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Saline growing conditions induce ripening of the non-ripening mutants *nor* and *rin* tomato fruits but not of *Nr* fruit

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Abstract

Tomato (*Lycopersicon esculentum* Mill.) plants cv. 'Rutgers', and their three nearly isogenic ripening mutant derivative lines *nor*, *rin* and *Nr*, were grown in sand culture irrigated with nutrient solution. Six-week-old plants were exposed to saline growing conditions (EC 15.5 mmohs/cm) by adding NaCl or NaCl + $CaCl_2$ to the nutrient solution. Ripening was induced in *nor* fruit under both saline conditions as indicated by fruit softness, red colour development, induction of a climacteric pattern of C_2H_4 production and an increase in 1-aminocyclopropane-1-carboxylic acid (ACC) content over that of the control. Similar stimulation of all ripening parameters was obtained in *rin* fruit, but only with NaCl treatment. It seems that the presence of Ca^{2+} in the saline solution blocked salt-induced *rin* fruit ripening. Neither saline treatment affected *Nr* fruit ripening. Furthermore, *Nr* fruit grown under non-saline conditions showed yellow colour development and produced C_2H_4 at a level comparable to that produced by 'Rutgers' fruit with no post-climacteric decline. The ACC content of *Nr* fruit was significantly higher than that of post-climacteric 'Rutgers' fruit. These data are discussed as to the possible role of saline treatment with or without Ca^{2+} in inducing ripening in the non-ripening mutants.

Keywords: Non-ripening lines *nor*, *rin*, *Nr*; Ripening; Saline treatments; Tomato

1. Introduction

Tomato fruit ripening is characterized by four clearly defined changes: chlorophyll degradation and carotenoid biosynthesis, increased respiration and ethylene production, softening and associated increases in pectolytic enzyme activity, and seed maturation (Tigchelaar et al., 1978). With the exception of seed maturation, these changes do not occur in non-ripening lines. These mutant lines have been separated into three types: never-ripe (*Nr*), ripening inhibited (*rin*), and non-ripening (*nor*) mutant lines (Tigchelaar et al., 1978).

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Each type is the result of a single mutation on a different chromosome, *Nr* on 9, *rin* on 5 and *nor* on 10 (McGlasson, 1985).

The *Nr* mutation does not totally inhibit ripening, but rather retards the onset of ripening. The respiratory climacteric and associated rise in ethylene production are reduced, and the level of pigmentation never reaches that in normally ripening lines. Fruit of *rin* and *nor*, however, are non-climacteric in both respiration and ethylene production (Tigchelaar et al., 1978).

When *rin* and *nor* tomato plants were stressed by the addition of 3 g l^{-1} NaCl to the nutrient solution, attached *nor* fruit exhibited a slight increase in ethylene production, PG (polygalacturonase) activity, and lycopene content (Mizrahi et al., 1982). This saline treatment had no effect on *rin* fruit. The physiological events surrounding the ability of saline treatments to initiate some ripening parameters in non-ripening tomato mutant lines are unknown.

It has also been reported that Na^+ displaced Ca^{2+} in plant cell membranes under saline growing conditions (Cramer et al., 1985), and several physiological disorders, due mainly to Ca^{2+} deficiency, developed under such conditions (Atta-Aly, 1988). Higher levels of Ca^{2+} supplementation to the tomato plants grown under saline conditions increased the plant's ability to withstand salt stress (Atta-Aly, 1988).

In addition, increasing the level of Ca^{2+} by exogenous application inhibited tomato fruit respiration, ethylene production and action, and ripening (Wills and Tirmazi, 1979). Exogenous ethylene treatments are not effective in reversing Ca^{2+} inhibition of ripening (Wills and Tirmazi, 1979). In addition, chelating Ca^{2+} by direct EDTA application to the fruit (Atta-Aly, 1988) or by adding it to the nutrient solution (Atta-Aly and El-Beltagy, 1992) induced all ripening parameters of *nor* and *rin* fruits.

In the present study, therefore, it was of interest to study the impact on the ripening behaviour of the non-ripening mutants *nor*, *rin* and *Nr* fruits of supplementing the tomato nutrient solution with NaCl, with or without $CaCl_2$.

