

Antioxidant system level in 'Braeburn' apple is related to its browning disorder

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Abstract. Many factors related to the occurrence of browning disorder in 'Braeburn' apple were investigated, including harvest maturity, cumulative temperature in growing season, and different orchard locations. The incidence of browning disorder was related to the harvest time of fruit and the activity of superoxide dismutase. Superoxide dismutase activity was lower in late harvested 'Braeburn' apple fruit that had a higher disorder incidence. The risk of browning disorder was higher after growing seasons with lower cumulative temperature and lower activities of superoxide dismutase and catalase in fruit. The fruit harvested from the orchard located in a colder area had lower catalase activity, lower lipid soluble antioxidant levels, and a higher risk of browning disorder.

Keywords: Antioxidant; 'Braeburn' apple; Browning disorder; Catalase; Superoxide dismutase.

Introduction

The internal browning disorder of 'Braeburn' apples (*Malus domestica* Borkh.) was first observed in 1978 in New Zealand, and was named "Braeburn browning disorder" (BBD) in 1993 by the New Zealand industry (Elgar et al., 1998). The browning disorder was also observed in 'Braeburn' apples growing in British Columbia, Canada (Lau, 1998) and Washington State, USA (Curry, 1996). Some preharvest and postharvest factors have been reported to be related to the development of BBD, such as a cool growing season, harvest maturity, storage atmosphere, and waxing (Elgar et al., 1998; Lau, 1998). BBD develops in controlled atmosphere (CA) storage (Padfield, 1975). However, a 2 or 3 week delay in air storage prior to placement into CA reduces the incidence of the disorder, suggesting that 'Braeburn' apple is sensitive to CA during first the 2-3 weeks of storage (Elgar et al., 1998).

Changes in antioxidant enzymes in response to stress in plants are well known, and more recently such changes have been related to some postharvest disorders, such as chilling injury in squash (Wang, 1995) and pear (Ju et al., 1994), superficial scald in apple induced by chilling (Du and Bramlage, 1994; Rao et al., 1998) and senescence of pear and apple (Brennan and Frenkel, 1977; Du and Bramlage, 1994). Superoxide dismutase (SOD, EC 1.15.1.1) catalyzes the dismutation of superoxide anions to produce hydrogen peroxide (H_2O_2), whereby SOD activity helps protect cells from damage by superoxide anion re-

action products. On the other hand, the product of dismutation, H_2O_2 , is also a potentially hazardous compound and can be metabolized to H_2O by a wide array of antioxidant enzymes such as catalase (CAT, EC 1.11.1.6) and peroxidase (POD, EC 1.11.1.7). However, when POD metabolizes H_2O_2 , it oxidizes hydrogen donors at the same time. A wide range of hydrogen donors, including polyphenols, can be oxidized by POD, and involvement of POD in enzymatic browning has been reported (Lopez-Serrano and Barcelo, 1997; Richard-Forgetand Gaillard, 1997). A lower CAT level in apples was reported to be related to superficial scald development (Rao et al., 1998)

Non-enzymic antioxidants also play a role in resistance to physiologic disorders caused by oxidative stress. Antioxidant compounds are found in all higher plants, and they include ascorbic acid, α -tocopherol, β -carotene, glutathione, and other flavonoids (Larson, 1988). Certain postharvest disorders of fruits and vegetables are likely affected by the antioxidant levels in their tissue. For example, superficial scald development of apples is related to endogenous antioxidant concentration and activity (Barden and Bramlage, 1994; Thomai et al., 1998). Chilling injury induced oxidative stress and reduced antioxidant compounds level in cucumber (Hariyadi and Parkin, 1991). Veltman et al. (1999) found that brown core in pears (*Pyrus communis* L. cv. Conference) occurred under CA conditions, soon after ascorbic acid had declined below a certain value.

In the present work, we examined the relationship between the antioxidant system (enzyme and non-enzyme) in fruit and BBD development with many factors related to BBD development, such as harvest maturity, cumulative temperature in growing season, and different orchard locations.

