果実の成熟あるいは傷害に伴うエチレン生成と青酸代謝との関係

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Cyanide Metabolism Involved in Ethylene Formation of Ripening or Wounded Fruit Tissues[1]

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Summary

Changes in β-cyanoalanine synthase activity, rate of ethylene production, ACC and CN^- content were determined in ripening and wounded fruit tissues. When fruits were examined at various ripening stages, apple fruits which had the highest rate of ethylene production, showed the greatest activity of β-cyanoalanine synthase, while satsuma mandarin peel showed the least enzyme activity.

During maturation of apple fruit on the trees, β-cyanoalanine synthase activity gradually increased until November 29, then showed a marked increase. The CN^- content and rate of ethylene production remained at constant levels before November 29 and increased thereafter. In wounded apple tissue, the rate of ethylene production reached a peak after 24 hours, while the CN^- content and β-cyanoalanine synthase activity peaked 36 hours after wounding. The rate of cyanide evolution from the cut sections of apple flesh was 2.67 ± 0.41 ng/g F. W./hr (1.71 ± 0.26 pmol/g F. W./min).

Concomitant changes in the ACC and CN^- content, rate of ethylene production and β-cyanoalanine synthase activity were also observed during the ripening process of fruits of Japanese persimmon and kiwifruit stored at 25°C.

The development of cyanide-resistant respiration in ripening or wounded friut tissues seemed to be closely related to the increase in β-cyanoalanine synthase activity.

Introduction

β-Cyanoalanine synthase, which catalyzes the reaction between cysteine and HCN to form β-cyanoalanine and H_2S, is widely distributed in higher plants(6, 13, 14, 17, 20, 32, 33), algae(14) and microorganisms(7, 8, 10, 12). β-Cyanoalanine is further converted to asparagine by β-cyanoalanine hydratase(9). These enzymes are considered to play a role in detoxifying HCN by converting nitrogen to the amide form.

The detoxification mechanism of HCN produced *in vivo* during metabolic turnover of cyanogenic glucosides in *Lotus* sp.(1), *Nandina domestica*(2) and *Manihot utilissima*(21) has also been reported. Recently Peiser *et al.*(22, 23) have suggested that the formation of $^{14}CN^-$ from[1-^{14}C]-1-aminocyclopropane-1-carboxylic acid(ACC) occurs during its conversion to ethylene *in vivo*. The radioactivity liberated during the metabolism of [1-^{14}C]ACC was converted in 62% yield to asparagine. HCN and β-cyanoalanine are thought to be possible intermediates in this conversion. Ethylene formation from ACC is well known in ripening fruits and wounded tissues(34). Here we report the possible involvement of cyanide metabolism in ethylene evolution in ripening or wounded fruit tissues. The relationship between the cyanide metabolism and cyanide-resistant respiration of such tissues(18) is also discussed.

Materials and Methods

Fruits were obtained from local markets, farmers, the Experimental Farm of Ehime

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University or the Fruit Tree Experiment Station of Ehime Prefecture. The fruits included Japanese persimmons(*Diospyros kaki* Thunb.), Japanese pears (*Pyrus serotina* Rehd. var. *culta*), apples (*Malus pumila* Mill. var. *domestica* Schneid.), banana(*Musa sapientum* L.), Wase satsuma mandarin (*Citrus unshiu* Marc. var. *praecox* Tanaka) and kiwifruit(*Actinidia chinensis* Planch.). They were either used immediately or were stored at 25°C until analysis.

In another experiment, apple fruit (cv. Ralls Janet)maturing on the trees were collected at intervals from the Experimental Farm of Ehime University. Wounded sections of apple flesh were prepared by cutting premature 'Ralls Janet' apple fruit into about 2 g sections, which were placed on moist paper in a petri dish. These were incubated at 25°C and analyzed at intervals.

Ethylene determination

A 500 mg section of flesh or peel was incubated for 4 hr in a 15 ml gas-tight vial at 25°C. One ml of gas was withdrawn from the vial and analyzed for ethylene in a Shimadzu GC 8 A gas chromatograph equipped with a FID detector and an activated alumina column.

ACC determination

A 1 g section of flesh or peel was extracted with 70% ethanol containing 0.05% 2-mercaptoethanol. The extracts were evaporated *in vacuo* to dryness and the residues were taken in 2 ml distilled water. An aliquot of the solution was used for ACC determination after the method of Lizada and Yang (19).

