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Enzymatic Browning of Foods

Quantitative Relationships between Browning and Food Constituents

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Enzymatische Bräunung in Lebensmitteln

Quantitative Beziehungen zwischen Bräunung und Lebensmittelinhaltsstoffen

Zusammenfassung. Quantitative Beziehungen zwischen enzymatischer Bräunung von Lebensmitteln und den verantwortlichen Inhaltsstoffen (z. B. Phenoloxidase, phenolische Substrate, Inhibitoren) werden diskutiert. Darüber hinaus wird über die Effekte äußerer Faktoren (z. B. Klima, Düngemittel, Phytohormone, Pesticide, γ-Bestrahlung, Lagerzeit und -temperatur) auf die Bräunung berichtet.

Summary. Quantitative relationships between enzymatic browning of foods and the responsible food constituents (e.g. phenol oxidase, phenolic substrates, inhibitors) are discussed. Attention is also given to the effects of extrinsic factors (e.g., climatic factors, fertilizers, phytohormones, pesticides, γ-irradiation, storage time and temperature) on the rates of browning.

Enzymatic browning following mechanical injury of plants is a serious problem during handling, storage, and processing of many foods. In the manufacture of some foods (e.g. tea, cacao, raisins, dates, cider) it is an essential part of the process.

The fundamental step in enzymatic browning is the oxidation of phenolic compounds to o-quinones in the presence of oxygen. This oxidation is brought about by the catalytic action of phenol oxidase (EC 1.14.18.1). The o-quinones then condense to form brown or black pigments.

Different cultivars of many fruits and vegetables at the stage of maturity are known to differ in their rates of browning. Changes in the rates of discoloration have been observed during development, during storage, and upon various treatments of fruits and vegetables. It is generally believed that differences in the rates of browning are caused by quantitative rather than qualitative differences of the responsible plant constituents. However, recent observations also indicate qualitative differences between phenol oxidases from different apple cultivars [1, 2].

Excellent reviews on the properties of plant phenol oxidases, the phenolic compounds involved in browning, and the control of browning by various treatments are available [3–8]. This review discusses the quantitative relationships between the rates of browning and the responsible factors in various foods. Effects of extrinsic factors on the rates of browning are also reported.

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Intrinsic Factors Contributing to the Rate of Browning

The rate of browning depends on the following factors: (a) concentration and substrate specificity of phenol oxidase(s), (b) concentration and type of phenolic compound(s), (c) concentration of naturally occurring inhibitor(s), (d) concentration of oxygen, (e) pH of the tissue, (f) temperature of the tissue, and (g) (as reported for potatoes, see below) concentration of lipid compounds.

Ascorbic acid probably is the most common naturally-occurring inhibitor of enzymatic browning in fruits and vegetables. It reduces the initial oxidation products, the o-quinones, back to the o-diphenols until it is quantitatively oxidized to dehydroascorbic acid. In addition to this effect, ascorbic acid is reported to inhibit the enzyme directly [9–11]. The latter effect is contradicted by Duden and Siddiqui [12] who conclude that the observed "inhibition" during the action of phenol oxidase in the presence of ascorbic acid is due to exhaustion (reaction-inactivation) of the enzyme.

Other naturally-occurring inhibitors, e.g. compounds containing sulfhydryl groups such as cysteine or glutathione, may act by reducing the o-quinones as described for ascorbic acid and/or by inhibiting the enzyme directly by blocking the copper of the active site. In addition, there are several reports on polypeptide inhibitors of phenol oxidase activity in the literature [7].

Relationships between Rate of Browning and Single Parameters

Phenol Oxidase. The quantitative relationships between the concentration of phenol oxidase and the rate of browning has been studied in apples [13–22], apri-

cots [18, 23], avocados [24–27], bananas [28–30], chillies [31], eggplants [32], macaroni [33], mangos [34], olives [35], peaches [36, 37], potatoes [38–57], snap beans [58, 59], sweet potatoes [60, 61] and wheat [62, 63]. The samples analyzed include fruits and vegetables during development and ripening [13, 14, 19, 20, 22, 30, 39–41], several cultivars of fruits and vegetables at the stage of maturity [13, 16–19, 21, 23–27, 31, 32, 34, 36, 42–46, 48, 50–55, 58, 59, 62, 63], different tissues of one fruit or tuber [13, 24, 43, 51, 53, 54], several cultivars of fruits and vegetables during storage at various temperatures [15, 17, 38, 40, 41, 46, 48, 51, 54, 56, 57, 61], fruits and vegetables treated with growth regulators [37, 60] and gamma-irradiation [28, 29, 34, 47], potato tubers of different specific gravities [49] and flour during pasta production [33].

