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Effect of Abscisic Acid on Banana Fruit Ripening in Relation to the Role of Ethylene

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ABSTRACT

The role of abscisic acid (ABA) in banana fruit ripening was examined with the ethylene binding inhibitor, 1-methylcyclopropene (1-MCP). ABA (0, 10^{-5}, 10^{-4}, or 10^{-3} mol/L) was applied by vacuum infiltration into fruit. 1-MCP (1 μL/L) was applied by injecting a measured volume of stock gas into sealed glass jars containing fruit. Fruit ripening, as judged by ethylene evolution and respiration associated with color change and softening, was accelerated by 10^{-4} or 10^{-3} mol/L ABA. ABA at 10^{-5} mol/L had no effect. The acceleration of ripening by ABA was greater at 10^{-3} mol/L than at 10^{-4} mol/L. ABA-induced acceleration of banana fruit ripening was not observed in 1-MCP treated fruit, especially when ABA was applied after exposure to 1-MCP. Thus, ABA's promotion of ripening in intact banana fruit is at least partially mediated by ethylene. Exposure of ABA-treated fruit to 0.1 μL/L ethylene for 24 h resulted in increased ethylene production and respiration, and associated skin color change and fruit softening. Control fruit (no ABA) was unresponsive to similar ethylene treatments. The data suggest that ABA facilitates initiation and progress in the sequence of ethylene-mediated ripening events, possibly by enhancing the sensitivity to ethylene.

Key words: Abscisic acid; Banana; Ethylene; 1-methylcyclopropene; Respiration; Ripening.

INTRODUCTION

Banana fruit shows a characteristic climacteric ripening pattern (Dominguez and Vendrell 1994; Marriott 1980). Fruit ripening is controlled by plant growth regulators (Parikh and others 1990; Salunkhe and others 1975). Abscisic acid (ABA) enhances ripening of both climacteric and nonclimacteric (Brady 1987; Palejwala and others 1985; Parikh and others 1986; Vendrell 1985). The effect of ABA on various ripening parameters may be related to

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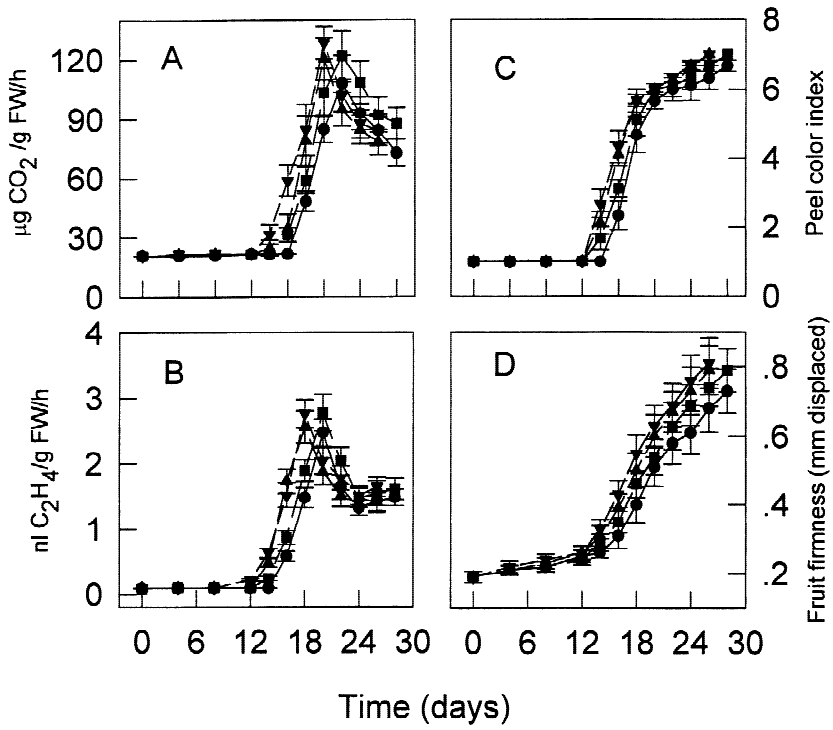