2. Material and methods

2.1. Plant material

Seeds of *Lycopersicon esculentum* Mill. cv. 'Rutgers' and its nearly-isogenic mutant derivatives, *nor*, *rin* and *Nr* (provided by Dr. R.A. Jones, Department of Vegetable Crops, University of California, Davis, CA) were sown in a peat moss, sand and vermiculite (1:1:1) mixture and transplanted after 5 weeks to 12-l plastic pots filled with coarse sand. Plants were grown in a heated greenhouse at 24°C during the day, and 18°C at night, and irrigated for 15 min every 90 min with 0.5 × Hoagland's nutrient solution (Epstein, 1972) until flowering, when they received full-strength solution until the experiment was terminated. Each pot was irrigated with approximately twice the pot volume at every watering. Excess nutrient solution was collected by gravity from the bottom and recycled.

2.2. Salinity treatments

One week after transplanting, the nutrient solution was supplemented with 7.5 g l^{-1} NaCl or 7.5 g l^{-1} NaCl:$CaCl_2$ (3:1). The electrical conductivity (EC) of the control solution was 1.5 mmohs cm^{-1} while that of the saline solutions was adjusted to 15.5 mmohs cm^{-1} immediately after preparation. The pH values of the solutions were initially adjusted to 6.5 with H_2SO_4. Both EC and pH were monitored every other day. All solutions were renewed at weekly intervals.

2.3. Fruit growth

Flowers were vibrated each day to ensure pollination, and date-tagged at anthesis. Fruit were harvested at mature green (MG), breaker (Br), red-ripe (RR) and over-ripe (OR) stages, i.e. 42, 54, 60 and 65 days after anthesis, respectively. Fruit of the non-ripening mutants were harvested at physiologically equivalent ages to 'Rutgers' fruits, classified by Atta-Aly (1988) and Atta-Aly and El-Beltagy (1992), and summarized as follows:

1. MG (mature green stage): almost full-size fruit, 45 days after anthesis.
2. PBr (physiologically at the breaker stage): first appearance of yellow pigment on the blossom end of *Nr* fruit, 65 days after anthesis; *nor* and *rin* fruits still green. By that time the wild-type fruit reached the over-ripe stage.
3. PRR (physiologically equivalent to red-ripe in cv. 'Rutgers'): 75 days after anthesis; *Nr* fruit are still only yellow at this stage, and *nor* and *rin* fruits are green-yellow in colour.
4. POR (physiologically over-ripe): 90 days after anthesis, *Nr* fruit are yellow-red, and *nor* and *rin* are pale yellow.

Colorimetric readings, firmness, respiration and ethylene production were determined on five replicates each of five fruits. Fruit samples were frozen and kept at −20°C until analyzed for ACC content.

2.4. Analysis of fruit

Fruit colour, as total reflectance of the green (30–35) and red (90–100) components on a scale of 0–100, was measured with an Agtron E5W reflectance spectrophotometer (Kader and Morris, 1978), and was also visually monitored. A non-destructive method was used to measure fruit firmness based on the extent of deformation in millimetres, 15 s after a 500-g load was placed on the fruit (Kavanagh and McGlasson, 1983).

Fruit were enclosed in sealed 500-ml containers (one fruit in each container) for about 2 h before 1 ml of gas was withdrawn from the head space for analysis of C_2H_4 and CO_2 concentrations, as previously described by Atta-Aly et al. (1987).

ACC levels were analyzed in 2 g of frozen pericarp tissue using a modified version (Atta-Aly et al., 1987) of the procedure described by Lizada and Yang (1979).

These experiments were replicated five times in a complete randomized design factorial during the winter and spring seasons at the University of California, Davis, CA. Data were subjected to statistical analysis, and L.S.D. (5%) values were calculated when significant differences were indicated by an *F*-test.

3. Results

Saline treatment during plant growth and fruit development significantly reduced fruit fresh weight in each of the four lines (Table 1). NaCl treatment reduced fruit fresh weight more than NaCl:$CaCl_2$, but this reduction was only statistically significant for 'Rutgers'. 'Rutgers' fruit and *Nr* fruit fresh weight was more severely affected than that of the other two lines.

With the exception of mature-green fruit, *nor* and *rin* fruits from saline treatments were significantly softer than those from control plants at each developmental stage (Table 2). Saline treatment did not produce significantly softer 'Rutgers' and *Nr* fruit.