Positive correlations [13–21, 24–29, 32–34, 36–47, 60, 62, 63] and no correlations [15, 18, 22, 23, 30, 31, 35, 38, 50–59, 61] have both been found. In the case of potatoes, negative correlations have also been reported [40, 41, 48, 49].

Phenolic Compounds. Attempts were made to correlate the rate of browning with the concentrations of total phenols, o-diphenols, catechins, chlorogenic acid, caffeic acid, tyrosine and dopamine.

Relationships between *total phenol* content and browning have been studied in apples [14, 19, 22], avocados [24], bananas [64], chillies [31], mangos [34], peaches [65–67], pears [68], potatoes [38, 39, 41, 42, 44, 47–49, 54, 56, 69], snap beans [58, 59], strawberry preserves [70], sweet potatoes [60] and wheat [63]. The samples analyzed include fruits and vegetables during development and ripening [14, 19, 22, 39, 41], several cultivars of different fruits and vegetables at the stage of maturity [19, 24, 38, 42, 44, 48, 54, 58, 59, 63, 66–68, 70], different tissues of one fruit or tuber [24, 54], several cultivars of different fruits and vegetables during storage at various temperatures [38, 41, 42, 48, 64, 69], fruits and vegetables treated with ethylene [47, 60] and gamma-irradiation [34], potato tubers of different specific gravities [49], and potato tubers after virus infection [56].

Positive correlations [22, 24, 34, 39, 41, 47, 49, 56, 58–60, 63, 65–70] and no correlations [14, 19, 31, 38, 41, 42, 44, 48, 54] have both been found. During storage of bananas, a negative correlation was found [64].

Relationships between browning and *o-diphenol* content were studied in apples [13, 15–18], apricots [18, 23], avocados [24], olives [35], and peaches [36, 37]. The samples analyzed included one apple cultivar during fruit development [13] or during storage at various temperatures [15, 17], several cultivars of different fruits at the stage of maturity [13, 16–18, 23, 24, 35, 36], different tissues of avocado fruits [24], and one peach cultivar treated with various growth regulators [37].

Positive correlations [13, 15–18, 23, 24, 36] and no correlations [15, 17, 18, 24, 37] have both been reported.

No correlation between browning and *catechin* content could be detected in one apple cultivar during fruit development [20] and in several apple cultivars at the stage of maturity [21]. By contrast, a positive correlation has been found in several pear cultivars at the stage of maturity [68].

Relationships between browning and *chlorogenic acid* content were studied in apples [15, 17, 19–21], chicory [71], peaches [36], pears [68], potatoes [38, 42, 50–53] and sweet potatoes [61, 72]. Samples analyzed include several apple cultivars during fruit development and ripening [19, 20], several cultivars of different fruits and vegetables at the stage of maturity [15, 17, 19, 21, 36, 38, 42, 44, 50–52, 68], different tissues of potato tubers [51–53], several cultivars of different fruits and vegetables during storage at various temperatures [15, 17, 38, 42, 51, 72] and chicory treated with gamma-irradiation [71].

Positive correlations [15, 17, 19, 20, 36, 61, 68, 72] and no correlations [15, 21, 38, 42, 44, 50–53, 71] have both been reported. It is remarkable that in all studies performed on relationships between concentration of chlorogenic acid or caffeic acid and the rate of browning of potatoes [38, 42, 44, 50–53], no correlations could be found.

The concentration of *dopamine* has been reported to be positively correlated with the rate of browning of bananas during ripening [30].

Relationships between browning and *tyrosine* content were studied in flour during macaroni production [33], several wheat cultivars at the stage of maturity [63], and in potatoes including several cultivars at the stage of maturity [43–45, 50–55, 73], different tissues of one tuber [43, 51–54], and several cultivars during storage at various temperatures [51, 54, 57].

