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Health-Promoting Phytochemicals in Fruits and Vegetables: Impact of Abiotic Stresses and Crop Production Practices

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ABSTRACT

Phytochemicals are the primary source of antioxidants in the human diet and play an important role in combating the damaging effects of oxidative stress and other adverse cell responses that can lead to a wide variety of chronic and degenerative illnesses. These phytochemicals typically consist of a wide array of phenolic compounds, ascorbic acid, alpha-tocopherol and carotenoids, and have been shown to promote health and provide protection against a growing list of diseases including various cancers and cardiovascular and neurodegenerative diseases. A significant part of the antioxidants found in plants is the products of plant secondary metabolism, and these antioxidants appear to have similar protective function in plants against oxidative damage caused by various stresses, as they do in animals, including humans. In response to stresses and, more importantly, as an adaptive mechanism, plants tend to shift toward secondary metabolism resulting in the accumulation of protective antioxidants. Accumulation of phytochemicals in response to various abiotic stresses such as high and low temperatures, water stress and high light has been studied in a wide range of plants. Thus, the use of mild and controlled environmental stresses may provide an opportunity to improve the health-promoting qualities of many commonly consumed fruits and vegetables. In addition, a number of factors such as plant nutrition, growing conditions (*e.g.*, open fields, protective environments and organic culture) and crop production and postharvest management practices have also been known to have a significant impact on the phytochemical composition of many fruits and vegetables. The purpose of this review is to characterize the nature of the relationship between these factors and the phytochemical accumulation in fruits and vegetables, which is important in developing potential strategies to improve their quality through enhanced health-promoting and nutritive value.

Keywords: antioxidants, crop management, diet, environmental stresses, organic practices, plant adaptation, plant nutrition, postharvest, phenolics, nutrition, secondary metabolites

CONTENTS

INTRODUCTION

The ability of plants to survive and thrive under varied environmental conditions may depend on their ability to produce secondary metabolites and antioxidants. The secondary metabolites comprise a vast and diverse group of compounds, and more than several thousands have been identified in only a small fraction of plant species thus far investigated (Wink 1999). An overwhelming body of evidence suggests that these metabolites help plants cope with a wide range of biotic and abiotic stresses which can typically elevate the levels of a number of reactive oxygen species that can be damaging to many cellular macromolecules including membrane lipids, proteins and the genetic material (Mittler 2002). However, it should be recognized that reactive oxygen species are routinely generated during normal plant function and there appears to be a balance between reactive oxygen species and antioxidants, unless the plants happen to be exposed to adverse abiotic and biotic factors in which case the reactive active species could dominate. Under situations involving plant stress, to counter the damaging effect of the oxidative stress and as a defense mechanism, plants have evolved to produce a vast number of antioxidants, many of which are secondary metabolites. A broad range of these antioxidants, rather than any specific ones, appear to be involved in conferring plant defense against environmental stresses (Munne-Bosch 2005).

Interestingly, these antioxidants in plant-based diets function in animals, including humans, in a fashion similar to their function in plants, possibly preventing oxidative

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Invited Review

damage and other cellular dysfunctions which are known to contribute to a number of chronic and degenerative diseases.

One of the challenges of aerobic life both for plants and animals is the ever-present threat of oxidative stress. Reactive oxygen species are typically produced due to incomplete reduction of oxygen during mitochondrial respiration, and are one of the major causes of cellular damage and, in the long term, the development of many commonly occurring chronic illnesses including cardiovascular disease, cancers, neurodegenerative diseases, arthritis, diabetes, cataracts and others (Halliwell 1987; Ames 1989; Taylor 1992; Ames *et al.* 1993; Joseph *et al.* 2000; Laaksonen and Sen 2000).

Fruits and vegetables are a rich source of phytochemicals with antioxidant properties (Cao *et al.* 1996; Prior and Cao 2000; Wolfe *et al.* 2008). They contain a wide array of phenolic compounds, carotenoids and vitamins such as vitamin C and vitamin E (Wang *et al.* 1996; Sun *et al.* 2002). Among these, phenolic compounds are the most abundant and are effective antioxidants, with an astonishing number of more than 8000 diverse phenolic compounds identified in plants thus far (Luthria, *et al.* 2006). In addition to their antioxidant role, phytochemicals are being increasingly known to modulate a multitude of cell functions which may all significantly contribute toward better health (Marchand 2002). Therefore, consumption of fruits and vegetables is thought to reduce the risk of many diseases, promote overall health (Steinmetz and Potter 1996; Lasheras *et al.* 2000; Prior and Cao 2000; Birt *et al.* 2001; Wolfe *et al.* 2008) and even possibly extend the human lifespan (Lagouge *et al.* 2006). In fact, Doll (1990) proposed a strong association between the incidence of cancer and diet and suggested that diet modification involving inclusion of fruits and vegetables is a possible solution in mitigating some of these health problems. Subsequently, numerous epidemiological studies have demonstrated a positive correlation between high consumption of fruits and vegetables and a reduced risk of a growing list of chronic diseases (Block *et al.* 1992; Ness *et al.* 1999).

The effectiveness of antioxidants depends on their reduction potential, their ability to generate stable radicals and delocalize unpaired electrons and to chelate transition metal ions which promote the formation of free radicals. Structurally, phenolic compounds possess all of these characteristics and hence, are effective as antioxidants. In addition, they are also known to inhibit the activities of many enzymes that are implicated in the formation of reactive oxygen species such as NADPH oxidase and xanthin oxidase (De Groot and Rauen 1998). However, what is thought to make the consumption of fruits and vegetables effective in disease prevention and health-promotion is the concerted and synergistic effects of their diverse phytochemicals in overcoming the damaging oxidative stress and other adverse cell responses. This may also explain the often observed lack of positive relationship between individual dietary supplements of antioxidants and the health benefits typically associated with fruits and vegetables (Liu 2004).

Because of their health-promoting qualities, fruits and vegetables have been the focus of a number of studies which have sought to characterize their phytochemical composition and their health benefits (Tomas-Barberan and Espin 2001; Lattanzio 2003; Schreiner 2005). In addition, with increasing awareness of the health benefits of fruits and vegetables in the daily diet, there is a growing interest in improving the quality of fruits and vegetables with regard to their phytochemical content. In fact, enhancing the health-promoting qualities of plants may turn out to be beneficial not only for human health but for plants as well in dealing with abiotic and biotic stresses (Demmig-Adams and Adams 2002). Although there is a great deal of attention focused on the antioxidant activities of these phytochemicals, there is a growing body of evidence on the complex nature of phytochemicals and their other possible modes of action in bringing about the positive effects on human health. Clearly, phytochemicals are involved in a number of cell functions including enzyme activities, cell cycle regulation, cell signaling pathways, inflammation and many others. Thus, it is important to note that the observed overall health-benefits are perhaps a result of a more complex and a much broader role played by phytochemicals in cell functions in addition to their well known antioxidant properties (Marchand 2002; Virgili and Marino 2008).

A number of factors affect the content of health-promoting antioxidants in fruits and vegetables including plant genotype and stage of growth (Kakes 1991) and complex abiotic and biotic factors (Dixon and Paiva 1995; Wink 2008). However, the scope of this review is limited to abiotic factors, and crop growing and management practices that could affect the health-promoting phytochemicals in plants. In the context of health-promoting qualities of fruits and vegetables, we discuss plant antioxidants, and for the purpose of discussion here, they will be considered as phytochemicals although most are secondary metabolites, some are vitamins.