Cyanide determination

A 500 mg section of flesh or peel was homogenized in 2 ml of 20% H_3PO_4 with a glass homogenizer and 0.5 ml of bromine-saturated water was added to the homogenate. After 15 min, 0.2 ml of 5% phenol solution was added. The BrCN thus formed was extracted with 5 ml of isopropylether. The same procedures were applied to the standard NaCN and distilled water. The extract was further diluted, if necessary, with isopropylether. A 2 μl aliqout of the isopropylether extract was injected into a Hitachi gas chromatograph 063 equipped with a ^{63}Ni(10 mCi) ECD detector. The glass column, 75 cm length × 3 mm inner diameter, was packed with Porapak Q(80-100 mesh).

The column, injection and detector temperatures were 125, 175 and 200°C respectively. The carrier gas was N_2 at a flow rate of 50 ml/min. The peak of BrCN was identified by comparing the retention time with the authentic compound, and by checking the retention time with other column packings such as Porapak N and Gaskuropack 54. Of these column packings, Gaskuropack 54 showed the highest sensitivity to BrCN. However Porapak Q was used for the quantitative analysis in this experiment.

The evolution of cyanide from wounded apple tissues was estimated by the Conway microdiffusion method. A 1 g sample of freshly cut sections (cv. Ralls Janet) was placed in the outer well and the cyanide evolved was absorbed in 1 ml of 0.1 N KOH in the center well at 30°C for 4 hours. Identical procedures without cut sections in the outer well were used as control. A 0.5 ml aliqout of the 0.1 N KOH solution was brominated and analyzed as described above.

β-Cyanoalanine synthase assay

A 1 g or 500 mg sample of flesh or peel was homogenized with a pre-freezed mortar and pestle in 12.5 ml of cold 0.05 M Tris-HCl buffer (pH 8.5) and 300 mg insoluble PVP. After centrifugation at 20,000 × *g* at 4°C for 10 min, the resulting supernatants were used for the enzyme assays. β-Cyanoalanine synthase activity was determined colorimetrically by measuring the reduction of methylene blue by the H_2S released from cysteine(6, 20). Identical assays lacking substrates and containing boiled enzyme were used as control.

All the analyses described above were replicated three times.

Results

Fig. 1 shows typical gas chromatograms of BrCN extracted with isopropylether from brominated NaCN and homogenate of Japanese persimmon flesh. The control revealed a very small peak at the same retention time as BrCN. The linearity of response of the ECD detector to BrCN ranged from 0.4 pg to

Table 1. The rates of ethylene production, ACC and CN^- content, and β-cyanoalanine synthase activities in various fruits at different ripening stages.

Species	Cultivars	Ripening stages[y]	Ethylene (nl/gF·W./hr)	ACC (nmol/gF·W.)	CN^- (μg/gF·W.)	β-Cyanoalanine synthase (H_2S μM/gF·W./hr)
Japanese persimmon (*Diospyros kaki* Thunb.)	Fuyu	3	0.35±0.04[x]	0.97±0.22	11.53±0.56	0.24±0.04
	Jiro	3	0.56±0.09	0.08±0.02	7.82±0.30	0.30±0.07
Japanese pear (*Pyrus serotina* Rehd. var. *culta*)	Nijisseiki	4	2.75±1.07	0.25±0.02	5.65±0.35	0.42±0.06
	Shinsetsu	2	0.17±0.02	0.12±0.04	1.70±0.05	0.36±0.02
Apple (*Malus pumila* Mill. var. *domestica* Schneid.)	Alps Otome	4	16.92±4.95	0.41±0.08	5.97±0.81	9.35±0.96
	Starking Delicious	4	18.24±2.69	1.85±0.06	6.12±0.57	10.02±1.61
	Ralls Janet	2	1.18±0.24	0.26±0.02	8.36±0.48	5.90±0.18
Banana (*Musa sapientum* L.)		2	2.01±0.26	0.56±0.21	16.03±0.74	0.19±0.05
Wase satsuma mandarin (*Citrus unshiu* Marc. var. *proecox* Tanaka)	Miyagawa[z]	3	0.92±0.05	0.13±0.05	1.34±0.39	0.07±0.02

[x] The peel was used for analyses.

[y] 1=before ripening, 2=initial stage, 3=middle stage, 4=peak stage, 5=after ripening

[z] mean±S.E.