Positive correlations [33, 43, 50–54, 63, 73] and no correlations [44, 45, 55, 57] have both been found.

Ascorbic Acid. The quantitative relationships between ascorbic acid content and rate of browning have been studied in apples [14, 19, 20, 22], bananas [30], mangos [34], peaches [37], potatoes [44, 74], strawberry preserves [70], sweet potatoes [72] and tea [75]. The samples analyzed include several cultivars of apples [14, 19, 20, 22] and bananas [30] during fruit development and ripening, several cultivars of apples [19], potatoes [44, 74], and tea [75] at the stage of maturity, one cultivar of sweet potatoes during storage [72] and several fruits treated with various growth regulators [37] and gamma-irradiation [34]. In most cases, the concentration of ascorbic acid was negatively correlated with the rate of browning [14, 30, 34, 44, 70, 72, 74, 75]. In some cases, no correlation could be found [19, 20, 22, 37].

Lipid Compounds. Relationships between enzymatic browning and lipid content have only been studied in potatoes. The negative correlation reported [56, 76–79] was interpreted to mean "within the cell, polyphenol oxidase enzymes located in the mitochondria are separated from their phenolic substrates located in the vacuole by lipoprotein membranes and any alteration of these membranes may result in greater susceptibility to darkening" [79].

pH and Temperature. The pH and temperature of the plant tissues may have considerable effects on the rate of browning. Of the foods listed in Table 1, only the tissue pH of potatoes, plums, and sweet potatoes coincide roughly with the pH optima of the corresponding phenol oxidases. In other foods, even little changes in the tissue pH greatly influence the enzyme activity (Table 1), and consequently the rate of browning. Using the same phenolic substrate, the pH optima of isolated enzymes do not necessarily coincide with the pH optima as measured in the corresponding plant homogenates (Table 1).

Considerable work has been reported on the thermal inactivation characteristics of phenol oxidases at high temperatures [80, 121, 122]. However, little is known on the temperature optima of the enzymes (Table 2), although these data may be of great interest in chosing storage or processing conditions to minimize browning reactions.

Relationships Between Rate of Browning and More Than One Parameter

Since the rate of browning depends, in some cases, mainly on the concentration of phenol oxidase, in other cases mainly on the concentration of phenolic compounds, and since the concentration of reducing substances (ascorbic acid) is also important, attempts were made to correlate more than one parameter with the rate of browning.

Weurman and Swain [14] demonstrated a positive correlation between the *ratio of total phenols/ascorbic acid* and browning of apples during fruit development.

Vamos-Vigyazo et al. [18] failed to show an apparent relationship between the *ratio of phenol oxidase/odiphenols* and browning of apples. For both apples and apricots, however, they found that, if the numerical values of the ratios are below 20, the rate of browning is a linear function of the enzyme concentration. If the numerical values of the ratios exceed 35, the rate of browning is a linear function of the o-diphenol concentration. The authors assume "that in the first case, the amount of substrate present in the fruit is sufficient for the formation of reaction products in a concentration high enough to inactivate the enzyme during the reaction before the substrate is depleted. In this case, enzyme inactivation is the limiting factor of the reaction. In the second case, even complete transformation of the substrate might not yield reaction products in a concentration sufficient to inactivate the enzyme. Consequently, substrate depletion must be the limiting factor of the reaction" [18].

With factorial analysis and multiple regression analysis, Schaller and Amberger [45] demonstrated that enzymatic browning of potatoes is essentially influenced by the concentrations of *phenol oxidase, total phenols, basic amino acids, dry matter, chlorogenic acid, and flavonols.* The influence of the basic amino acids on the rate of browning could not be explained.

Of the two main phenolic compounds in potatoes, chlorogenic acid and tyrosine, the latter is thought to be the major substrate in the browning reactions. Although chlorogenic acid is readily oxidized by potato phenol oxidase, its oxidation products are yellow or yellow-brown, whereas tyrosine yields dark brown and subsequently black pigments [52, 53, 130]. Based upon kinetic studies of the reactions catalyzed by potato phenol oxidase [131], a positive correlation between calculated *tyrosine turnover* and enzymatic browning of potatoes could be demonstrated [44, 132]. For this calculation, the concentrations of phenol oxidase, tyrosine, chlorogenic acid, and ascorbic acid have been considered.