Figure 1. Effect of ABA treatment on respiration **(A)**, ethylene evolution **(B)**, skin color change **(C)**, and softening **(D)** of banana fruit. Each value is the mean for six measurements, and vertical bars indicate standard errors. ●, 0; ■, 10^{-5}; ▲, 10^{-4}; and ▼, 10^{-3} mol/L ABA.

ethylene evolution (Riov and others 1990). However, the mechanism by which ABA stimulates ethylene production is not clear. Some investigators suggest that ABA has a direct effect on ethylene biosynthesis, predominantly through enhancement of ACC synthesis (Goren and others 1993; Riov and others 1990; Tan and Thimann 1989). Others suggest that its stimulative effect is indirect, resulting from acceleration of senescence (Jackson and Osborne 1972; Lieberman and others 1977). Most studies dealing with stimulation of ethylene production by ABA have used excised tissues (Goren and others 1979; Jackson and Osborne 1972; Lieberman and others 1977; Vendrell 1985). It is not clear whether ABA also stimulates production in intact fruit.

1-Methylcyclopropene (1-MCP) is a highly effective compound among recently developed inhibitors of ethylene action in fruits and ornamentals (Golding and others 1988; Porat and others 1995; Serek and others 1995; Sisler and others 1996a,b; Song and others 1997). 1-MCP acts by binding irreversibly to ethylene receptors, thereby blocking ethylene-induced ripening and senescence (Sisler and Blankenship 1996; Sisler and Serek 1997).

In this work, ABA and 1-MCP were applied to intact banana fruit to characterize effects of ABA on fruit ripening associated with endogenous ethylene evolution, and especially to examine whether ABA-induced ripening is mediated by ethylene.

Materials and Methods

Plant Material

Hands of mature green bananas (*Musa sapientum* L.) were purchased at the Rocklea Central Market in Brisbane (Australia). Hands were cut into individual fingers, dipped for 3 min in 500 μL/L prochloraz (Sportak) fungicide solution, and then dried. Sportak gives good control of postharvest banana fruit diseases (Wade and others 1993). Fruit was sorted for freedom from visual defects and uniformity of weight and shape before use in these experiments.

Treatments

Fruit was randomly allocated into three lots for the following treatments. The first lot was used for ABA treatments according to the method of Vendrell (1985). ABA treatment was by vacuum infiltration at −80 kPa for 20 min with 0 (control), 10^{-5}, 10^{-4}, or 10^{-3} mol/L ABA. This application method resulted in increased fruit weight of about 0.4%. After infiltration, the fruit was kept in a controlled shelf-life evaluation room at 20°C and 90% relative humidity (RH). The same controlled conditions were maintained for all other experiments. The second lot of fruit was treated with 1 μL/L 1-MCP for 12 h without and with subsequent treatment with 10^{-3} mol/L ABA as described previously. 1-MCP was applied by

