2.0	
Prickly pear[b] (Cosmulescu, Trandafir and Nour,2014)	1.53 - 3.02	0.90-3.43		
Broccoli florets[a] **(**Ferreyra, Rius and Casati,2012)	3.21		2.410.74	
Broccoli stems[a] (Ferreyra, Rius and Casati,2012)	0.80			
Broccoli leaves[a] (Ferreyra, Rius and Casati,2012)	6.70		8.14	
Brown algae (from SMG)[c] (Shi et al.,2017)				
Brown algae (from SMA) [c](Shi et al.,2017)		6.02		6.75
Peach blossoms [c](Field, Lee and Holbrook, 2001)		4.21		4.10
Mountain Hawthorn (root) [c](Pandey et al., 2016)	93.03-44.06.		18.44 - 6.64	
Mountain Hawthorn (twig) [c](Pandey et al., 2016)	19.07	31.75	29.70 - 16.04	
Mountain Hawthorn (leaf) [c](Pandey et al., 2016)	10.32	23.09	29.52 - 25.89	
Mountain Hawthorn (fruit) [c](Pandey et al., 2016)	17.94	28.59	34.81 - 29.23	
Chicory family:(Cartea et al., 2010)		13.17		
Cichorium intybus l.[b](Cartea et al., 2010)			0.480 - 0.948	
Sonchus asper l.[b](Cartea et al., 2010)	0.480-0.594		0.594	
Picris hieracioides l.[b](Cartea et al., 2010)	0.699 - 0.747		0.445 - 0.890	
Tephrosia purpurea (Linn.) Pers. **(pea family)** [c](Cartea et al., 2010)	0.418 - 0.630			
Cayenne cherry leaves [c] (Santos et al.,2011)			21.88	
Baccharis dentata (aster family)[b] (Jakovljevic, Stankovic and Topuzovic, 2013)	19.77; 15.03; 15.17	18.92	12.20; 11.37;	15.17
Walnut green husks (Dai et al., 2014; Munialo et al., 2019)	14.01	15.53; 16.07; 12.53	18.90 20.10	17.47; 16.03; 21.73 25.13
Leafy liverworts: [c](Sartor et al., 2013)		25.19		
F. himalayensis [c](Sartor et al., 2013)	1.85		0.52	
C. gollani [c](Sartor et al., 2013)				16.68
S. crenulata [c](Sartor et al., 2013)			8.39	18.07
Eucommia ulmoides Oliver (small tree) [c] (kumar and Pandey, 2013)			5.98	20.77
	17.5 - 21.3		7.82)	
			9.5 - 14.5	
		11.4 - 14.6		

Abbreviations: [a] = values are represented as Catechin Equivalents (mg/g), [b] = values are represented as quercetin equivalent (mg/g); [c] = values are represented as Rutin Equivalent (mg/g); SS = spring-summer, SW = summer-winter, SA = summer-autumn, AS = autumn-spring, WS = winter-summer, SMG = São Miguel Island, SMA = Santa Maria Island

A resulting ninety-two articles pertained to a seasonal or flavonoid/phenolic focus published within the stated time frame. After duplicate s were removed, ninety articles were screened to remove non-food plants, review articles, or data unrelated to total flavonoid content resulting in 29 articles. The full papers of eleven of these studies could not be sourced for review and four out of 18 studies had different missing data. Thus, the remaining 14 studies were then grouped by total flavonoids (Table 1) and flavonoid subgroups (Table 2). Seven studies

Determination of seasons

Seasons were determined by identifying the country in which the study was conducted and the months of the year for sample collection. Studies using terms such as "dry and rainy seasons" either specified relevant months or were found via internet search for the specified country. Data were then organised by season (spring, summer, autumn, winter), and across plant varieties and time of year. Flavonoid subclass data were attributed to season in Tables 1 and 2, to visualise the variability of flavonoid contents across seasons (Tables 1 and 2).