Extrinsic Factors Contributing to the Rate of Browning

Enzymatic browning of fruits and vegetables is influenced by extrinsic factors, such as climatic factors, fertilizers, plant growth regulators (phytohormones), antibiotics, pesticides, nucleotides, gamma-irradiation, time and temperature of storage, and oxygen concentration in the storage or processing atmosphere.

Climatic Factors. Of the climatic factors (e.g. rainfall, sunshine, temperature), the effects of rainfall on enzymatic browning and on its responsible factors were studied. Increasing amounts of rainfall (or irrigation) increased the rate of browning of potatoes, which was paralleled by increases in phenol oxidase and substrate concentrations and by a decrease in ascorbic acid content [51–53, 133–136]. Increasing rainfall also decreased the ascorbic acid content of turnips [136], gooseberries [137], red currants [137] and strawberries [137, 138]. The reverse was found for rose fruits [139]. No clear effect of rainfall on the ascorbic acid content of apples, cherries and pears could be found [137].

Fertilizers. The effects of fertilizers on the rate of browning have been studied extensively in potatoes. Fertilization with *nitrogen* (applied as $Ca(NO_3)_2$, KNO_3, NH_4NO_3, or urea) is generally correlated posi-

Table 1. Tissue pH of some fruits and vegetables and pH optima of the corresponding phenol oxidases

Food	Tissue pH	pH optimum of		Enzyme activity % at tissue pH	Reference
		Purified or partially purified enzyme	Vegetable or fruit homogenate		
Apple	2.8–4.0				[14, 80–82]
		5.0[a]			[85]
		5.1 and 7.0–7.3[a, b]			[86–88]
			6.1–6.6[a]		[20, 83]
Grape	3.4				[89]
		5.0 with a shoulder at 7.3[b]			[90]
		5.9–6.3[c]		~50	[89–91]
		5.7[d]			[91]
Mango	2.9–3.2 (preclimacteric)			0	[34, 92]
	4.2–5.2 (ripe)			30	[34, 92]
		6.5–7.0[c, e, f]			[34, 93]
Orange juice	4	7–8[g]		25	[94]
Peach	3.4–4.2	5.9–7.2[c]		0–9	[37, 80, 95–97]
Pear	3.9				[80]
		4.0[a]		85	[98]
		6.2[c]		30	[99]
		7.0[c]			[100]
Potato	5.6–6.4				[43, 44, 82, 101–105]
		5.0 with a shoulder at 7.0[a]			[106]
		4.3 with a shoulder at 5–7[a, h]			[107. 108]
		4.0–6.0[b]			[108]
		5.0[b]			[109]
		6.0 with a shoulder at 4–5[b]			[110, 111]
		7.0[c, i]		~50	[112, 115]
		4.5–8.0[c]			[107, 108]
		5.8[c]			[113]
		6.5–7.5[f]			[114]
		4.5–6[g]			[107]
			6.0–7.0[a]		[83]
			8.2[i]		[116]
Plum	3.8	4.3[c]		90	[117]
Red beet	6.2		6.5–7.0[c]		[118]
Sweet potato	5.5–7.0				[61]
		6.0–7.0[h]			[119]
			4-5[c]		[120]

[a] chlorogenic acid, [b] 4-methylcatechol, [c] catechol, [d] pyrogallol, [e] dopamine, [f] p-cresol, [g] D,L-dopa, [h] caffeic acid, [i] L-tyrosine