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Materials and Methods

Materials and Treatments

1. *Effect of different harvest times (1997)*. Apple fruit were harvested from five orchards of local growers at three times: during commercial standard harvest (ST), and at two weeks earlier (E) or two weeks later (L) than commercial standard harvest. Fruit from each orchard's replicate was randomized into ten fruit samples for maturity determination, percent of red coloration on skin surface (Red %; by visual estimation) and starch index (0 to 9; Lau, 1998). Harvest criterion for E fruit, Red %: 60, starch index: 1; for ST fruit, Red %: 75, starch index: 3; and for L fruit, Red %: ≥ 80 , starch index: 4. Fruit obtained each time from each orchard replicate were randomized into five fruit samples. The flesh tissues of samples were taken without peel with a cork borer (10 mm diameter) and cut into 5-8 mm thick disks, which were then frozen and ground into small pieces in liquid N₂ and stored at -80°C.

2. *Effect of growing season temperature (1997, 1998 and 1999) and orchard location (1999)*. Temperature data for 1997, 1998 and 1999 were collected from the Agriculture and Agri-Food Canada Research Centre in Summerland, BC and used for calculating cumulative temperature as degree-days $>10^{\circ}\text{C}$ base temperature (DD10) between May 1 and the harvest date. A commercial grower was selected in Summerland for sampling in 1997, 1998 and 1999. Two commercial orchards (G1 and G2) were selected from the south region of the Okanagan valley and three other orchards (G3, G4 and G5) from the north region. Thirty 'Braeburn' apples were harvested each year or in each orchard at two weeks later than standard harvest, and then the fruits were divided into five replicates of six fruits each. Flesh tissues were taken without peel from six fruits with a cork borer (10 mm diameter) and cut into 5-8 mm thick disks. The disks were frozen and ground into small pieces in liquid N₂ and stored at -80°C.

The incidence of 'Braeburn' browning disorder was determined on 20 to 30 fruits for the treatments outlined in Sections 1 and 2.

Extraction and Assay of SOD and POD

Frozen apple tissue (5 g) was homogenized with 15 ml 0.05 M phosphate buffer (pH 7.0) containing 10% PVPP and 0.1 M EDTA. The homogenate was centrifuged at 15,000 g for 15 min at 4°C. The supernatant was used for SOD and POD assays.

SOD activity was determined by measuring inhibition of the photochemical reduction of nitroblue tetrazolium (NBT) using the method of Beauchamp and Fridovich (1971). The reaction mixture (3 ml) was composed of 13 mM methionine, 0.075 mM NBT, 0.1 mM EDTA, 0.002 mM riboflavin, and 0.1 ml of enzyme extract in 50 mM phosphate buffer (pH 7.8). The mixture in the tube was placed on a rotating tube holder in a light box for 7 min. The absorbance was read at 560 nm with a spectrophotometer (Beckman, model DU-640). One unit of SOD activity was defined as the amount of enzyme that inhibits the NBT

photoreduction by 50%. The activity of SOD was presented as unit / min / mg protein.

POD activity was measured by the method of Vetter et al. (1958) as modified by Gorin and Heidema (1976). The assay mixture contained 0.1 ml enzyme extract, 1.35 ml 100 mM MES buffer (pH 5.5), 0.05% H₂O₂ and 0.1% p-phenylenediamine. Changes in absorbance were recorded at 485 nm for 3 min with the spectrophotometer. The activity of POD was presented as $\Delta\text{OD}_{485\text{ nm}}/\text{min}/\text{mg protein}$.

Extraction and Assay of CAT Activity

Fresh apple flesh tissue (5 g) was homogenized in 15 ml of Tris-HCl buffer (pH 8.5) including 2 mM EDTA, 10% (w/v) PVPP. The homogenate was centrifuged at 15,000 g for 15 min at 4°C. Supernatant was used for the activity measurement. CAT activity was determined by following the disappearance of H₂O₂ in the enzyme reaction mixture (Brennan and Frenkel, 1977; Du and Bramlage, 1995). The enzyme extract (0.25 ml) was added to 2 ml assay mixture (50 mM Tris-HCl buffer pH 6.8, containing 5 mM H₂O₂). The reaction was stopped by adding 0.25 ml 20% titanous tetrachloride (in concentrated HCl, v/v) after 10 min at 20°C. A blank was prepared by addition of 0.25 ml 20% titanium tetrachloride at zero time to stop the enzyme activity. The absorbance of the reaction solutions was read at 415 nm against water. CAT activity was determined by comparing absorbance against a standard curve of H₂O₂ from 0.25 to 2.5 mM. The activity of CAT was presented as H₂O₂ mM /min /mg protein.