Table 2: Seasonal variation of flavonoid subgroups throughout the year from edible plant varieties (seasons adjusted to country of study)

Flavonoid subclass	Food source	Spring	Summer	Autumn	Winter
Anthocyanin (Marrelli et al., 2018)			**0.05 - 0.34 µgQE/100g d.m**		**0.12-0.26µgE/100gd.m**
Rutin			**48.6, 98.9, 0.43**		
Rutin(Jakovljevic,Stankovicand Topuzovic, 2013)	**B.dentata**	**1.465 mg/g d.m.**	**mg/g f.w.**	**1.596 mg/g d.m.**	**2.677 mg/g d.m.**
Rutin (Dai et al, 2014)	**Walnut Green Husks**	**28.49 - 6.00 mg/100g 13.9 mg/g**	**1.802 mg/g d.m. 1.66 - 4.85 mg/100g 11.5 - 9.8 mg/g**		
Rutin				**10.3 - 10.6 mg/g**	
Myricetin			**1.15, 1.78, 1.11**		
Myricetin (Dai et al, 2014)	**Walnut Green Husks**	**7.79 - 6.68 mg/100g**	**mg/g f.w.**		
Pinocembrin (Luo et al., 2016)				**0.255 -**	**0.098 - 0.121 mM**
3-O-methylgalangin (Luo et al., 2016)	**H.stenophyllum**	**0.151 -**	**0.212 - 0.141 mM**	**0.098 mM**	**0.252 - 0.222 mM**
Kaempferol3-O-rhamnoglucoside	**H.stenophyllum**	**0.172 mM**	**0.109 - 0.141 mM**	**0.118 -**	**0.68 ng/mg**
Kaempferol(akovljevic,Stankovicand,Topuzovic, 2013)		**0.116 - 0.66 mM**	**3.21 ng/mg**	**0.218 mM**	**0.099 mg/g d.m.**
Quercetin-3-O-rhamnoglucoside	**B.dentata**		**0.537 mg/g d.m.**		**8.99 ng/mg d.e.**
Quercetin (Jakovljevic,Stankovicand Topuzovic, 2013)	**B.dentata**	**0.583 mg/g d.m.**		**0.215 mg/g d.m.**	
Apigenin (Jakovljevic,Stankovicand Topuzovic, 2013)	**B.dentata**	**26.66 ng/mg d.e.**	**0.38 - 0.27 mg/g 0.525 mg/g d.m. 1.75 – 2.93 mg/100g**		**0.078 mg/g d.m.**
Catechin (Dai et al, 2014)	**Walnut Green Husks**			**0.33 - 0.42 mg/g**	
Epicatechin (Dai et al, 2014)	**Walnut Green Husks**	**0.62 mg/g 0.580 mg/g d.m. 3.65 - 3.33 mg/100g 0.72 - 0.66 mg/100g**	**0.45 - 0.76 mg/100g**	**0.210 mg/g d.m. 2.65 – 3.34 mg/100g 0.50 - 0.53 mg/100g**	

RESULTS

Season and flavonoid content

Several studies have shown that seasonal flavonoid contents vary according to type and part of the plant, the characteristics of the environment and the growth stage [3,19,24]. *Brassica* vegetables (i.e. broccoli), contained a higher average total flavonoid content (12.1 mg/g catechin equivalent (CE) dry weight (dw))

during the spring-summer period compared to the summer-winter period (3.13 mg/$g_{CE\ dw}$)(3) (Table 1). Similarly, Portuguese kale (also from the *Brassica* family), had higher total flavonoid content in spring-summer (12.0 mg/$g_{CE\ dw}$) compared to summer-winter (7.4 mg/g_{CEdw} .)(3). Broccoli florets and stems had higher flavonoid content during spring (3.21 mg/g_{CE}, 0.80 mg/g_{CE}) compared to autumn (2.41 mg/g_{CE}, 0.74 mg/g_{CE}) in another study(12). Broccoli leaves produced the highest total flavonoid content of its plant parts in both spring and autumn, with a greater total flavonoid content produced in autumn compared to spring (8.14 mg/g_{CE}, 6.70 mg/g_{CE})(12). The potential health implications of these variations may be minimal since *Brassica* vegetables (broccoli, brussels sprouts, cabbage, cauliflower and kale) are generally minor dietary sources of flavonoids (24).

Autumn season and flavonoid content

Autumn appears to be the most plentiful season for flavonoid content in the reviewed studies (Table 1). Autumn yielded the highest total flavonoid contents in Mountain Hawthorn twig, leaf and fruit, with the fruit having the highest flavonoid content (34.81 - 29.23 mg/g rutin equivalent (RE)) compared to summer (13.17 mg/g_{RE})(25). C*rataegus sp*., commonly known as hawthorn, is native to Europe, Asia, and North Africa, where the berries are used both for food and medicinal purposes, the herbal medicinal having beneficial effects on the cardiovascular system (26). Total flavonoid content increased rapidly in early autumn but reduced in mid-autumn(25). This is similar to *Tephrosia purpurea* (Linn.) Pers, related to the pea family, which also manifests maximum total flavonoid content in autumn (21.88 mg/g_{RE}) compared to summer (18.92 mg/g_{RE}) or winter (15.17 mg/g_{RE})(9).