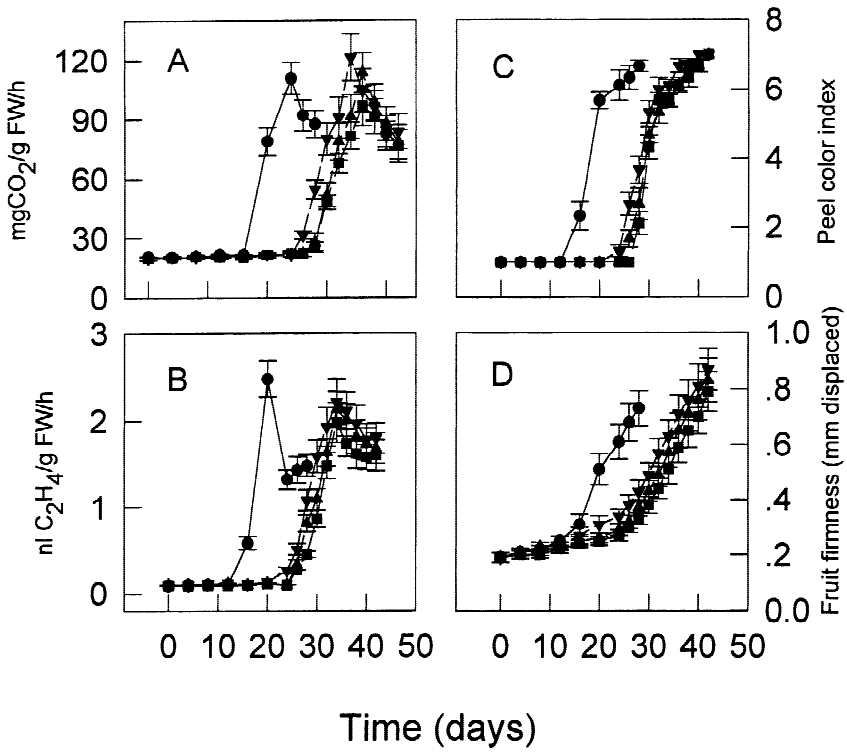

Figure 2. Effect of ABA and 1-MCP treatments on respiration **(A)**, ethylene evolution **(B)**, skin color change **(C)**, and softening **(D)** of banana fruit. Each value is the mean for six measurements, and vertical bars indicate standard errors. ●, Control (water); ■, 1-MCP treatment; ▲, 1-MCP with subsequent ABA treatment; and ▼, ABA with subsequent 1-MCP treatment.

injecting a measured volume of concentrated stock gas into 2.5L glass jars containing fruit. Treatment with 1 µL/L 1-MCP for 12 h essentially eliminates µL/L-induced banana ripening (Jiang and others 1999). Fruit placed for 12 h at 20°C before water vacuum infiltration was used as the control. In addition, to examine the effect of pretreatment with ABA on 1-MCP–treated fruit, a portion of the fruit from the second lot was treated with 10^{-3} mol/L ABA. This was the most effective concentration in the preceding experiment. The fruit was sealed for 12 h in glass jars with 1 µL/L 1-MCP before subsequent shelf-life evaluation at 20°C and 90% RH. Fruit in the third lot was used to test the response of ABA-treated fruit to ethylene. Fruit was vacuum infiltrated with 0 (control) and 10^{-3} mol/L ABA and then exposed to 0.1 or 1 µL/L ethylene for 24 h in glass chambers. Thereafter, fruit was held in the shelf-life evaluation room at 20°C and 90% RH. Peel color, fruit firmness, and ethylene and carbon dioxide production were monitored throughout the evaluation period for both control and treated fruit.

Assessments

At each assessment time, six pieces of fruit from control and each of the treatments were assessed for skin color and fruit firmness. Peel color of individual fruit pieces was scored on a scale of 1 (green), 2 (breaker), 3 (<25% color change), 4 (25–50% color change), 5 (>50% but <100% color change), 6 (fully yellow), and 7 (yellow with black spots) (Paull 1996). A skin color index was calculated using the formula Σ(color scale × percentage of fruit within each color class). Fruit firmness was evaluated by the nondestructive deformation method of Macnish and others (1997). Ethylene evolution and respiration were measured in six replicates. One-milliliter gas samples were taken from glass jars in which one finger of banana fruit was sealed for 2 h at 20°C and analyzed for carbon dioxide or ethylene by gas chromatography (Paull 1996).

Each treatment was made up of six replicate banana fingers, and these six fruits were repeatedly assessed over the duration of the experiment.