SECONDARY METABOLITES AND PLANT ADAPTATION

Secondary metabolism plays an important role in the ability of plants to adapt to benign changes in environmental conditions as well as to a number of abiotic and biotic stresses, ultimately leading to plants' fitness to thrive under varied environmental conditions. Plants grown in protective environmental conditions (growth chamber) need to adapt to normal unprotective conditions such as greenhouse or field conditions. Plants may accomplish this by accumulating antioxidants including secondary metabolites. Recent findings show that plants may adapt by activating a number of key genes involved in the biosynthesis of antioxidants (Oh *et al.* 2009a). When lettuce plants, grown under protective conditions [near 100% RH at 22/18°C (day/night)] in a growth chamber, were transferred to unprotective conditions [60-70% RH at 22/18°C (day/night)], PAL (phenylalanine ammonia-lyase) and γ-TMT (γ-tocopherol methyl transferase) genes responsible for the biosynthesis of most phenolic compounds and α-tocopherol, respectively, were rapidly activated. Thus, secondary metabolites, having antioxidant properties, and other antioxidants are likely to play a role in helping plants adapt to varying, albeit benign, environmental conditions. The activation of these antioxidant genes may be triggered by environmental perturbation, including environmental stresses. PAL, a key gene involved in the phenylpropanoid pathway leading to the biosynthesis of most pehenolic compounds, is also activated by environmental stresses (**Fig. 1**). Furthermore, a number of antioxidants are known to protect the photosynthetic apparatus both under normal growing conditions and under a wide range of environmental stresses (Demmig-Adams *et al.* 1999). Tender lettuce plants [grown in protective environment – near 100% RH at 22/18°C (day/night)] without adaptation did not perform well when exposed to unprotective environmental conditions [60-70% RH at 22/18°C (day/night)], as reflected by their lower shoot and root growth (Oh *et al.* 2009a). Blocking the PAL activity impaired lettuce plant growth even under normal growing conditions, suggesting the importance of phenylpropanoids in plant's ability to adapt to fluctuating environmental conditions (**Fig. 1**). Similarly, in kale and spinach, Lefsrud *et al.* (2005) found that fluctuating growing temperatures had a significant impact on the content of various antioxidants. Lettuce plants grown under varying environmental conditions outdoors had significantly higher phenolic content compared to those grown under greenhouse conditions (Romani *et al.* 2002). Acclimation of begonia plants, grown in subdued light, to full sun resulted in an increased activity of a number of antioxidant enzymes (Burritt and Mackenzie 2003). Thus, perturbations in environmental conditions, whether benign or stressful, can lead to the activation of secondary metabolism in plants.

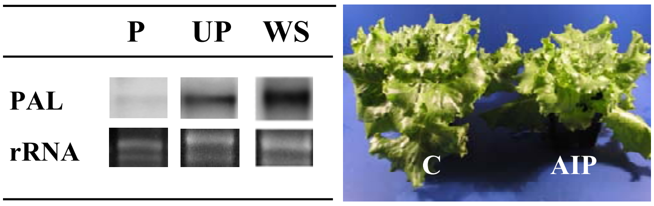

Fig. 1 Expression of PAL gene (left panel) in lettuce grown under protective (P) conditions, similar to *in vitro* conditions [~100% RH at 22/18°C (day/night)], unprotective (UP) conditions, same as in P but with 60-70% RH, and water stress (WS), imposed by withholding irrigation for 7 days. Lettuce plants (right panel) with AIP (2-aminoindan 2-phosphonic acid, 10 µM), a PAL inhibitor and without AIP (C) grown under unprotective growing conditions. From **Oh MM, Trick HN, Rajashekar CB** (2009a) Secondary metabolism and anti-oxidants are involved in environmental adaptation and stress tolerance in lettuce. *Journal of Plant Physiology* **166**, 180-191, with kind permission from Elsevier GmbH.

ENVIRONMENTAL STRESSES AND PHYTOCHEMICALS

A number of environmental stresses including high light, UV, water stress, extremes of temperature, and nutrient stress can affect the antioxidant content of plants (Dixon and Paiva 1995; Zobayed *et al.* 2007; Oh *et al.* 2009b). Of the abiotic stresses, high light may play a dominant role in enhancing phytochemical content in plants. In a recent study using various environmental stress shocks to increase the phytochemical content in lettuce just prior to harvest, high light was found to be a more powerful agent in inducing accumulation of various phenolic componds than high or low temperatures (**Fig. 2**). This may be because plants accumulate a number of phenolic compounds and other antioxidants as a protective measure against damaging high light and UV. In fact, light plays an important role in the synthesis of many antioxidants such as carotenoids, flavonoids, anthocyanins and α-tocopherol (Hrazdina and Parsons 1982; Lancaster 1992; Alba *et al.* 2000; Demmig-Adams and Adams 2002; Hormaetxe *et al.* 2005; Lester 2006). Studies on tomatoes have shown that high light can lead to the accumulation a number of phenolic compounds, ascorbate, lycopene and β-carotene in fruit tissues (Gautier *et al.* 2008). Also, in green tissues, anthocyanins are known to play a protective role against high light-induced photo-oxidation and photobleaching of chlorophyll, and hence, accumulate in response to high light (Steyn *et al.* 2004). High light has been shown to increase the amount of various phenolic compounds including flavonoids, quercetin and luteolin derivatives in lettuce (Hohl *et al.* 2001) and in other plant species (Grace *et al.* 1998; Yaginuma *et. al.* 2002; Tattini *et al.* 2004). Both light intensity and quality play an important role in inducing the accumulation of phytochemicals in plants, notably anthocyanins in many fruits (Dussi *et al.* 1995; Tomas-Braberan and Espin 2001) and others in a wide range of species (see **Table 1**). In our studies on lettuce, brief exposure of plants to high light increased the total phenolic content three-fold, accompanied by large increases in both caffeic acid derivatives and flavonoids (**Fig. 2**; Oh *et al.* 2009b). The accumulation of these compounds along with antioxidants such as α-tocopherol and ascorbic acid in lettuce was associated with activation of PAL, γ-TMT and L-GalDH (L-galactose dehydrogenase) genes involved in their biosynthesis. This suggests that the accumulation of these antioxidants in response to environmental stresses is under the transcriptional control. Using microarray analysis in *Arabidopsis*, Kimura *et al.* (2003) showed that more than 100 genes were activated rapidly in response to high light, many of which are known to be involved in the biosynthesis of phenolic compounds including flavonoids. Also, many of these genes were activated by water stress in *Arabidopsis*.

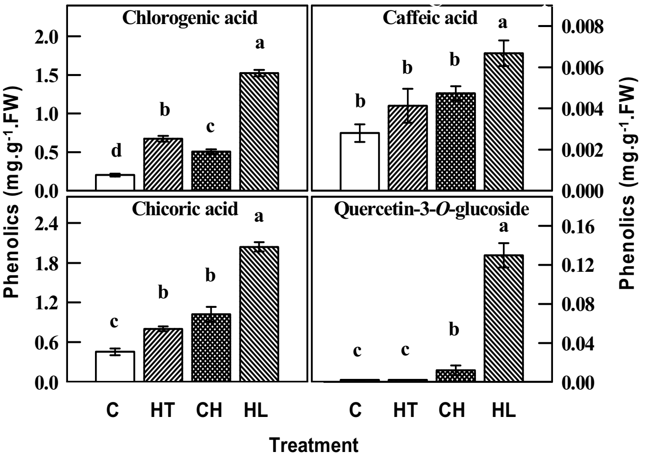

Fig. 2 Concentration of phenolic compounds in lettuce subjected to various environmental stress shocks: heat shock-HT (40°C for 10 min.), chilling-CH (4°C for 1 day) and high light-HL (800 µmolm^{-2}s^{-1} for 1 day) and grown without the stress shocks (C). From **Oh MM, Carey EE, Rajashekar CB** (2009b) Environmental stresses induce health-promoting phytochemicals in lettuce. *Plant Physiology and Biochemistry* **47**, 578-583, with kind permission from Elsevier Masson SAS.