Assay of Protein Content

Total protein was determined by the method of Bradford (1967) using bovine serum albumin as the standard.

Extraction and Measurements of Lipid and Water Soluble Antioxidant Activities

Frozen fruit tissue (5 g) was homogenized in 5 ml hexane and 5 ml water for one minute. The homogenate was then centrifuged at 15,000 g for 15 min at 4°C. The hexane phase in the supernatant was carefully removed and placed into a test tube for assay of lipid soluble antioxidants (LSA) activity. The water phase in the bottom of the centrifuge tube was diluted by 10 times after filtration for assay of water soluble antioxidants (WSA) activity.

A stable free radical, 1,1-diphenyl-2-picrylhydrazyl (DPPH), was used to determine antioxidant activity (Blois, 1958; Yen and Duh, 1994). A 0.5 ml aliquot of the hexane extract (for LSA activity assay), or 0.2 ml of the water extract (for WSA activity assay) and 1.0 ml of DPPH (6×10^{-5} M in methanol), were incubated at room temperature for 30 min. The absorbance of the reaction solution was read at 517 nm using a Beckman DU640 UV-VIS spectrophotometer. Different concentrations of α -tocopherol in hexane (for LSA) or in methanol (for WSA) were used to make standard curves. DPPH was reacted with 0.5 ml hexane or 0.2 ml water as a control, the difference of $\text{Abs}_{\text{control}} - \text{Abs}_{\text{sample}}$ was used for the

antioxidant activity calculation. Antioxidant activity of LSA or WSA was presented as tocopherol equivalent μg / 100 g fresh weight.

Results and Discussion

Effect of Harvest Maturity on Antioxidant Enzyme Activities and the Incidence of Browning Disorder (1997)

Susceptibility of fruit to BBD was related to harvest date. Previous studies reported a higher incidence of BBD in late harvested fruit than in early harvested fruit (Burmeister and Roughan, 1997; Lau, 1998; Elgar et al., 1999). In the present experiment, the incidence of BBD was the highest in the L fruit and lowest in the E fruit (Figure 1). The incidence of BBD in ST fruit was intermediate (Figure 1A) and not significantly different from E and L fruit. The enzyme activity of POD was highest in ST fruits (Figure 1B) compared to E and L fruit. SOD activity in fruit was reduced at later harvest dates (Figure 1B). The activity was the highest in E fruit and lowest in fruit harvested later. The change in SOD activity showed a negative relationship with BBD development. A similar process in pear (*Pyrus communis* L. cv. Conference) was found by Lenthéric et al. (1999), where the activity of SOD fell about fivefold when the fruit was picked two weeks later than standard commercial maturity. However, POD activity was the highest in pear fruit harvested later.

Effect of Cumulative Temperature of Growing Season on Antioxidant Enzyme Activities, and the Incidence of Browning Disorder (1997, 1998, and 1999)

Lau (1998) traced the relationship between BBD development and cumulative temperature (degree-days $>10^\circ\text{C}$) in the growing season and reported that fruits in CA storage were highly susceptible to BBD when the season was <1300 degree-days $>10^\circ\text{C}$ between May 1 and harvest. In this study, it was warmer in 1998, and cooler in 1997 and 1999 (Table 1). The incidence of BBD was lower in 1998 than in 1997 (1/3 lower) and 1999 (1/2 lower). Antioxidant enzyme activities were higher in 1998. SOD activity was fourfold higher than that in 1997 and 1999, and CAT was

threefold higher than in 1999. There was no marked difference in POD activity among the different years. The ratios of SOD/POD and SOD/CAT were higher in 1998 as well. This suggests that SOD was more sensitive to temperatures during the growing season and that the activity was much influenced by the cool season.