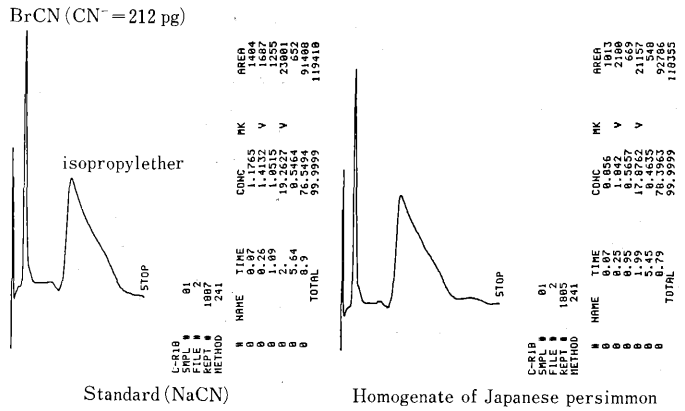

Fig. 1. Typical gas chromatograms of BrCN derived from the brominated NaCN and homogenate of Japanese persimmon flesh (cv. Jiro).

1 ng CN^- per injection. Table 1 shows rates of ethylene production, ACC and CN^- content and β-cyanoalanine synthase activities of various fruits at different ripening stages. The rate of ethylene production and β-cyanoalanine synthase activity were especially high in 'Alps Otome' and 'Starking Delicious' apples at the peak stages of ripening. In contrast, the level of enzyme activity in the peel of Wase satsuma mandarin was low.

Fig. 2 shows the changes in β-cyanoalanine synthase activity, rate of ethylene production and CN^- content in 'Ralls Janet' apple fruit maturing on the trees. The enzyme activity increased gradually until November 29, then showed a marked increase. The CN^- content remained unchanged until November 29, and then increased. The rate of ethylene production followed the change in CN^- content.

Fig. 3 shows the effect of wounding on β-cyanoalanine synthase activity, rate of ethylene production and CN^- content of apple flesh tissues. The rate of ethylene production reached a maximum after 24 hours, while CN^- content and β-cyanoalanine synthase activity peaked 36 hours after wounding. In another experiment, the rate of cyanide evolution from the cut sections of apple flesh was 2.67±0.41 ng/g F.W./hr.

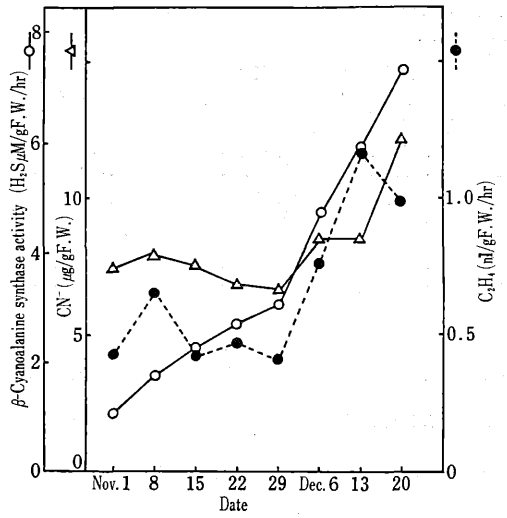

Fig. 2. Changes in the ethylene production, CN^- content and β-cyanoalanine synthase activity in apple fruit (cv. Ralls Janet) maturing on the trees.

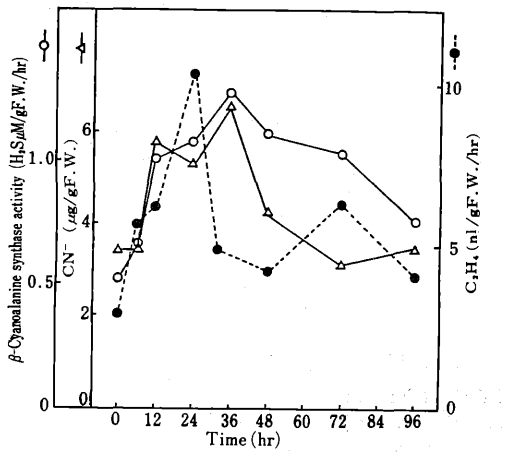

Fig. 3. Changes in the ethylene production, ACC and CN^- content, and β-cyanoalanine synthase activity in the cut sections of apple flesh (cv. Ralls Janet).