Plants are protected against UV light by the accumulation of a number of phenolic compounds especially flavonoids, which typically accumulate in epidermal tissues and can strongly absorb UV-B wavelengths (Dixon and Paiva 1995). Numerous studies have shown the importance of phenylpropanoids in protecting plants against UV. More conclusive evidence of the role played by phenylpropanoids in protecting plants against UV has come from the use of *Arabidopsis* mutants, sensitive to UV, that do not accumulate various flavonoids (Li *et al.* 1993; Lois and Buchanan 1994; Fiscus *et al.* 1999) or from a mutant, tolerant to UV, which accumulates UV absorbing pigments (Bieza and Lois 2001). Irradiation of parsley cell cultures with UV resulted in a large flavonoid accumulation resulting from the rapid activation PAL and CHS (chalcone synthase) genes, involved in phenylpropapanoid pathway which is the major source of phenolic compounds in plants (Chappell and Hahlbrock 1984). Natural UV from solar radiation can be a significant factor in the accumulation of several phenolic compounds. Studies using plastic films to block UV radiation under field conditions in lettuce showed a marked reduction in the total phenolic content and the antioxidant capacity, reflecting a sharp decline in a number of flavonoids, while exposure of lettuce to natural UV radiation led to an increase in cyanidin and quercetin contents by more than 4-fold, luteolin by more than 7-fold and caffeic acid by nearly 2-fold (Garcia-Macias *et al.* 2007). Similar positive results of natural UV on the total phenolic content have also been noted in tomatoes (Luthria *et al.* 2006). These studies suggest a strong effect of UV and in fact, a great part of the accumulation of phenolic compounds due to natural solar radiation in lettuce may be due to its UV component (Garcia-Macias *et al.* 2007; Tsormpatsidis *et al.* 2008). **Table 1** summarizes the positive effect of light on the antioxidant accumulation in a number of horticultural species. While many studies demonstrate the importance of UV in inducing higher accumulation of these chemicals, white light (typically has a UV component) and visible light are also likely to produce a similar effect.

Other environmental stresses including water deficits, low and high temperature stresses and nutritional levels can also affect the antioxidant and phytochemical content of plants. Drought stress has been shown to result in the accumulation of a number of phytochemicals including many phenolic compounds, α-tocopherol and ascorbic acid (Keles and Oncel 2002; Kirakosyan *et al.* 2003; Hernandez *et al.* 2004; Tattini *et al.* 2004; Zobayed *et al.* 2007). A detailed summary of a broader effect of water stress on a wide range of secondary metabolites in plants has been presented by

Table 1 Accumulation of antioxidants in various plant species in response to irradiation.

Irradiation	Plant species	Antioxidants	References
UV	Lettuce	Total phenolics Total anthocyanins Total flavonoids Cyanidin Quercetin Luteolin Caffeic acid	Garcias-Macias *et al.* 2007; Tsormpatsidis *et al.* 2008
	Tomato	Total phenolics Caffeic acid	Luthria *et al.* 2006
	Spinach	Total phenolics	Schirrmacher *et al.* 2007
	Onion (postharvest)	Quercetin Ascorbic acid Flavonoids	Higashio *et al.* 2007
	Grapes (postharvest)	Resveratrol	Langcake and Pryce 1997; Cantos *et al.* 2000; Versari *et al.* 2001; Kolb *et al.* 2003
	Peanut	Resveratrol	Chung *et al.* 2003
	Potatoes	Resveratrol	Lippman *et al.* 2000
	Apples (postharvest)	Anthocyanins Flavonols Proanthocyanidins	Dong *et al.* 1995
	Strawberry (postharvest)	Anthocyanins	Higashio *et al.* 2005
	Peach (postharvest)	Anthocyanin	Kataoka and Beppu 2004
White light	Tomato (postharvest)	Carotenoids	Gautier *et al.* 2008
	Apples (postharvest)	Anthocyanins Flavonols Proanthocyanidins	Dong *et al.* 1995
	Lettuce	Chlorogenic acid Chicoric acid Caffeic acid Luteolin-7-*O*-glucoside Quercetin-3-*O*-glucoside	Oh *et al.* 2009b
	Pea	Flavonol glyosides	Hrazdina and Parsons 1982
Light (visible)	Cucumber	Total phenolics	Yaginuma *et al.* 2002
	Safflower	Luteolin-7-*O*-glucoside	Yaginuma *et al.* 2002

Gershenzon (1984). In a field study, higher concentrations of total phenolics and anthocyanins were observed in grape berries under non-irrigated conditions than under irrigated conditions (Esteban *et al.* 2001). In lettuce, some of the key genes PAL, γ-TMT and L-GalDH, involved in the biosynthesis of phenolic compounds, α-tocopherol and ascorbic acid, respectively, have been shown to be activated by water stress, suggesting that the accumulation of these antioxidants in response to stress may be controlled by gene action (Oh 2008).

Accumulation of phytochemicals is also sensitive to temperature, and is often variable depending on the plant species (Schreiner 2005). For example, accumulation of ascorbic acid in plants is typically favored at lower temperatures. However, the accumulation of β-carotene in cool season crops is favored at cooler temperatures while warmer temperatures appear to be more optimal for warm season crops such as melons and tomatoes (Keles and Oncel 2002; Lefsrud *et al.* 2005; Lester 2006; Rosales *et al.* 2006; Gautier *et al.* 2008). Thus, temperature appears to play a more important role in the accumulation of many carotenoids than does light in a number of vegetables. Also, the accumulation of anthocyanins in many fruits is perhaps dependent on the fluctuations in day and night temperatures (Tomas-Barberan and Espin 2001). Low temperatures have also been shown to induce accumulation of a number of phenolic compounds in several plant species (Hasegawa *et al.* 2001; Kirakosayan *et al.* 2003; Pennycooke *et al.* 2004). Oh *et al.* (2009b) showed that exposing lettuce just prior to harvest to high or low temperature shocks could elevate its total phenolic content and antioxidant capacity resulting from an increase in the concentrations of many phenolic compounds.

STRATEGIES TO AUGMENT PHYTOCHEMICALS-ENVIRONMENTAL STRESSES, GROWING AND MANAGEMENT PRACTICES

Environmental stresses

Since various environmental stresses have been shown to induce a host of protective antioxidants in plants, they may be used as an effective strategy to enhance the health-promoting phytochemicals in fruits and vegetables. Although some of these environmental stresses cannot be imposed under field conditions, some can be, including regulated water stress and modulation of the intensity and quality of light in crop production systems especially those involving high tunnels, greenhouse or reflective mulches (Ju *et al.* 1999; Atkinson *et al.* 2005). Schreiner (2005) has suggested that crop management practices can increase individual phytochemical content significantly in some cruciferous vegetables and outlined some of these practices involving environmental and nutritional factors such as temperature, irrigation, radiation, fertilization and growing season. Using regulated deficit irrigation in strawberry, Atkinson *et al.* (2005) found that the application of water stress late in the crop growth stage resulted in an increase in the polyphenol antioxidants, ellagic acid and ellagitannins. Similarly, use of deficit irrigation in grapes was found to increase total phenolics, tannins and anthocyanins in the berries, although the results varied depending on the year and sampling dates (Esteban *et al.* 2001). In a growth chamber study using lettuce, plants were treated with various mild stresses including high temperature, chilling and high light just prior to harvest. All these stresses increased the total phenolic content and individual phenolic compounds such as chlorogenic acid and chicoric acid. Consistently, of these stresses, high light produced the largest increases in the total phenolics, caffeic acid derivatives and flavonoids (**Fig. 2**). The accumulation of these antioxidants appear to be as a result of *de novo* synthesis as PAL gene was activated in response to all the stresses (Oh *et al.* 2009a, 2009b). Interestingly, in addition to enhancing the phytochemical content, environmental stress could also induce certain phenolic compounds, thereby changing the composition of phytochemicals. Both chilling and high light induced luteolin-7-*O*-gulcoside and quercetin-3-*O*-glucoside in lettuce. High light was especially more effective in increasing the quercetin-3-*O*-glucoside content by more than 6-fold over the chilling-treated plants (**Fig. 2**). Also, lettuce grown in open field consistently produced more phenolic componds including both caffeic acid derivaties such as chlorogenic and caffeic acids and flavonoids such as quercetin-3-*O*-glucoside and luteolin-7-*O*-glucoside compared to that grown in high tunnels or greenhouses (Romani *et al.* 2002; Oh 2008). Similarly, field grown tomatoes had higher ascorbic acid content compared to those grown in the greenhouse (Currence 1940). While environmental stresses generally have a favorable impact on the phytochemical content of many crops, it is important to recognize that they can also produce an adverse effect on the plant growth and yield. For this reason, the stresses have to be mild enough and applied in such a way that there is no appreciable adverse effect on the yield. If crops are subjected to mild stresses just before harvest, their effects on plant growth and biomass accumulation tend to be minimal (Oh *et al.* 2009b).