Antioxidant enzymes SOD, POD and CAT convert the potentially dangerous O_2^- and H_2O_2 to water through their combined action. A balance of these enzymes provides an efficient system to prevent oxidative damage. Response of SOD to environmental stress against superoxide damage has been well documented (Scandalios, 1993). Temperatures and light conditions lead to increased SOD

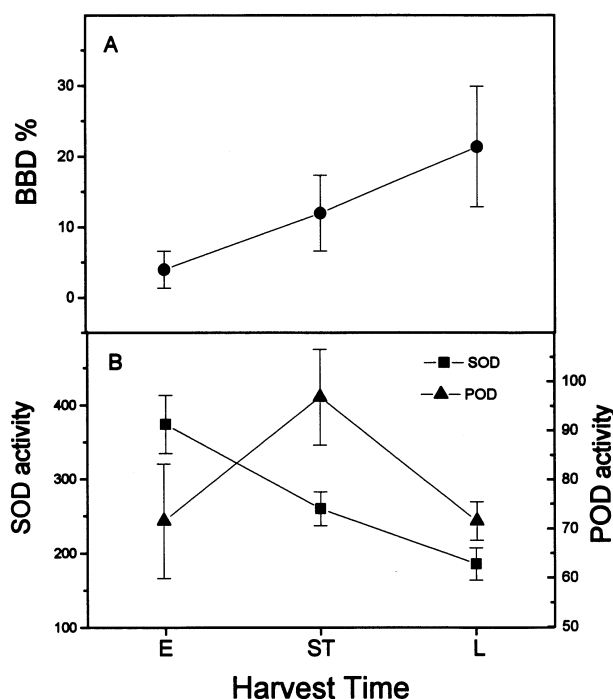


Figure 1. The incidence of BBD and the activities of SOD and POD in 'Braeburn' apples harvested at different times. Commercial standard harvest (ST), and two weeks earlier (E) or two weeks later (L) than commercial standard harvest. Bars show standard error. (The values of BBD % were average of five orchards; the values of enzyme activity were average from three measurement each of five orchards.)

Table 1. Incidence of 'Braeburn' browning disorder (BBD) after CA storage (1.5% O_2 + 1.2% CO_2) at 0°C for 1.5 months and antioxidant enzyme activities at harvest in the fruit from the same orchard in three different years (1997, 1998 and 1999).

	DD $>10^\circ\text{C}$	BBD %	SOD	POD	CAT	SOD/POD	SOD/CAT
1997	1106.8	33 (n=30)	142.5 (\pm 14.9)	70.9 (\pm 2.5)*	ND	2.0	-
1998	1489.5	12 (n=30)	626.6 (\pm 40.8)	64.5 (\pm 4.4)	6.63 (\pm 0.02)	9.7	94.5
1999	1131.5	25 (n=30)	156.4 (\pm 8.4)	39.9 (\pm 8.4)	2.06 (\pm 0.10)	3.9	75.9
98 / 97		2.8	4.4	0.9	-		
98 / 99		2.1	4.0	1.6	3.2		

DD $>10^\circ\text{C}$: Degree-Days above 10°C between May 1 and harvest; SOD: Unit/min/mg protein; POD: $\text{A}_{485\text{nm}}$ /min/mg protein; CAT: H_2O_2 $\mu\text{mole}/\text{min}/\text{mg}$ protein; ND: not done.

*: Standard error (n=3).

activity and may protect against sunscald of vegetables and fruits (Rabinowitch and Sklan, 1980). Higher SOD activity has been associated with reduced chilling injury in squash (Wang, 1995). Lenthéric et al. (1999) reported that the activity of CAT in pear (*Pyrus communis* L. cv. Conference) fell by half when the fruit was picked two weeks later with increasing maturity. In our study, SOD and CAT activities were lower following a cool season, and the activity of SOD was lower in the fruit at a late harvest date. The decrease in these enzyme activities after a cool season or in the more mature apple fruit may lead to a higher susceptibility to peroxidation and a higher susceptibility to BBD. The antioxidant enzyme system seems to have been one of the factors in resistance to BBD, and higher activity of the system may prevent its development.

Effect of the Location of Orchards on Antioxidant System and the Incidence of Browning Disorder (1999)

Preliminary studies in New Zealand indicate that the incidence and severity of BBD are higher in fruit grown in colder or higher altitude districts regions, and that larger variations in incidence can occur among the orchards within regions (Elgar et al., 1998; 1999). Results in Canada were similar. The incidence of BBD (Table 2) was markedly lower in the south region, a warmer area, and higher in the north. Within the cooler northern region incidence of the disorder for G5 was less than for the other two growers.