Both saline treatments significantly induced red colour development in *nor* fruit while only NaCl treatment showed a significant increase in red colour development in *rin* fruit (Fig. 1). In contrast, neither saline treatment increased colour development in 'Rutgers' or *Nr* fruit over the control. The *nor* fruit from NaCl-treated plants showed a significant increase in colour development over the control 10 days earlier than *rin* fruit (i.e. 65 versus 75 days after anthesis, respectively). Ninety days after anthesis, *rin* and *nor* fruits from NaCl-treated plants reached about 88% of the colormeter readings of red-ripe 'Rutgers' fruit. Whole *Nr* fruit were completely yellow 75 days after anthesis and the colormeter reading 90 days after anthesis reached only 65% of that observed for red-ripe 'Rutgers' fruit.

Table 1
Fresh weights of tomato fruits growing in nutrient solution, or supplemented with NaCl or NaCl:$CaCl_2$

Tomato lines	Fruit fresh weight[a] (g)		
	Control	NaCl:$CaCl_2$	NaCl
'Rutgers'	92.18a	46.90b	37.70c
nor	87.05a	55.98b	54.58b
rin	97.40a	58.90b	51.90b
Nr	94.50a	36.98c	35.18c

Measurements were made 65 days after anthesis and values are the means of 25 fruits.
[a] Values followed by the same letter are not statistically different at the 5% level.

Table 2
Softness of tomato fruits growing in nutrient solution, or supplemented with NaCl or NaCl:$CaCl_2$

Tomato lines	Fruit softness (mm deformation)												L.S.D.[a]
	Control				NaCl:$CaCl_2$				NaCl				
	A	B	C	D	A	B	C	D	A	B	C	D	
'Rutgers'	0.7	1.0	2.2	3.4	1.2	1.5	3.5	4.3	1.1	1.7	2.5	3.5	0.8
nor	0.7	0.8	0.8	0.7	0.9	1.8	1.8	1.3	1.1	1.6	1.5	1.6	0.2
rin	0.7	1.0	1.7	1.1	1.1	1.6	2.0	2.2	1.2	1.7	2.1	2.6	0.6
Nr	0.8	1.9	2.3	2.2	1.0	2.3	2.7	2.2	1.2	1.8	2.5	2.7	0.5

Ripening stages are: (A) mature green, (B) breaker, (C) red-ripe and (D) over-ripe stages of the normal ripening for 'Rutgers', or at the physiologically equivalent ages of its nearly isogenic mutant derivatives, *nor*, *rin* and *Nr*. Values are the means of 25 fruits.
[a] L.S.D. values were at the 5% level.

Both saline treatments significantly increased fruit respiration over the control in 'Rutgers', *nor* and *Nr* fruits (Fig. 2). This increase was especially pronounced at the first visible sign of colour development. The only significant increase in *rin* fruit respiration was observed on the fruit of NaCl-treated plants 75 and 90 days after anthesis. At the mature-green stage (A), a significant increase in CO_2 production over the control was only observed for 'Rutgers' fruit from the NaCl treatment and for *Nr* fruit from both saline treatments. At the first visible sign of ripening (B), both saline treatments significantly induced 'Rutgers', *nor* and *Nr* fruit respiration over the control. At 75 days after anthesis (C), *rin* fruit from NaCl-treated plants showed the first sign of ripening and produced significantly higher amounts of CO_2 than that of control. At the same time, differences between treatments in *nor* and *Nr* fruits were diminished. At the over-ripe stage (D), the only remaining significant difference among treatments was for *rin* fruit from NaCl-treated plants. Saline treatments accentuated the normal climacteric rise in CO_2 production during ripening of 'Rutgers' fruit. A similar pattern was not observed in any of the mutant fruits, although some saline treatments did induce ripening of *rin* and *nor* fruit.