Plant nutrition

Plant nutrition can be an important factor affecting the accumulation of various phytochemicals. A number of studies have reported that nitrogen and sulfur nutrition could affect the phytochemical accumulation involving glucosinolate and various carotenoids (Aires *et al.* 2006; Kopsell *et al.* 2007; Li *et al.* 2007). Nitrogen deficiency that can lead to poor growth and the reduced protein synthesis has been proposed to affect the nitrogen balance in plants, which may favor secondary metabolism and the accumulation of a number of phenolic compounds and glucosinolates (Gershenzon 1984; Schreiner 2005). Consistent with these results, in a field study with lettuce, increased fertility (nitrogen) through either application of organic or commercial fertilizers resulted in reduced total phenolics as reflected by diminished levels of caffeic acid derivatives and flavonoids (Oh 2008). Similar responses with phosphorus and sulfur deficiencies have also been reported in some plant species (see review by Gershenzon 1984). Conversely, increasing available nitrogen has been found to increase the ascorbic content in a number of vegetable crops (Lee and Kader 2000) and carotenoid content in carrots (Hochmuth *et al.* 1999). Reports of nutrient effects on phytochemical composition of plants vary with the plant species (Kalt 2005) and are often variable, partly due to the fact that they are derived largely from field studies with variable cultural, management and environmental conditions. Nonetheless, based on results from many studies, one can conclude that soil fertility levels with regard to major and micro nutrients do play a role in influencing the phytochemical accumulation in fruits and vegetables (Tomas-Barberan and Espin 2001; Lester 2006). Thus, it is possible to control fertility levels by appropriate crop management practices to improve the health-promoting qualities of fruits and vegetables.

Organic practices

Comparisons of nutritional quality between organic food and its conventional counterparts have produced inconclusive findings due to the lack of well-designed studies and the intrinsic complexity of farming systems (Bourn and Prescott 2002; Magkos *et al.* 2003). Managing production systems for improved food quality can be rather challenging as a host of genetic and environmental factors, cultural practices, and production methods can differentially impact various quality attributes of food crops (Dumas *et al.* 2003; Zhao *et al.* 2006). Nevertheless, recently emerging evidence suggests that organically grown fruits and vegetables might contain higher levels of health-promoting phytochemicals (Olsson *et al.* 2006; Mitchell *et al.* 2007; Sousa *et al.* 2008). Although a meta-analysis of literature data arrived at a similar conclusion (Zhao *et al.* 2007), because of the complexity involved in organic production system, which can alter a number factors such as soil biology, water and nutrient availability and plant-pest interactions, it is safe to say that its effect on the phytochemical composition in plants is still not very clear and certainly, less than conclusive (Oh 2008).

It has been estimated that organic vegetables may contain 10-50% higher defense-related secondary metabolites than conventionally grown vegetables (Brandt and Mølgaard 2001). Since phytochemicals tend to accumulate in response to an array of biotic and abiotic stresses, elevated levels in organic versus conventional produce have been attributed to the relatively "stressful" conditions in organic systems, including possible increases of herbivore and pathogen pressure caused by limited use of pesticides under organic management (Carbonaro *et al.* 2002; Asami *et al.* 2003; Young *et al.* 2005; Tarozzi *et al.* 2006) as well as lower nitrogen availability resulting from the slow-release property of organic nutrient inputs (Sousa *et al.* 2008; Zhao *et al.* 2009). A comparative study of organic and conventionally grown processing tomatoes showed consistently higher levels of quercetin and kaempferol in organic tomato over a 10-year period, and a rise in the levels of these flavonoids within the organic system in the final 4 years of the study as compost application rates were reduced (Mitchell *et al.* 2007). The dramatic increase of phytochemical content under organic production in this long-term study was linked directly to the level of readily available nitrogen in soil and it was suggested that the phytochemical enhancement might be compromised if over-fertilization occurred in organic systems. A decrease of flavonoid and phenolic acid concentrations has been observed in leaves of organically grown barley as a result of increasing fertilization rates using farmyard manure or cattle slurry (Norbaek *et al.* 2003). Similarly, studies on lettuce showed that the crop grown under organic management resulted in an increase in certain phenolic compounds only in open fields but not in high tunnels, and also increased organic fertilizer application tended to have a negative effect on its phytochemical content (Oh 2008).

In addition to disease and pest management and nutrient availability, Lundegardh and Martensson (2003) proposed that the underlying difference between organic and conventional farming systems is the soil microbiological activity that might fundamentally affect phytochemical biosynthesis and thus health benefits of plant food. The study of Malusà *et al.* (2004) revealed that organic amendment increased phenolics in the grape skin compared with conventional fertilization, whereas polyphenol content varied significantly among organic treatments with higher contents in the inoculant treatments containing "mycorrhiza and plant growth promoting bacteria."

To date, few studies have taken a holistic approach to examine the systematic impact of organic management on phytochemical enhancement. Along with organic amendment, cover crops, crop rotation, and reduced tillage achieved by the use of cover crops can be well integrated into organic systems. How these organic management practices may synergistically influence the production of phytochemicals in fruit and vegetables is not well understood. According to Lombardi-Boccia *et al.* (2004), conventional plums contained higher total phenolic content than organically fertilized plums when the same tillage practice was employed in both production systems. However, when comparing organic plums under different soil management systems including tilled soil, clover covered soil, and natural meadow covered soil, clover mulch led to the highest level of phenolic acids, while natural meadow mulch resulted in enhanced contents of tocopherols, β-carotene and total polyphenols.

Within the framework of "organics", there are many production conditions, and they can significantly vary both within and among farms and regions. This underscores the highly variable, multiple complex factors involved in organic culture and the associated management systems. For example, organic management strategies have been demonstrated to suppress soil-borne disease and improve soil physical, chemical, and biological properties and processes (Mäder *et al*. 2002; van Diepeningen *et al*. 2006; Liu *et al*. 2007). Without an understanding of the key components of organic farming with regard to their effect on food quality, it will be difficult to control the specific elements in organic systems to enhance phytochemical contents. In other words, the question of whether organic farming can improve food quality as opposed to conventional production is perhaps less critical than identifying specific contributing factors that can be manipulated in production systems to enhance food quality (Zhao *et al*. 2006). This requires interdisciplinary efforts to elucidate the interconnectedness of crop health, soil fertility and biodiversity, and food quality which may help in developing the best management practices for organic farming systems.