Several plants yield higher flavonoid concentrations in the cooler months of winter. Two cabbage varieties differed from the general spring-summer (SS) favouring *Brassica* family with equal or greater total flavonoid content in the summer-autumn-winter (SAW) period(3). This was observed for both savoy (4.1 mg/g_{CEdw}. (SS), 4.1 mg/g $_{CEdw}$ (SAW)) and white cabbage (2.5 mg/g_{CEdw} (SS), 3.2 mg/g_{CEdw} (SAW)), but not for Portuguese tronchuda cabbage(3). Higher total flavonoid content was also found in SAW in turnip leaves (8.7 mg/g_{CEdw}) and roots (2.0 mg/g_{CEdw}) compared to SS (5.5 mg/g_{CEdw}, 1.6 mg/g_{CEdw})(3). A study in leaves of cayenne cherry (*Eugenia uniflora* L. (Myrtaceae)) identified significantly higher flavonoid content in winter (21.73 mg/g_{RE}) compared to autumn (18.90 mg/g_{RE}), spring (15.17 mg/g_{RE}) and summer (12.53 mg/g_{RE})(27). These results also showed that flavonoid levels were directly correlated ($p<0.01$) with evaporation and inversely correlated ($p<0.05$) with humidity and cloudy weather(27). Flavonoid content increased in the dry season, possibly due to increased daylight (27). A Brazilian study identified the highest flavonoid content in *Baccharis dentata* of the aster family during both the wet (summer) and dry (winter) periods (25.19 mg/g quercitin equivalent (QE), 25.13 mg/g_{QE}) compared to spring (14.01 mg/g $_{QE}$) and autumn (20.10 mg/g $_{QE}$)(17).

Specific flavonoids and seasonal variation

In total, seven studies focussed entirely on or included seasonal variation of specific flavonoids, including rutin, anthocyanins, myricetin, pinocembrin, 3-*O*-methylgalangin, k aempferol 3-*O*-rhamnoglucoside, quercetin-3-*O*-rhamnoglucoside, apigenin, catechin and epicatechin (Table 2)(11, 17-23). Rutin was the most commonly studied flavonoid(11, 17, 18, 23), showing highest content in spring in two Chinese studies (18, 23) on *Eucommia ulmoides oliver* leaf and Walnut green husks, and winter in a Brazilian study(17) on *Baccharis dentata(Vell.) G.M. Barroso*. Rutin also had the highest abundance in walnut leaves in mid-summer in a Romanian study (98.9 mg/100g fresh weight (fw)) compared to the beginning (48.6 mg/100g_{fw}) and end of the season (43.6 mg/100g_{fw})(11). This was similar for myricetin, (178.0 mg/100g_{fw} in mid-summer compared to season start (115.6 mg/100g_{fw}) and end (111.4 mg/100g_{fw})(11).

DISCUSSION

Genotype and environmental interactions in Brassicas

This review investigated the seasonal availability of flavonoids amongst dietary and medicinal plant species to identify optimal periods of consumption. Flavonoid variability is affected by a complex range of factors, including temperature, UV-B radiation, nutrient availability, water availability, altitude, biotic and abiotic stresses, genotype, time of harvest, fluctuations during development, geographic location and various other habitat conditions, all of which may affect production, presence and variation of flavonoid levels (3, 11, 19, 20, 25, 28-30). The findings of this review indicate that flavonoids occur in fluctuating and various concentrations throughout the year and may vary according to growing season. Brassica vegetables in particular have shown substantial variations in several studies (3, 19, 31). Bhandari and Kwak (2014) examined the associations between cultivar, plant part and growing season, with total flavonoids in twelve commercial broccoli cultivars and found cultivar-dependant variations of total flavonoids, determined by genotype with specific cultivar-season interactions(12). Similarly, Aires et al. (2011) demonstrated a similar relationship among six *Brassica* vegetables (*Brassica oleracea L. and Brassica rapa L.*)(3). Significant differences (*P* <

0.05) were observed in total flavonoids between climate seasons of spring-summer and summer-autumn-winter across *Brassica* vegetable types, apart from savoy cabbage(3). Though an association between genotype and environment was established in these studies, other as-yet understudied growth parameters may also influence flavonoid availability. For example, Reilly et al. (2013) found a correlation between increasing flavonoid content and longer maturation time in broccoli florets(31), indicating cultivar, plant part and duration of growth within favourable growing conditions can influence total availability of flavonoids in broccoli, being greater at the time of sprouting compared to its green stage(31).