Results and Discussion

Treatment with ABA

Vacuum infiltration of ABA into banana fruit at 10^{-5}, 10^{-4}, or 10^{-3} mol/L yielded varied responses in terms of respiration and ethylene evolution and associated skin color changes and fruit softening (Figure 1). Treatment with 10^{-3} mol/L ABA stimulated an earlier rise in both ethylene evolution and respiration. ABA at 10^{-5} mol/L was not effective, as judged by similarity of response to the control treatment. The 10^{-4} mol/L ABA treatment had a similar

Table 1. Time (Days) to Inception of the Climacteric Rises in Ethylene Production and Respiration and to Changes in Skin Color (Score of 2–3) and Fruit Softening (Deformation by 0.30–0.35 mm)

ABA Concentration (mol/L)	Ethylene	Respiration	Color	Softening
0	16.8a	18.5a	19.6a	19.1a
10^{-5}	15.7ab	17.3ab	18.7ab	18.4ab
10^{-4}	13.1c	15.2c	16.8c	16.3c
10^{-3}	12.8cd	14.8cd	16.3cd	15.6cd

Means within a column followed by the same letter are not significantly different at the 5% level.

Table 2. Time (Days) to Inception of the Climacteric Rises in Ethylene Production and Respiration and to Changes in Skin Color (Score of 2–3) and Fruit Softening (Deformation by 0.30–0.35 mm)

Treatments	Ethylene	Respiration	Color	Softening
Control	16.0d	17.1d	18.7d	17.6d
1 µL/L 1-MCP	27.4a	29.9a	32.2a	30.9a
1-MCP with subsequent ABA treatment	27.1ab	28.2b	31.0ab	29.1b
ABA with subsequent 1-MCP treatment	25.9c	26.6c	28.5c	27.3c

Means within a column followed by the same letter are not significantly different at the 5% level.

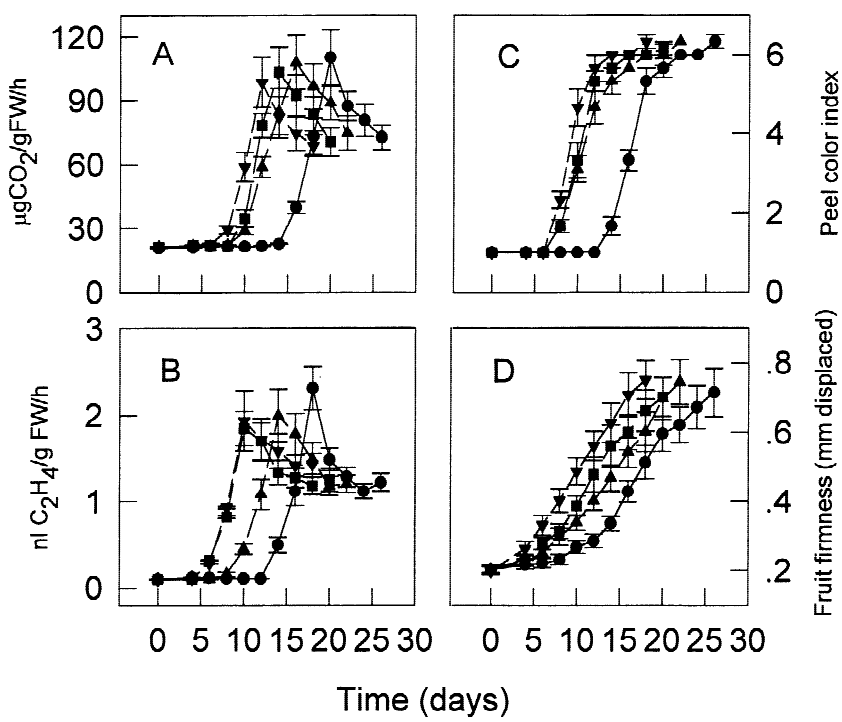

Figure 3. Effect of ethylene treatment on respiration **(A)**, ethylene evolution **(B)**, skin color change **(C)**, and softening **(D)** of banana fruit. Each value is the mean for six measurements, and vertical bars indicate standard errors. ●, Exposure of control (no ABA treatment) fruit to 0.1 µL/L ethylene; ■, exposure of control fruit to 1 µL/L ethylene; ▲, exposure of ABA-treated fruit to 0.1 µL/L ethylene; and ▼, exposure to ABA-treated fruit to 1 µL/L ethylene.