Postharvest handling

Just as in the field, the quality of fruits and vegetables with regard to phytochemical content and composition can be affected during their postharvest handling, storage and processing. Thus, by using appropriate approaches, it is possible to maintain or even improve the quality of fruits and vegetables including the composition of health-promoting phytochemicals during postharvest stage. Generally, to extend the postharvest life of fruits and vegetables, various methods involving low temperatures, irradiation, heat treatment, and controlled atmosphere and chemicals are commonly used (Tomas-Barberan and Espin 2001; Schreiner and Huyskens-Keil 2006). However of these approaches, the use of low temperatures is by far the most commonly used method. Low temperatures can have a major effect on the phytochemical content of fruits and vegetables, especially on the phenylpropanoid pathway which is the source of most of the phenolic compounds. There is considerable evidence to show that a host of phenolic compounds accumulate during cold storage in a wide range of fruits and vegetables (for review, see Lattanzio 2003). Just as during the preharvest stages, a significant part of phenylpropanoid pathway is activated during postharvest period in response to low temperatures, including PAL, a key gateway enzyme to this pathway. The accumulation of these secondary metabolites may be as a result of *de novo* synthesis as the PAL gene and others involved in the biosynthesis of phenylpropanoids have been shown to be activated at low temperatures in a number of plant species (Christie *et al.* 1994; Steyn *et al*. 2004)). However, a complicating factor with low temperature storage is that fruits and vegetables are invariably susceptible to chilling injury, the severity of which depends on the species and on the length of cold storage. Indeed, fruits of most species, including the temperate ones, are likely to show chilling injury symptoms, if stored for a long enough time. In addition, the stage and maturation of fruits during storage can also have an effect on the accumulation of phytochemicals (Schreiner and Hyuskens-Keil 2006).

In addition to low temperatures, use of γ and UV irradiation during postharvest stage, typically used to control food-borne pathogens, has also been known to increase various phytochemicals, especially, phenolic compounds (Tomas-Barberan and Espin 2001; Schreiner and Hyusen-Keil 2006). UV irradiation can activate PAL and many other enzymes involved in phenylpropanoid pathway similar to low temperatures (Tomas-Barberan and Espin 2001; Pluskota *et al*. 2005) resulting in the accumulation of phenolic compounds including resveratrol in grapes (Takayanagi *et al*. 2004) and quercetin in onions (Higashio *et al*. 2007). The response in grapes was associated with activation of some of the key genes involved in its biosynthesis such as PAL and stilbene synthase (Takayanagi *et al*. 2004). UV irradiation has also been useful in improving fruit color by anthocyanin accumulation in some fruit species including strawberries, apples, sweet cherries and peach (Dong *et al*. 1995; Kataoka *et al*. 1996; Kataoka and Beppu 2004).

CONCLUSION AND FUTURE PERSPECTIVES

Many factors including abiotic and biotic stresses, plant nutrition and crop management practices can significantly affect the phytochemical content and composition of fruits and vegetables. Studies show that various environmental factors can activate genes involved in the biosynthetic pathways of secondary metabolism leading to the accumulation of numerous phytochemicals. Of these, high light and UV, in particular, are known to produce significant impact on improving the nutritional and heath-promoting qualities. In addition, findings from numerous studies have shown the potential for improving the quality of fruits and vegetables in relation to their health-promoting phytochemicals, through use of appropriate cultural and management practices which may involve regulating abiotic stresses and other practices both during pre- and postharvest stages. However, in many cases, these results from field studies are difficult to interpret and do not typically allow for the identification of the direct role of individual factors in influencing the health-promoting quality of fruits and vegetables because of the varied inherent complexities and interactions involved under field conditions. Also, very few controlled studies have focused on understanding the effects of various factors, abiotic, biotic and others, that directly affect the phytochemical composition and content of these crops. Obviously this knowledge forms the basis for developing strategies to effectively influence the phytochemical content and hence, the quality of crops. To date, in the absence of such information, there have been very few studies which have attempted to integrate or optimize some of these factors to attain the best phytochemical advantage.

Indeed under field conditions, many environmental conditions, perhaps with the exception of water stress, are difficult to control. Yet in many ways, the possibility of exploiting environmental stresses to improve health-promoting qualities of fruits and vegetables is quite promising. This is particularly true under protective crop production systems such as those involving greenhouse and high tunnels where, in addition to the supply of water, other environmental factors including light (quality and intensity) and temperature (in greenhouses) can be regulated. As environmental factors can play an important role on phytochemical accumulation, the quality of food crops is expected to depend not only on the growing season but also on the geographical region of their cultivation. In addition, it is important to recognize that imposing less than optimal environmental conditions or environmental stresses is likely to produce a negative impact on crop growth and development and ultimately, the yield. Obviously, in the interest of producing crops with high health-promoting qualities, a balance between crop quality and yield needs to be maintained. Indeed, recent studies on lettuce have shown that the adverse effects of environmental stresses can be minimized or even eliminated by employing mild stresses over a brief period of time just prior to harvest. Also, the use of postharvest treatments to improve the quality of food crops can obviate this problem. Unlike under field conditions, environmental parameters can be better controlled during postharvest stage. Although there are some studies that show significant quality improvements in fruits and vegetables during postharvest stage, especially, in response to light, yet very little information is available to develop standardized postharvest procedures involving environmental factors. The focus in extending postharvest life of fruits and vegetables will have to be to develop new and to identify the existing postharvest practices that maintain or improve their quality, not just defined by aesthetics, taste, flavor, etc., but also by the health-promoting characteristics.

Under filed conditions, besides environmental considerations, other factors such as plant nutrition, various soil factors and biotic stresses are also likely to affect the plants' response in relation to phytochemicals. Hence, naturally, the crop management and production practices, which in many ways incorporate many of the above factors in various proportions, are bound to affect this response, as has been shown in a number of field studies. With growing interest in plant based-diet and health, we can anticipate that crop and cultivar-specific research will result in cultural and management practices that optimize phytochemical composition along with other crop quality factors and yield in order to consistently provide consumers with fruits and vegetables rich in heath-promoting qualities and nutrition.

REFERENCES

Aires A, Rosa E, Carvalho R (2006) Effect of nitrogen and sulfur fertilization on glucosinolates in the leaves and roots of broccoli sprouts (*Brassica oleracea* var. *italica*). *Journal of the Science of Food and Agriculture* **86**, 1512-1516

Alba R, Cordonnier-Pratt MM, Pratt LH (2000) Fruit-localized phytochromes regulate lycopene accumulation independently of ethylene production in tomato. *Plant Physiology* **123**, 363-370

Ames BN (1989) Endogenous oxidative DNA damage, aging, and cancer. *Free Radical Research Communications* **7**, 121-128

Ames BN, Shigenaga MK, Hagen TM (1993) Oxidants, antioxidants and the degenerative diseases of aging. *Proceedings of the National Academy of Sciences USA* **90**, 7915-7922

Asami DK, Hong YJ, Barrett DM, Mitchell AE (2003) Comparison of the total phenolic and ascorbic acid content of freeze-dried and air-dried marionberry, strawberry, and corn grown using conventional, organic, and sustainable agricultural practices. *Journal of Agricultural and Food Chemistry* **51**, 1237-1241

Atkinson CJ, Netsby R, Ford YY, Dodds PAA (2005) Enhancing beneficial antioxidants in fruits: A plant physiological perspective. *BioFactors* **23**, 229-234

Bieza K, Lois R (2001) An *Arabidopsis* mutant tolerant to lethal ultraviolet-B levels show constitutively elevated accumulation of flavonoids and other phenolics. *Plant Physiology* **126**, 1105-1115

Birt DF, Hendrich S, Wang W (2001) Dietary agents in cancer prevention: flavonoids and isoflavonoids. *Pharmacology and Therapeutics* **90**, 157-177

Block G, Patterson B, Subar A (1992) Fruit, vegetables, and cancer prevention: A review of the epidemiological evidence. *Nutrition and Cancer* **18**, 1-29