tively with the rate of browning [46, 51–53, 76, 133, 140]. This is paralleled by increased concentrations of phenol oxidase [51, 53, 116, 141], chlorogenic acid [133], and tyrosine [51–53, 133], and by a decrease in ascorbic acid content [136, 142]. *Potassium* fertilization (KCl or K_2SO_4) is generally correlated negatively with the rate of browning of potatoes [46, 52, 69, 116, 129, 141, 143]. This is paralleled by decreased concentrations of phenol oxidase [46, 51, 129, 144], total phenols [69], o-diphenols [116, 141], chlorogenic acid [145], and tyrosine [52, 116, 141], and by increased ascorbic acid content [129]. *Phosphorus* (applied as Na_2HPO_4 or $CaHPO_4/Ca_3(PO_4)_2$) was correlated positively with the rate of browning and the tyrosine content of potatoes [51]. The ascorbic acid content was increased by phosphorus fertilization [143], but the effect on phenol oxidase was not clear [51, 116, 141]. The tendency of potato tubers to darkening decreased when manure + N:P:K fertilization was used, expecially when potassium was applied as KCl [143]. Recommended *N:P:K or N:K ratios* to minimize enzymatic browning of potatoes are 1:1.25:1.6 [146] or $1:\geqq 1$ [147], respectively. On the other hand, fertilization with an N:P:K ratio of 1:0.75:0.45 produced the highest ascorbic acid content in the tubers [148]. *Chlorine* fertilization (applied as $CaCl_2$ or NH_4Cl) resulted in decreased potato browning [133] and decreased chlorogenic acid content [145]. The effect of *copper* (Applied as $CuSO_4$, or Cu-EDTA) on potato discoloration is not clear. Positiv correlations [116] and no correlations [149] have both been found. The o-diphenol content increased and the tyrosine content decreased

Table 2. Temperature optima of phenol oxidases

Food	Temperature optimum, °C		Reference
	Purified or partially purified enzyme	Vegetable or fruit homogenate	
Apple	40[a]		[123]
		25–30[b]	[83]
Apricot		25[b]	[83]
Banana	37[a]		[124]
Barley	65[a]		[125]
Beet	25[a]		[126]
Grape	25–30[a]		[89]
Mushroom	42[a]		[127]
Peach	37[a]		[97]
Potato	22[a]		[113]
		>35[c]	[128]
		~50[d]	[129]
		55[e]	[116]
		30[f]	[116]
Plum	25–30[a]		[117]

[a] catechol, [b] chlorogenic acid, [c] pyrogallol, [d] substrate not indicated, [e] potato slices without added exogenous substrate, [f] L-tyrosine

with increasing amounts of copper application [116], the ascorbic acid content was enhanced [150]. *Boron* fertilization decreased enzymatic browning of potatoes [78]. *Magnesium* (applied as $MgSO_4$) decreased [46] or did not affect [151] potato discoloration. No effects on phenol oxidase [116, 141], o-diphenols [151] or tyrosine [151] could be found. Ascorbic acid concentration was enhanced [152]. *Molybdenum* and *zinc* fertilization also increased the ascorbic acid content of potatoes [150, 153], the effect of *manganese* (applied as $MnSO_4$) on ascorbic acid was not clear [152].

I am not aware of information on the effects of fertilizers on the rate of browning of fruits and vegetables other than potatoes. However, there are several reports dealing with the effects of fertilization on the responsible food constituents. *Nitrogen* application had a decreasing effect on the concentrations of phenol oxidase in cherries [154], total phenols in rice [155], and ascorbic acid in apples [156, 157], cantaloupes [136], grapefruit juice [136] and pepper [136]. *Potassium* decreased the ascorbic acid content of turnips [136]; no effects on lettuce and peas could be found [136]. *Manganese* fertilization enhanced the ascorbic acid content of tomatoes [158], but no effect on spinach was noted [136]. *Molybdenum* and *zinc* applications failed to show an appreciable effect on the ascorbic acid content of lettuce and peas [136], but zinc enhanced the ascorbic acid concentration in tomatoes [136].

Phytohormones. The effects of phytohormones on enzymatic browning have been studies in peaches, potatoes and sweet potatoes. A negative correlation was found between the application of gibberellic acid (GA-3), ethylene (applied as 2-chloroethane phosphonic acid), or Alar and the discoloration of peaches [37, 159]. All three phytohormones did not affect the concentrations of o-diphenols [37] and ascorbic acid [37, 160]. Ethylene (applied as gas) was correlated positively with the rate of browning of sweet potatoes [60]. This was paralleled by increases in the concentrations of phenol oxidase [60, 161], total phenols [60], and chlorogenic acid [162]. 2,4-Dichlorophenoxyacetic acid (2,4-D) decreased the browning tendency of potato tubers, although no effect on phenol oxidase activity could be found [163]. Maleic hydrazide (MH) was found to increase potato discoloration [79]; GA-3, kinetin, and indole acetic acid (IAA) lowered the ascorbic acid content of potatoes [164].