Figs. 4 and 5 show the changes in β-cyanoalanine synthase activity, rate of ethylene production, CN^- and ACC content of fruits of Japanese persimmon (cv. Jiro) and kiwifruit (cv. Hayward) during storage at 25°C.

In Japanese persimmon, rate of ethylene production and CN^- content reached maximum levels on the ninth day, and then decreased. β-Cyanoalanine synthase activity reached a maximum level on the third day, then decreased gradually. ACC content reached a peak on the third day, decreased until the ninth day, and then increased slightly.

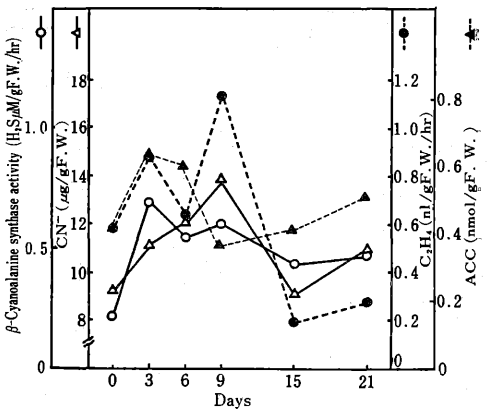

Fig. 4. Changes in the ethylene production, ACC and CN^- content, and β-cyanoalanine synthase activity in Japanese persimmon fruit (cv. Jiro) stored at 25°C.

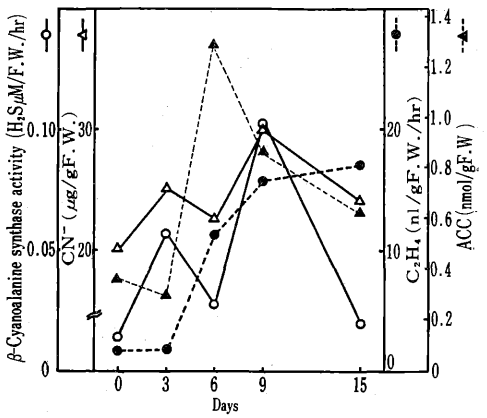

Fig. 5. Changes in the ethylene production, ACC and CN^- content, and β-cyanoalnine synthase activity in kiwifruit (cv. Hayward) stored at 25°C.

In kiwifruit, rate of ethylene production increased from the third to the fifteenth day, while β-cyanoalanine synthase activity and CN^- content reached maximum levels on the ninth day and then decreased. ACC content reached a maximum level on the sixth day.

Discussion

Cyanide metabolism in higher plants has been extensively investigated(5, 6, 9, 13, 14, 17). When exogenously applied to plant tissues, HCN is effectively converted to β-cyanoalanine(6, 20, 32, 33), which is further hydrolyzed to asparagine(9). The enzymes which catalyze these reactions are referred to as β-cyanoalanine synthase and β-cyanoala-

nine hydratase respectively.

Miller and Conn (20) examined many plants, both cyanogenic and non-cyanogenic, and found that both classes of plants contained β-cyanoalanine synthase, although there was no known source of cyanide in the non-cyanogenic plants. The role of the detoxifying mechanism in cyanogenic plants is obvious, but the role of these enzymes in non-cyanogenic plants is still unknown. However, Gewitz *et al.* (15) have reported the formation of hydrogen cyanide from histidine in the presence of amino acidoxidase and peroxidase. Solomonson and Spehar(25) reported that hydroxylamine and glycolate were a source of cyanide. Recently Peiser *et al.* (22, 23) suggested that cyanide is formed during the conversion of ACC to ethylene.

Since ethylene is a ubiquitous plant hormone, cyanide production and metabolism may not be confined to cyanogenic plants but may be distributed widely throughout the plant kingdom.