Bourn D, Prescott J (2002) A comparison of the nutritional value, sensory qualities, and food safety of organically and conventionally produced foods. *Critical Reviews in Food Science and Nutrition* **42**, 1-34

Brandt K, Mølgaard JP (2001) Organic agriculture: Does it enhance or reduce the nutritional value of plant foods? *Journal of the Science of Food and Agriculture* **81**, 924-931

Burritt DJ, Mackenzie S (2003) Antioxidant metabolism during acclimation of *Begonia* x *erythrophylla* to high light levels. *Annals of Botany* **91**, 783-7994

Cantos E, Gracia-Viguera C, Pascal-Teresa S de, Tomas-Barberan FA (2000) Effect of postharvest ultraviolet irradiation on resveratrol and other phenolics of cv. Napoleon table grapes. *Journal of Agricultural and Food Chemistry* **48**, 4606-4612

Cao G, Sofic E, Prior RL (1996) Antioxidant capacity of tea and common vegetables. *Journal of Agricultural and Food Chemistry* **44**, 3426-3431

Carbonaro M, Mattera M, Nicoli S, Bergamo P, Cappelloni M (2002) Modulation of antioxidant compounds in organic vs conventional fruit (peach *Prunus persica* L., and pear, *Pyrus communis* L.). *Journal of Agricultural and Food Chemistry* **50**, 5458-5462

Chappell J, Hahlbrock K (1984) Transcription of plant defense genes in response to UV light or fungal elicitor. *Nature* **311**, 76-78

Christie PJ, Alfenito MR, Walbot V (1994) Impact of low-temperature stress on general phenylpropanoid and anthocyanin pathways: enhancement of transcript abundance and anythocyanin pigmentation in maize seedlings. *Planta* **194**, 541-549

Chung I-M, Park M-R, Chun J-C, Yun S-J (2003) Resveratrol accumulation and resveratrol synthase gene expression in response to abiotic stresses and hormones in peanut plants. *Plant Science* **164**, 103-109

Currence TM (1940) A comparison of tomato varieties for vitamin C content. *Proceedings of the American Society for Horticultural Sciences* **37**, 901-906

De Groot H, Rauen U (1998) Tissue injury by reactive oxygen species and the protective effects of flavonoids. *Fundamental and Clinical Pharmacology* **12**, 249-255

Demmig-Adams B, Adams WW III (2002) Antioxidants in photosynthesis and human nutrition. *Science* **298**, 2149-2153

Demmig-Adams B, Adams WW III, Ebbert V, Logan BA (1999) Ecophysiology of the xanthophyll cycle. In: Frank HA, Young HA, Britton G, Cogdell RJ (Eds) *The Photochemistry of Carotenoids-Advances in Photosynthesis and Respiration* (Vol 8), Kluwer Academic Publishers, Dordrecht, Netherlands, pp 245-269

Dixon RA, Paiva NL (1995) Stress-induced phenylpropanoid metabolism. *Plant Cell* **7**, 1085-1097

Doll R (1990) An overview of the epidemiological evidence linking diet and cancer. *Proceedings of the Nutrition Society* **49**, 119-131

Dong YU, Mitra D, Kootstra A (1995) Postharvest simulation of skin color in Royal Gala apple. J*ournal of the American Society for Horticultural Science* **120**, 95-100

Dumas Y, Dadomo M, Lucca GD, Grolier P (2003) Effects of environmental factors and agricultural techniques on antioxidant content of tomatoes. *Journal of the Science of Food and Agriculture* **83**, 369-382

Dussi MC. Sugar D, Wrolstad RE (1995) Characterizing and quantifying anthocyanins in red pears and the effect of light quality on fruit color. *Journal of the American Society for Horticultural Science* **120**, 785-789

Esteban MA, Villanueva M, Lissarrague JR (2001) Effect of irrigation on changes in the anthocyanin composition of the skin of Tempranillo (*Vitis vinifera* L) grape berries during ripening. *Journal of the Science of Food and Agriculture* **81**, 409-420

Fiscus EL, Philbeck R, Britt AB, Booker FL (1999) Growth of Arabidopsis flavonoid mutants under solar radiation and UV filters. *Environmental and Experimental Botany* **41**, 231-245

Garcia-Macias P, Ordidge M, Vysini E, Waroonphan S, Battey N, Gordon MH, Hadley P, John P, Lovegrove JA, Wagstaffe A (2007) 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* **55**, 10168-10172

Gautier H, Diakou-Verdin V, Benard C, Reich M, Buret M, Bourgaud F, Poessel JL, Caris-Veyrat C, Genard M (2008) How does tomato quality (sugar, acid, and nutritional quality) vary from ripening stage, temperature, and irradiance? *Journal of Agricultural and Food Chemistry* **56**, 1241-1250

Gershenzon J (1984) Changes in the levels of plant secondary metabolites under water and nutrient stress. *Recent Advances in Phytochemistry* **18**, 273-320

Grace SC, Logan BA, Adams WW III (1998) Seasonal differences in foliar content of chlorogenic acid, a phenylpropanoid antioxidant, in *Mahonia repens*. *Plant, Cell and Environment* **21**, 513-521

Halliwell B (1987) Oxidants and human disease: some new concepts. *FASEB Journal* **1**, 358-364

Hasegawa H, Fukasawa-Akada T, Okuno T, Niizeki M, Suzuki M (2001) Anthocyanin accumulation and related gene expression in Japanese parsley (*Oenanthe stolonifera*, DC) induced by low temperature. *Journal of Plant Physiology* **158**, 71-78

Hernandez I, Alegre L, Munne-Bosch S (2004) Drought-induced changes in flavonoids and other low molecular weight antioxidants in *Citrus clusii* grown under Mediterranean field conditions. *Tree Physiology* **24**, 1303-1311

Higashio H, Hirokane H, Sato F, Tokuda S, Uragami A (2005) Effect of UV irradiation after the harvest on the content of flavonoid in vegetables. *Acta Horticulturae* **682**, 1007-1012

Higashio H, Hirokane H, Sato F, Tokuda S, Uragami A (2007) Enhancement of functional compounds in *Allium* vegetables with UV radiation. *Acta Horticulturae* **744**, 357-361

Hochmuth GJ, Brecht JK, Bassett MJ (1999) Nitrogen fertilization to maximize carrot yield and quality on a sandy soil. *HortScience* **34**, 641-645

Hohl U, Neubert b, Pforte H, Schonof I, Bohm H (2001) Flavonoid concentrations in the inner leaves of head of lettuce genotypes. *European Food Research and Technology* **213**, 205-211

Hormaetxe K, Esteban R, Bercerril JM, Garcia-Plazola JI (2005) Dynamics of the alpha-tocopherol pool as affected by external (environmental) and internal (leaf age) factors in *Buxus sempervirens* leaves. *Physiologia Plantarum* **125**, 333-344

Hrazdina G, Parsons GF (1982) Induction of flavonoid synthesizing enzymes by light in etiolated pea (*Pisum sativum* cv. Midfreezer) seedlings. *Plant Physiology* **70**, 506-510

Joseph JA, Denisova NA, Bielinski D, Fisher DR, Shukitt-Hale B (2000) Oxidative stress protection and vulnerability in aging: putative nutritional implications for intervention. *Mechanisms of Ageing and Development* **116**, 141-153

Ju Z-Q, Duan Y-S, Ju Z-G (1999) Effects of covering the orchard floor with reflecting films on pigment accumulation and fruit coloration in 'Fuji' apples. *Scientia Horticulturae* **82**, 47-56

Kakes P (1991) The genetics and ecology of variation in secondary plant substances. In: Rozema J, Verkleij JAC (Eds) *Ecological Responses to Environmental Stresses*, Kluwer, The Netherlands, pp 234-249