I am not aware of further information on the effects of phytohormones on enzymatic browning of food. However, there are a number of reports on the effects of phytohormones on the concentrations of phenol oxidase, ascorbic acid, and total phenols. 2,4-D decreased the phenol oxidase activity of artichokes [165] and tomatoes [166], but had no effect on wheat phenol oxidase [167, 168]. GA-3 stimulated the monophenol oxidase [169] but not the o-diphenol oxidase activity [168, 169] of wheat phenol oxidase; the effect on barley phenol oxidase was not clear [170]. GA-3 increased the ascorbic acid content of cherries [171–173] and grapes [174]. In the latter case, this increase was only observed after 5 and 10 days; after 30 days, a decrease was found. The total phenol content of grapes remained unaffected by GA-3 [174]. When applied as a gas, ethylene did not affect the phenol oxidase activity of carrots [161], parsnips [161], and turnips [161], and increased the ascorbic acid content of tomatoes [175]. When applied as 2-chloroethane phosphonic acid, the effect of ethylene on dwarf pea [176] and wheat [168] phenol oxidase was not clear; the ascorbic acid content of cherries remained unaffected [171]. Daminozide and kinetin did not affect the ascorbic acid content of cherries [171] and the phenol oxidase activity of wheat [168], respectively. Abscisic acid (ABA) was found to decrease the o-diphenol oxidase of wheat phenol oxidase [168].

Antibiotics. The influence of antibiotics on enzymatic browning was studied in potatoes. The positive correlation between chloramphenicol or streptomycin and the rate of browning was paralleled by increased phenol oxidase concentration [177, 178]. Cycloheximide increased the monophenol oxidase activity [169] but decreased the o-diphenol oxidase activity [179] of wheat phenol oxidase. Actinomycin D also increased the monophenol oxidase in wheat [169], but the o-diphenol oxidase remained unaffected [179]. The latter effect was also found for cordycepin (3′-deoxyadenosine) [179].

Fungicides, Insecticides, and Nematocides. A negative correlation was found between the application of the *fungicide* pentachloronitrobenzene (PCNB) and the tendency to darkening of potato tubers [54, 73]. This was paralleled by a decrease in the tyrosine content, whereas phenol oxidase activity remained unaffected [54, 73]. The effect of PCNB on total phenols was not clear [54, 73].

Application of the *insecticide* Tritox against the Colorado beetle resulted in increasing rate of browning of potato tubers [180].

Conspicious browning of potato tubers was observed when contacted with the *nematocides* 1,3-dichloropropane/1,2-dichloropropane (D-D), 1,2-dibromoethane (EDB), or 1,2-dibromo-3-chloropropane (DBCP) [181, 182]. The phenol oxidase activity did not change during the first 6 hours; thereafter, it was gradually reduced [181].

Nucleotides. ATP was found to prevent enzymatic browning of potatoes [183–186], apples [184], avocados [184], mushrooms [184], and peaches [184]. The concentration of phenol oxidase was not affected [184] nor did ATP inhibit the color formation from catechol by purified phenol oxidase [183]. NAD^+ and NADH had the same effects on enzymatic browning of potatoes as ATP [186]; ADP, AMP, and $NADP^+$ had little or not influence [186]. The results are consistent with the hypothesis that NADH is formed in slices of fruits or vegetables treated with ATP and/or NAD^+, and that NADH is probably the reducing compound responsible for color inhibition [168].

γ-Irradiation. γ-Irradiation was found to be positively correlated with the rate of browning of bananas [28, 29], mangos [34], and potatoes [47]. This effect is associated with increased concentrations of phenol oxidase in bananas [28, 29], mangos [34], and potatoes [47], total phenols in mangos [34] and potatoes [47, 105, 187, 188, 189], chlorogenic acid in potatoes [187, 190], and tyrosine in potatoes [191]. It is also associated with decreased ascorbic acid content in mangos [92] and potatoes [187, 192]. No effects [187, 188, 193] as well as no clear effects [189, 193, 194] of gamma-irradiation on the browning of potatoes and responsible potato constituents have also been reported. The total phenol content of irradiated sweet potatoes increased, whereas the phenol oxidase activity was not affected [188, 195]. The discoloration of prepacked cut endive, chicory and onions was slightly intensified by irradiation [71, 196, 197]. During storage, however, the discoloration remained stable, whereas browning of non-irradiated samples worsened [196]. Phenol oxidase and chlorgenic acid concentrations of chicory were not affected by irradiation [71, 196], the ascorbic acid content of endive was lowered [196, 197]. In an extensive study on gamma-irradiation of subtropical fruits no appreciable effects of irradiation on ascorbic acid content of mangos, papayas, litchis and strawberries could be detected [198–200].