In this experiment, we used a highly sensitive gas chromatographic analysis for cyanide determination, similar to that reported by many others(3, 4, 31). In most of the previous work, the alkaline solution which had absorbed cyanide liberated from the source materials by distillation or diffusion methods was homogenated. In this study, tissue homogenates were brominated directly and the BrCN thus formed was extracted with isopropylether. There is, thus, a possibility that the cyanide measured by this method may be derived not only from free cyanide but also from conjugated forms or from other non-cyanogenic compounds. The cyanide content in fruits or peel estimated by this method ranged from approximately 1.3 μg/g F. W. for the peel of satsuma mandarin (Table 1) to 30 μg/g F. W. for the flesh of kiwifruit (Fig. 5). However, our further investigation revealed that most of the estimated cyanide is probably derived from water and alcohol insoluble membrane-bound fractions (unpublished data). So it is inferred that most of the cyanide comes from conjugated or bound forms and that free cyanide exists in very low levels in the tissues. Cyanide evolution from the wounded sections of apple flesh was 2.67±0.41 ng/g F. W./hr (1.71± 0.26 pmol/g F. W./min) when they were incubated at 30°C for 4 hours in Conway microdiffusion dishes. This rate of cyanide evolution is very low when compared with the *in vivo* rate of ethylene formation in plant tissues, which generally ranges from 5 pmol/g F. W./min to 50 pmol/g F. W./min depending on the tissue source. The low rate of cyanide evolution may be partly due to high levels of β-cyanoalanine synthase activity (8.0 nmol to 25.0 nmol H_2S/g F. W./min), which rapidly and effectively metabolize and remove cyanide from the tissues.

Our present results confirmed that ethylene formation from ACC in ripening and wounded fruit tissues is closely related to cyanide metabolism, as suggested by Peiser *et al.* (22, 23). Solomos and Laties(26) reported that cyanide mimicked ethylene action in initiating the climacteric respiration and ripening of avocados. Further, they found that ethylene and cyanide triggered a rise in respiration in potato tubers(27). These facts suggest a close relationship between ethylene biosynthesis and cyanide metabolism. Apple fruits, which are a climacteric type, showed the highest β-cyanoalanine synthase activity. In contrast, the peel of satsuma mandarin, which is a non-climacteric type, showed the lowest activity (Table 1). Since non-climacteric fruits show neither a climacteric rise in respiration nor an increase in evolution of ethylene during their ripening processes, they may not require cyanide metabolism during this time.

Solomos and Laties(28, 29) reported that a functional cyanide-resistant electron path is necessary for ethylene to enhance plant respiration. Many cases of the development of cyanide resistant-respiration in slices and in intact fruits and storage organs in response to ageing and ethylene have been reported(11, 16, 18, 28, 29, 30).

Our present results show that β-cyanoalanine synthase activity increased concomitantly with ethylene and cyanide formation in ripening and wounded fruit tissues. Therefore the development of cyanide-resistant

respiration in such tissues should be in part due to the increased cyanide metabolizing ability of β-cyanoalanine synthase. In this context, it is interesting to note that β-cyanoalanine synthase is localized in mitochondria (17, 33), and that the cyanide-resistant, alternative oxidase pathway is also located in the mitochondrial inner membrane, together with the cytochrome pathway(18). Rychter *et al.* (24) reported that while mitochondria from whole potato tubers are normally cyanide-sensitive, mitochondria from ethylene-treated tubers developed cyanide resistance. This indicates a close connection between the cyanide metabolizing function of β-cyanoalanine synthase and the development of cyanide-resistant respiration. Further investigations to elucidate the role of β-cyanoalanine synthase in the development of an alternative path of respiration are needed.

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果実の成熟あるいは傷害に伴うエチレン生成と青酸代謝との関係

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摘　要

果実の成熟あるいは傷害に伴うエチレン生成に関連して，β-シアノアラニン合成酵素の活性，ACC 及び CN^- 含量の変化を調査した．調査した果実のうちで，エチレン生成の著しいリンゴ果実で，β-シアノアラニン合成酵素活性が最も高く，早生ウンシュウミカンの果皮で活性が最も低かった．樹上で成熟しているリンゴ果実では，β-シアノアラニン合成酵素の活性は11月29日まで徐々に増加し，その後活性が急に増加した．エチレン生成量と CN^- 含量は11月29日を境に，その後増加する傾向が認められた．リンゴの果肉切片では，エチレン生成量は切断後24時間目にピークに達したが，β-シアノアラニン合成酵素の活性と CN^- 含量は36時間後にピークに達した．リンゴの果肉切片から発生する CN^- 量を測定したところ，2.67±0.41 ng/g F.W./hr (1.71±0.26 pmol/g F.W./min) であった．25℃ で貯蔵したカキ及びキウイフルーツ果実でも，成熟過程において，ACC 及び CN^- 含量，エチレン生成量，β-シアノアラニン合成酵素活性は付随的に変化した．成熟果実や傷害を受けた果実で見られるシアン耐性呼吸の発達は，β-シアノアラニン合成酵素活性の増加と密接に関係しているように思われた．