The activities of the antioxidant enzymes SOD and POD in fruit among the different orchards (Figure 2) did not relate to BBD development. However, the differences in CAT activity among the different orchards did relate ($r = -0.8186$, $P = 0.09$). In fruit from G1 and G2 in the warmer area, CAT activity was significantly higher than in G3 and G4, two orchards in the cooler area. CAT activity in G5, an orchard in the cooler area, was slightly higher than G3 and G4, but lower than G1 and G2 (no significant difference with G1).

Differences in LSA and WSA activities in fruit from different orchards were also found (Figure 3). LSA activity was highest in G1. The activity of LSA in G2 and G5 was

Table 2. Incidence of 'Braeburn' browning disorder (BBD) in fruit from different orchards after storage in CA conditions (1.5 % O₂ + 1.2% CO₂) at 0°C for 4 months.

Region in Okanagan	Orchard	BBD (%)	Mean (%)
South	G1 (n=30)	0	6.7
	G2 (n=30)	13.3	
North	G3 (n=80)	42.6	35.4
	G4 (n=80)	35.4	
	G5 (n=80)	28.3	

Significance

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** : Significant at $P \leq 0.01$ within column. Percentage values were arcsine square root transformed before analysis.

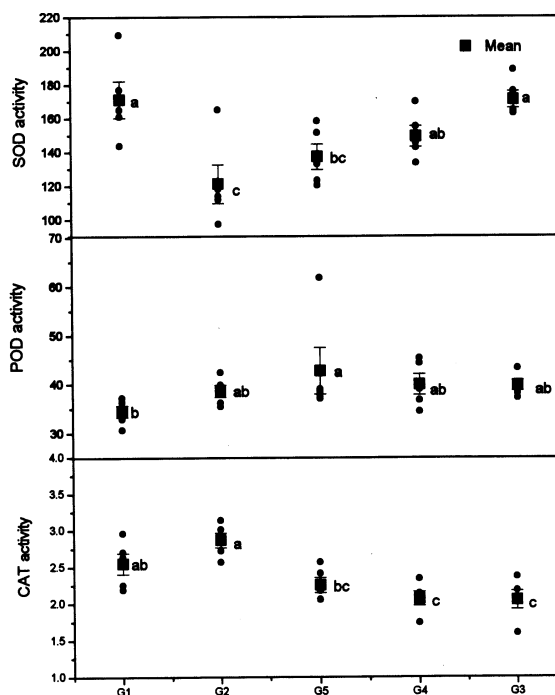


Figure 2. SOD, POD and CAT activity in 'Braeburn' apples harvested from different orchards. Data with no letter in common are significantly different at 5% level. Duncan's multiple range test. Bars show standard error (n=3).

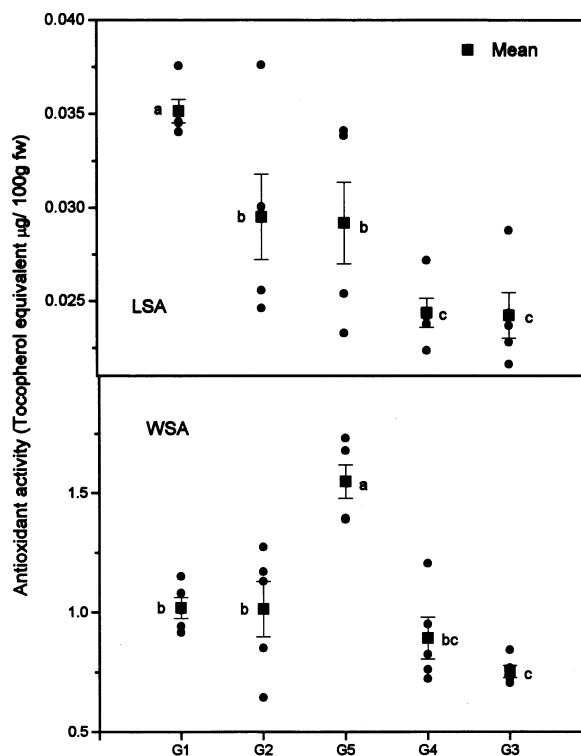


Figure 3. LSA and WSA activity in 'Braeburn' apples harvested from different orchards. Data with no letter in common are significantly different at 5% level. Duncan's multiple range test. Bars show standard error (n=3).

at a similar level and significantly higher than in G3 and G4. A strong negative correlation emerged between LSA activity and BBD incidence, $r = -0.9473$ ($P = 0.014$). WSA activity was the highest in G5 and the lowest in G3. WSA activity in G1 and G2 were at the same level, intermediate between G3 and G5, and slightly higher than G4. Although WSA activity was higher than LSA activity (over 30 times), WSA activity was not associated with BBD development.