Temperature, location, and flavonoids

Among the reviewed articles, temperature was one of the most important factors in determining flavonoid content. Lisete et al. (2018) found a difference within species among brown algae samples from different geographical locations(30). Brown algae *(Phaeophyceae)* from the Santa-Maria island produced the highest total flavonoids in both winter and summer seasons, with lower average seawater temperature (15.6 °C in the winter and 22.2 °C in the summer) compared to São Miguel Island (16.7 °C in the winter and 24.4 °C in summer)(30). In contrast, Marelli et al. (2017) found no significant difference in flavonoid content among edible chicory plants in response to eco-physiological factors (location, altitude and temperature) *(P* < 0.001)(28). Altitude similarly showed no significant effect on flavonoid content in blueberry varieties "Duke" and "Brigitta" (21). However, a lower altitude (650 m) with optimum temperatures (20–26°C during the day and 16°C at night) increased time of ripening and consequent anthocyanin production earlier in development, though flavonoids were regulated by plant development and genotype, rather than environmental conditions(21). These results somewhat conflict with a study on Cayenne Cherry Leaf by Santos et al. (2011), who reported that flavonoid content is positively correlated with climatic evaporation (*P* <0.01), though inversely correlated with humidity and cloudiness (*P* <0.05)(27). Furthermore, highest total flavonoid content was found in the dry season at the end of winter, while lowest in mid-autumn (beginning of the dry season)(27). Thakur and Kapila (2017) found higher total flavonoid accumulation in leafy liverwort cultivars were associated with lower temperatures, higher light conditions and water stress(29). Higher flavonoid content was also observed towards the end of the growing season (winter/spring), with lower variation of flavonoid content during winter and towards the end of the growing season(29).

UV radiation and water stress

Light exposure and water conditions are noteworthy factors that can influence flavonoid availability and variability. For example, Alves et al. (2017) found total flavonoid content of prickly pear (*Oppunita Spp*) cultivars to be highest in the dry season (autumn-spring)(10). This may reflect an adapted protective mechanism to abiotic stresses such as drought, heat and ultra-violet radiation in semiarid regions to ensure plant survival(10). Similar adaptations have been observed in semiarid environments in amaranth, with greater flavonoid levels produced in response to incremental drought stress (32). The presence of UV light enhances the production and variability of flavonoids, reflecting their role in absorbing short solar wavelengths. UV light causes upregulation in flavonoid biosynthesis when UV-radiation is either abundant or absent(33). High light conditions and water stress can resemble a favourable environment for anthocyanin biosynthesis, which occurs in the presence of environmental stresses (10, 22). Anthocyanin accumulation and biosynthesis is visible in autumn leaves during senescence, where anthocyanins enable protection from photooxidative damage while promoting nutrient retrieval, similar to that produced in the fruit (22, 34). Accumulation of anthocyanins has been further demonstrated in blueberries and bilberries where exposure to sunlight and UV radiation with lower daytime temperatures encourages anthocyanin production at higher altitudes(21).

Limitations

The large level of heterogeneity amongst the small number of reviewed studies is a significant limitation of this review. Soil type, salinity, flavonoid extraction methods, duration of light exposure, growing conditions, precipitation, maturation and planting/collection time among other factors can influence flavonoid content. More studies, with more consistency of methodologies will enable a more lucid account of the potential for seasonality to inform flavonoid intake studies. Furthermore, studies to date include only a small range of edible plants, leaving a relatively large gap in our understanding of content variations in the major dietary flavonoid sources identified previously(24). Whilst it is clearly plausible that seasonal availability is a significant determinant of flavonoid intake and consequent health impacts, there is a paucity of specific studies to explore this in any great detail.

CONCLUSION AND RECOMMENDATIONS

Despite the number of limitations included within this review, the findings of this review provide preliminary empirical evidence about the seasonal flavonoid variation within some of the plant species. The variability and availability of flavonoids can be affected by genotype, stages of growth and

environmental stresses among flavonoid composition and content. Abiotic stresses can affect flavonoid biosynthesis, typically for anthocyanins. The present study indicates a need for further research into the comparable growing seasons of fruit, vegetable, and medicinal plant species, to clarify environmental parameters to ensure optimal growth conditions for nutritional benefit.

Finally, many previous studies have reported variations of total flavonoid content, rather than that of specific individual flavonoids. Given the variability in physiological effects dependant on specific flavonoid type, studies investigating content of individual flavonoid also are warranted to enable translation of content variation into meaningful insights and potential health impacts.

CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

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