Kalt W (2005) Effects of production and processing factors on major fruit and vegetable antioxidants. *Journal of Food Science* **70**, R11-R19

Kataoka I, Beppu K (2004) UV irradiance increases development of red skin color and anthocyanin in 'Hakuho' peach. *HortScience* **39**, 1234-1237

Kataoka I, Beppu K, Sugiyama A, Tiara S (1996) Enhancement of coloration of Satohnishiki sweet cherry fruit by postharvest irradiation with ultraviolet rays. *Environment Control in Biology* **34**, 313-319

Keles Y, Oncel I (2002) Response of antioxidative defense system to temperature and water stress combinations in wheat seedlings. *Plant Science* **163**, 783-790

Kimura M, Yamamoto YY, Seki M, Sakurai T, Sato M, Abe T, Yoshida S, Manabe K, Shinozaki K, Matsui M (2003) Identification of Arabidopsis genes regulated by high light-stress using cDNA microarray. *Phytochemistry and Photobiology* **77**, 226-233

Kirakosyan A, Seymour E, Kaufman PB, Warber S, Bolling S, Chang SC (2003) Antioxidant capacity of polyphenolic extracts from leaves of *Crataegus laevigata* and *Crataegus monogyna* (hawthorn) subjected to drought and cold stress. *Journal of Agricultural and Food Chemistry* **51**, 3973-3976

Kolb CA, Kopecky J, Pfundel EE (2003) UV screening by phenolics in berries of grapevine (*Vitis vinifera*). *Functional Plant Biology* **30**, 1177-1186

Kopsell DA, Barickman TC, Sams CE, McElroy JS (2007) Influence of nitrogen and sulfur on biomass production and carotenoid and glucosinolate concentration in water cress (*Nasturtium officinale* R. Br.). *Journal of Agricultural and Food Chemistry* **55**, 10628-10634

Laaksonen DE, Sen CK (2000) Exercise and oxidative stress in diabetes mellitus. In: Sen CK, Packer L, Hanninen OOP (Eds) *Handbook of Oxidants and Antioxidants in Exercise*, Elsevier, Amsterdam, pp 1105-1136

Lagouge M, Argmann C, Gerhart-Hines Z, Meziane H, Lerin C, Daussin F, Messadeq N, Milne J, Lambert P, Elliott P, Geny B, Laakso M, Puigserver P, Auwerx J (2006) Resveratrol improves mitochondrial function and protects against metabolic disease by activating SIRT1 and PGC-1alpha. *Cell* **127**, 1109-1122

Lancaster JE (1992) Regulation of skin color in apples. *Critical Review in Plant Sciences* **10**, 487-502

Langcake P, Pryce RJ (1977) The production of resveratrol and the viniferins by grapevines in response to ultraviolet irradiation. *Phytochemistry* **16**, 1193-1196

Lasheras C, Fernandez S, Patterson AM (2000) Mediterranean diet and age with respect to overall survival in institutionalized nonsmoking elderly people. *American Journal of Clinical Nutrition* **71**, 987-992

Lattanzio V (2003) Bioactive polyphenols: Their role in quality and storability of fruit and vegetables. *Journal of Applied Botany* **77**, 128-146

Lee SK, Kader AA (2000) Preharvest and postharvest factors influencing vitamin C content of horticultural crops. *Postharvest Biology and Technology* **20**, 207-220

Lefsrud MG, Kopsell DA, Curran-Celentano J (2005) Air temperature affects biomass carotenoid pigment accumulation in kale and spinach grown in a controlled environment. *HortScience* **40**, 2026-2030

Lester GE (2006) Environmental regulation of human health nutrients (ascorbic acid, beta-carotene, and folic acid) in fruits and vegetables. *HortScience* **41**, 59-64

Li J, Ou-Lee TM, Raba R, Amundson RG, Last RL (1993) Arabidopsis flavonoid mutants are hypersensitive to UV-B irradiation. *Plant Cell* **5**, 171-179

Li S, Schonhof I, Krumbein A, Li L, Stutzel H, Schriener M (2007) Glucosinolate concentration in turnip (*Brassica rapa* ssp. *rapifera* L.) roots as affected by nitrogen and sulfur supply. *Journal of Agricultural and Food Chemistry* **55**, 8452-8457

Lippmann B, Mascher R, Balko C, Bergmann H (2000) UV induction of *trans*-resveratrol biosynthesis in the leaves of greenhouse and *in vitro* grown potatoes (*Solanum tuberosum* L.). *Journal of Applied Botany* **74**, 160-163

Liu RH (2004) Potential synergy of phytochemicals in cancer prevention: Mechanism of action. *Journal of Nutrition* **134**, 3479S-3485S

Liu B, Tu C, Hu S, Gumpertz M, Ristaino JB (2007) Effect of organic, sustainable, and conventional management strategies in grower fields on soil physical, chemical, and biological factors and the incidence of Southern blight. *Applied Soil Ecology* **37**, 202-214

Lois R, Buchanan BB (1994) Severe sensitivity to ultraviolet radiation in an *Arabidopsis* mutant deficient in flavonoid accumulation. II. Mechanisms of UV-resistance in *Arabidopsis*. *Planta* **194**, 504-509

Lombardi-Boccia G, Lucarini M, Lanzi S, Aguzzi A, Cappelloni M (2004) Nutrients and antioxidant molecules in yellow plums (*Prunus domestica* L.) from conventional and organic productions: a comparative study. *Journal of Agricultural and Food Chemistry* **52**, 90-94

Lundegardh B, Martensson A (2003) Organically produced plant foods – Evidence of health benefits. *Acta Agriculturae Scandinavica, Section B* **53**, 3-15

Luthria D, Mukhopadhyay S, Krizek DT (2006) Content of total phenolic acids in tomato (*Lycopersicon esculentum* Mill.) fruits as influenced by cultivar and solar UV radiation. *Journal of Food Composition and Analysis* **19**, 771-777

Mäder P, Fliebach A, Dubois D, Gunst L, Fried P, Niggli U (2002) Soil fertility and biodiversity in organic farming. *Science* **296**, 1694-1697

Magkos F, Arvaniti F, Zampelas A (2003) Organic food: nutritious food or food for thought? A review of the evidence. *International Journal of Food Sciences and Nutrition* **54**, 357-371

Malusà E, Laurenti E, Ghibaudi E, Rolle L (2004) Influence of organic and conventional management on yield and composition of grape cv. 'Grignolino.' *Acta Horiculturae* **640**, 135-141

Marchand L (2002) Cancer preventive effects of flavonoids – a review. *Biomedicine and Pharmacotherapy* **56**, 296-301

Mitchell AE, Hong YJ, Koh E, Barrett DM, Bryant DE, Denison RF, Kaffka S (2007) Ten-year comparison of the influence of organic and conventional crop management practices on the content of flavonoids in tomatoes. *Journal of Agricultural and Food Chemistry* **55**, 6154-6159

Mittler R (2002) Oxidative stress, antioxidants and stress tolerance. *Trends in Plant Science* **7**, 405-410

Munne-Bosch S (2005) The role of alpha-tocopherol in plant stress tolerance. *Journal of Plant Physiology* **162**,743-748

Ness A, Egger M, Powles J (1999) Fruit and vegetables, and ischaemic heart disease: systematic review or misleading meta-analysis? *European Journal of Clinical Nutrition* **53**, 900-902

Norbaek R, Aaboer DBF, Bleeg IS, Christensen BT, Kondo T, Brandt K (2003) Flavone C-glycoside, phenolic acid, and nitrogen contents in leaves of barley subject to organic fertilization treatments. *Journal of Agricultural and Food Chemistry* **51**, 809-813

Oh MM (2008) Plant adaptation and enhancing phytochemicals in lettuce through environmental stresses. PhD thesis, Kansas State University, Manhattan, KS, 175 pp