Storage Time and Temperature. A survey of the literature on the effects of storage time and temperature on enzymatic browning of foods and its responsible factors shows a number of papers dealing with apples [15, 17, 19], beets [201], carrots [201], dates [202], horseradishes [201], mangos [34], mushrooms [203], potatoes [38, 40, 41, 47, 48, 51, 54, 69, 105, 128, 144, 190, 194, 204–213] and sweet potatoes [60, 61, 72, 214]. Much of the evidence is confusing or contradictory. Both increases and decreases in the discoloration and the concentration of responsible plant constituents have been reported for the same storage time and/or storage temperature. However, two general conclusions may be drawn from the literature data.

Firstly, storage time seems to have a greater influence on changes of the browning tendency than storage temperature. For example, storage of apples at different temperatures for 6 months resulted in a decrease of browning tendency during the initial 4 months, followed by an increase thereafter (this was noted irrespective of storage temperature) [15, 17]. Also, the susceptibility of potato tubers to browning increased in most cases during 6 months storage irrespective of storage temperature.

Secondly, the changes in the rates of browning are difficult to correlate with the changes in the concentration of a single plant constituent, e.g. phenol oxidase or phenolic substrate.

Oxygen. A positive correlation between oxygen concentration of the processing or storage atmosphere and enzymatic browning has been demonstrated for snap beans [59, 215].

Conclusions

Ascorbic acid, sulfur dioxide and heat treatment are frequently used in industry to control enzymatic browning of foods. The use of ascorbic acid increases the cost of food processing, sulfur dioxide may give rise to undesirable off-flavors, and some phenol oxidases are relatively heat stable (e.g. apple phenol oxidase with a half-life of 12 min at 70 °C [6]). During the past two decades some novel procedures have been suggested that do not appear to be economic for large scale use, e.g. the use of o-methyltransferases to convert o-diphenols to the corresponding methoxy-derivatives (that do not serve as substrates for phenol oxidase) or the use of 3,4-dioxygenases, which catalyze the ortho- or meta-fission of aromatic rings, thereby destroying the phenol oxidase substrates.

The availability of fruit and vegetable cultivars with slow rates of browning seems highly desirable to avoid

or minimize postharvest browning of foods. As already pointed out, enzymatic browning is influenced by various factors such as cultivar, climate, and cultural conditions. Thus, one may obtain fruits or vegetables with susceptibility to enzymatic browning of varying degree dependent, at one extreme, on whether a high-browning cultivar is grown at a high-browning center in a high-browning year, or, at the other extreme, whether a low-browning cultivar is grown at a low-browning centre in a low-browning year. The question arises as to whether it is possible to breed fruit or vegetable cultivars with slow rates of browning irrespective of the growing centre and growing year.

Since enzymatic browning of potatoes is most extensively studied, we may draw some conclusions from these results. Of the potato constituents responsible for discoloration, phenol oxidase and ascorbic acid appear to show strong cultivar dependencies, whereas the content of phenolic substrates depends mainly on location and/or climatic factors [42, 50, 51, 53, 134, 216, 217]. Therefore, it should be possible to breed potato cultivars with low enzyme and/or high ascorbic acid concentrations. These cultivars should have slow rates of browning irrespective of growing center and growing year. Wild potato species are known to contain more ascorbic acid than cultured species, and some subspecies of wild potatoes have already been considered to be suitable for breeding edible potato species with high ascorbic acid content [218]. As already reported above, fertilization also greatly influences the rate of browning. High levels of potassium decrease and high levels of nitrogen increase the browning tendency of the tubers. Thus, potato cultivars with low phenol oxidase and/or high ascorbic acid concentrations could be cultivated with high potassium and low nitrogen fertilization to yield tubers with slow rates of browning. Whether the above conclusions are also valid for fruits and for vegetables other than potatoes remains to be clarified.

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