Higher levels of CAT and LSA activity were associated with a lower incidence of BBD in different orchards. G2 had the same level of LSA as G5 but a lower incidence of BBD. However, G2 did have higher CAT activity.

Antioxidant compounds are important in prevention of pollution damage and disease in plants (Al-Saikhan et al., 1995). Meir and Bramlage found that antioxidant activity in "Cortland" apple peel was strongly correlated with superficial scald development. The contents of antioxidant compounds in the peel tissue of cucumber, such as ascorbic acid, glutathione, α -tocopherol and β -carotene, declined with development of chilling injury (Hariyadi and Parkin, 1991). The core browning of "Conference" pear frequently occurs in CA storage. It was reported that ascorbic acid levels in fruits related to the browning development (Veltman and Van Schaik, 1997; Lenthéric et al., 1999; Veltman et al., 1999). The content of glutathione in pear fruit was found to be related to harvest maturity and core browning of fruit (Lenthéric et al., 1999). Ascorbate and glutathione are WSA compounds. However, there was no clear association between WSA activity and BBD development in that study.

Activated oxygen species in plant cells can react with unsaturated fatty acids to cause peroxidation of membrane lipids in the plasmalemma or intracellular organelles. Peroxidation damage of the plasmalemma leads to leakage of cellular contents, rapid desiccation, and cell death in plant tissue (Scandalios, 1993). The plasmalemma peroxidation damage results in leakage of phenolic compounds from the vacuole, facilitating the polyphenoloxidase reaction. The browning and cavities in pears under high CO_2 were reported to be related to membrane lipid peroxidation in fruit tissues (Veltman et al., 1999). Therefore, reducing the accumulation of activated oxygen species in tissues may be important for the prevention of peroxidation damage. Antioxidant enzymes SOD, CAT and POD can convert the potentially dangerous $\text{O}_2^{\cdot-}$ and H_2O_2 to water, and reduce the injury by oxygen stress. Many water soluble and lipid soluble reductive compounds in plant tissues have antioxidant ability and can scavenge activated oxygen species via autoxidation reactions. LSA, being in the same soluble phase with membrane lipid, may fight lipid peroxidation more efficiently than WSA. Burton and Ingold (1984) reported that β -carotene, as an LSA, inhibited lipid peroxidation by scavenging the lipid hydroperoxyl radical. This may be the reason why LSA activity was associated with BBD development but WSA was not, even though the level of LSA was much lower.

Conclusion

This study confirmed several factors that related to BBD development. SOD activity was lower in more mature 'Braeburn' apple fruit that had a higher BBD incidence. (CAT activity also decreased with maturity.) Higher cumulative temperature during the growing season reduced the incidence of BBD, and this was perhaps associated with the higher activities of SOD and CAT in the higher cumulative temperature season. Different BBD incidences in different orchard locations related to the activity of CAT and the level of LSA. We suggest that the high activity of antioxidant enzymes (SOD and CAT) and high level of LSA in 'Braeburn' apple fruits improves the resistance of fruit to BBD development.

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蘋果 'Braeburn' 果實褐心病與其抗氧化系統之關係

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本研究對多種與蘋果 'Braeburn' 果實褐心病有關的因素，像採收成熟度，生長季積溫和果園所在區域進行了調查。發現果實的抗氧化系統與 'Braeburn' 果實褐心病有關。不同採收期褐心病發病率不同與超氧化歧化酶的活性有關。在成熟度高的果實超氧化歧化酶的活性低而發病率高。在生長季積溫低的年份，果實的超氧化歧化酶和過氧化氫酶的活性低，而有較高的發病危險性。冷涼地區果園的果實過氧化氫酶的活性低，並且脂溶性抗氧化物的水平低，而果實容易發生褐心病。

關鍵詞： 抗氧化；蘋果 'Braeburn'；果實褐心病；過氧化氫酶；超氧化歧化酶。