Oh MM, Trick HN, Rajashekar CB (2009a) Secondary metabolism and antioxidants are involved in environmental adaptation and stress tolerance in lettuce. *Journal of Plant Physiology* **166**, 180-191

Oh MM, Carey EE, Rajashekar CB (2009b) Environmental stresses induce health-promoting phytochemicals in lettuce. *Plant Physiology and Biochemistry* **47**, 578-583

Olsson ME, Andersson CS, Oredsson S, Berglund RH, Gustavsson KE (2006) Antioxidant levels and inhibition of cancer cell proliferation in vitro by extracts from organically and conventionally cultivated strawberries. *Journal of Agricultural and Food Chemistry* **54**, 1248-1255

Pennycooke JC, Cox S, Stushnoff C (2004) Relationship of cold acclimation, total phenolic content and antioxidant capacity with chilling tolerance in petunia (*Petunia* x *hybrida*). *Environmental and Experimental Botany* **53**, 225-232

Peto R, Doll R, Buckley JD, Sporn MB (1981) Can dietary beta-carotene materially reduce human cancer rates? *Nature* **290**, 201-208

Pluskota WE, Michalczyk DJ, Gorecki RJ (2005) Control of phenylalanine ammonia-lyase gene promoters from pea by UV radiation. *Acta Physiologiae Plantarum* **27**, 229-236

Prior RL, Cao G (2000) Antioxidant phytochemicals in fruits and vegetables: Diet and health implications. *HortScience* **35**, 588-592

Romani A, Pimnelli P, Galardi C, Sani G, Cimato A, Heimler D (2002) Polyphenols in greenhouse and open-air-grown lettuce. *Food Chemistry* **79**, 337-342

Rosales MA, Ruiz JM, Hernandez J, Soriano T, Castilla N, Romero L (2006) Antioxidant content and ascorbate metabolism in cherry tomato exocarp in relation to temperature and solar radiation. *Journal of the Science and Food Agriculture* **86**, 1545-1551

Schirrmacher G, Schnitzler WH, Grassmann J (2007) Influence of UV-light on the antioxidative capacity of extracts from *Spinacia oleracea* L. and *Gynura bicolor* (Wild.) DC. *Acta Horticultrae* **747**, 357-364

Schreiner M (2005) Vegetable crop management strategies to increase the quantity of phytochemicals. *European Journal of Nutrition* **44**, 85-94

Schreiner M, Huyskens-Keil S (2006) Phytochemicals in fruits and vegetables: Health promotion and postharvest elicitors. *Critical Review in Plant Sciences* **25**, 267-278

Sousa C, Pereira DM, Pereira JA, Bento A, Rodrigues MA, Dopico-Grarcia S, Valentao P, Lopes G, Ferreres F, Seabra RM, Andrade PB (2008) Multivariate analysis of tronchuda cabbage (*Brassica oleracea* L. var. *costata* DC) phenolics: influence of fertilizers. *Journal of Agricultural and Food Chemistry* **56**, 2231-2239

Steinmetz KA, Potter JD (1996) Vegetables, fruit, and cancer prevention: a review. *Journal of the American Dietetic Association* **96**, 1027-1039

Steyn WJ, Holcroft DM, Wand SJE, Jacobs G (2004) Regulation of pear color development in relation to activity of flavonoid enzymes. *Journal of the American Society for Horticultural Science* **129**, 6-12

Sun J, Chu Y, Wu X, Liu RH (2002) Antioxidant and antiproliferative activities of common fruits. *Journal of Agricultural and Food Chemistry* **50**, 7449-7454

Takayanagi T, Okuda T, Mine Y, Yokotsuka K (2004) Induction of resveratrol biosynthesis in skins of three grape cultivars by ultraviolet irradiation. *Journal of the Japanese Society for Horticultural Science* **73**, 193-199

Tarozzi A, Hrelia S, Angeloni C, Morroni F, Biagi P, Guardigli M, Cantelli-Forti G, Hrelia P (2006) Antioxidant effectiveness of organically and non-organically grown red oranges in cell culture systems. *European Journal of Nutrition* **45**, 152-158

Tattini M, Galardi C, Pinelli P, Massai R, Remorini D, Agati C (2004) Differential accumulation of flavonoids and hydroxycinnamates in leaves of *Ligustrum vulgare* under excess light and drought stress. *New Phytologist* **163**, 547-561

Taylor A (1992) The role of nutrients in delaying cataracts. *Annals of the New York Academy of Sciences* **669**, 111-123

Tomas-Barberan F, Espin CJ (2001) Phenolic compounds and related enzymes as determinants of quality in fruits and vegetables. *Journal of the Science of Food and Agriculture* **81**, 853-876

Tsormpatsidis E, Henbest RGC, Davis FJ, Battey NH, Hadley P, Wagstaffe A (2008) UV irradiance as a major influence on growth, development and secondary products of commercial importance in Lollo Rosso lettuce 'Revolution' grown under polyethylene films. *Environmental and Experimental Botany* **63**, 232-239

van Diepeningen AD, de Vos OJ, Korthals GW, van Bruggen AHC (2006) Effects of organic versus conventional management on chemical and biological parameters in agricultural soils. *Applied Soil Ecology* **31**, 120-135

Versari A, Parinello GP, Torneilli GB, Ferrarini R, Giulivo C (2001) Stilbene compounds and stilbene synthase expression during ripening, wilting, and UV treatment in grape cv. Corvina. *Journal of Agricultural and Food Chemistry* **49**, 5531-5536

Virgili F, Marino M (2008) Regulation of cellular signals from nutritional molecules: a specific role for phytochemiclas, beyond antioxidant activity. *Free Radical Biology and Medicine* **45**, 1205-1216

Wang H, Cao GH, Prior RL (1996) Total antioxidant capacity of fruits. *Journal of Agricultural and Food Chemistry* **44**, 701-705

Wink M (1999) Introduction: biochemistry, role and biotechnology of secondary metabolites. In: Wink M (Ed) *Biochemistry of Plant Secondary Metabolism. Annual Plant Reviews* (Vol 2), Sheffield Academic Press, Sheffield, UK, 358 pp

Wink M (2008) Plant secondary metabolism: Diversity, function and its evolution. *Natural Product Communications* **3**, 1205-1216

Wolfe KL, Kang X, He X, Dong M, Zhang Q, Liu RH (2008) Cellular antioxidant activity of common fruits. *Journal of Agricultural and Food Chemistry* **56**, 8418-8426

Yaginuma S, Shiraishi T, Ohya H, Igarashi K (2002) Polyphenol increases in safflower and cucumber seedlings exposed to strong visible light with limited water. *Bioscience, Biotechnology and Biochemistry* **66**, 65-72

Young JE, Zhao X, Carey EE, Welti R, Yang S, Wang W (2005) Phytochemical phenolics in organically grown vegetables. *Molecular Nutrition and Food Research* **49**, 1136-1142

Zhao X, Carey EE, Benbrook C (2007) The influence of organic production on nutritional quality of fruit and vegetables: a meta-analysis. *HortScience* **42**, 885

Zhao X, Carey EE, Wang W, Rajashekar CB (2006) Does organic production enhance phytochemical content of fruit and vegetables? Current knowledge and prospects for research. *HortTechnology* **16**, 449-456

Zhao X, Nechols JR, Williams KA, Wang W, Carey EE (2009) Comparison of phenolic acids in organically and conventionally grown pac choi (*Brassica rapa* L. *Chinensis* group). *Journal of the Science of Food Agriculture* **89**, 940-946

Zobayed SMA, Afreen F, Kozai T (2007) Phytochemical and physiological changes in the leaves of St. John's wort plants under a water stress condition. *Environmental and Experimental Botany* **59**, 109-116