effect to the 10^{-3} mol/L ABA treatment. ABA-induced stimulation of banana fruit ripening was more obvious when judged by time to inception of rises in ethylene evolution and respiration and to changes in skin color and fruit softening (Table 1). For both the higher ABA concentrations, the preceding ripening-related processes were significantly advanced. Also, the respiration maximum in ABA-

Table 3. Time (Days) to Inception of the Climacteric Rises in Ethylene Production and Respiration and to Changes in Skin Color (Score of 2–3) and Fruit Softening (Deformation by 0.30–0.35 mm)

Treatments	Ethylene	Respiration	Color	Softening
Exposure of control fruit to 0 µL/L ethylene	16.8a	18.5a	19.6a	19.1a
Exposure of ABA-treated fruit to 0 µL/L ethylene	12.8bc	14.8bc	16.3bc	15.4bc
Exposure of control fruit to 0.1 µL/L ethylene	12.9b	15.4b	17.8b	16.6b
Exposure of ABA-treated fruit to 0.1 µL/L ethylene	10.4d	12.6d	14.7d	13.7d
Exposure of control fruit to 1 µL/L ethylene	8.1e	9.3e	11.6e	10.3e
Exposure of ABA-treated fruit to 1 µL/L ethylene	7.7ef	8.7ef	10.8ef	9.4ef

Means within a column followed by the same letter are not significantly different at the 5% level.

treated fruit was slightly greater than that of control fruit (Figure 1).

Treatment with ABA and 1-MCP

1-MCP reportedly binds irreversibly to ethylene receptor sites (Sisler and Blankenship 1996). In an earlier study, treatment with 1 µL/L 1-MCP for 12 h markedly delayed ethylene-induced banana ripening (Jiang and others 1999). As judged from trends in ethylene evolution, treatment with ABA had no significant effect on fruit pretreated with 1-MCP (Figure 2). Thus, stimulation of banana fruit ripening by ABA (Figure 1, Table 1) can be largely attributed to ethylene-mediated responses. However, either with ABA application immediately before or after 1-MCP treatment, respiration associated with fruit softening was slightly advanced compared with 1-MCP alone (Table 2). That is, the climacteric rise in respiration and fruit softening was possibly more responsive to treatment with ABA than the ethylene climacteric rise was. Stimulation of some aspects of fruit ripening by ABA that do not coincide with advanced ethylene production may reflect control by a phytohormone balance rather than by a single phytohormone (Vendrell 1985; Vendrell and Buesa 1989).

Response of ABA-treated Fruit to Ethylene

Treatment with ABA only slightly stimulated ethylene biosynthesis of the treated banana fruit (Figure 1, Table 1). It is, therefore, possible that ABA modulates the sensitivity of banana fruit to ethylene. Color change and fruit softening depend on both the presence and perception of ethylene (Blankenship and Sisler 1993). The threshold ethylene concentration to initiate banana ripening is between 0.1 and 1.0 µL/L (Bury and Bury 1962, Inaba and Nakamura 1988, Liu 1976). Exposure of ABA-treated fruit to 0.1 µL/L ethylene for 24 h accelerated the rise in ethylene production and respiration associated with changes in skin color and fruit softening compared with fruit treated with ethylene alone (Figure 3, Table 3). Similarly, a combined treatment of ABA at 10^{-3} mol/L and ethylene at 1 µL/L advanced ripening more than ethylene alone (Figure 3, Table 3). Thus, these data suggest that ABA may trigger enhanced sensitivity to ethylene (see Figure 1, Table 1 and Figure 3, Table 3). This conclusion reinforces the importance of phytohormone balance in controlling fruit ripening (Gertman and Fuchs 1972, Vendrell and Buesa 1989). Because initiation of ripening in climacteric fruit is triggered by ethylene, ABA may act as a coordinator during the climacteric process.

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