Ethylene production by 'Rutgers' and *Nr* fruit from all treatments increased dramatically with the first sign of fruit ripening (Fig. 3). 'Rutgers' fruit produced the normal climacteric increase and decrease in ethylene production during fruit ripening, while ethylene production by *Nr* fruit appeared to plateau after the initial rise associated with the first sign of ripening. The saline treatments accentuated ethylene production over the control by 'Rutgers' fruit while reducing it below the control for *Nr* fruit. Ethylene production by control fruit of *nor* and *rin* remained much lower than that produced by the other two lines for all ripening stages. Both saline treatments stimulated ethylene production by *nor* fruit, but the NaCl treatment had a more pronounced effect than the NaCl:$CaCl_2$ treatment. The NaCl treatment was also the only saline treatment that stimulated ethylene production by *rin* fruit, even though ethylene production from *nor* and *rin* fruit from saline treatments was significantly lower than in 'Rutgers' or *Nr* fruit.

ACC levels generally increased as ripening progressed (Fig. 4). The greatest increase occurred in *Nr* fruit, followed by a much smaller increase in 'Rutgers' fruit. In these fruits, the saline treatments increased ACC levels over the control. This was clearly noticed 75 and 90 days after anthesis with more pronounced levels for those exposed to NaCl:$CaCl_2$ treatment. ACC levels were also increased with NaCl treatment in *nor* and *rin* fruit, and with NaCl:$CaCl_2$ treatment in *nor* fruit, to a level equal to that observed in over-ripe 'Rutgers' fruit.

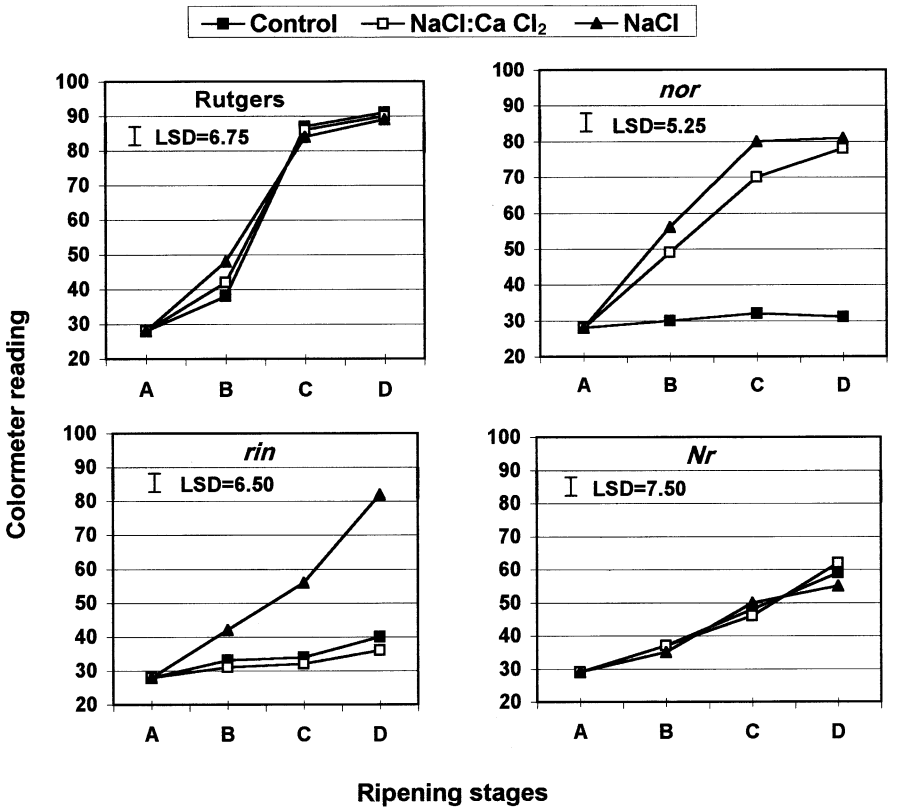

Fig. 1. Colour development of tomato fruits growing in nutrient solution or supplemented with NaCl or NaCl:$CaCl_2$. Ripening stages are classified as previously described in Table 2 and each value is the mean of 25 fruits. The L.S.D. values are indicated as vertical bars at the 5% level.

4. Discussion

The reduction in tomato fruit fresh weight grown under saline conditions could be due to the reduced size of those plants, and subsequent reduction in photosynthetic area. Fruit produced under saline conditions have reduced water content (Sharaf and Hobson, 1986), probably resulting from reduced water uptake during the expansive stage of fruit cell growth (Flowers et al., 1977). Addition of NaCl to the growing media significantly reduced bean (Greenway and Munns, 1980) and tomato (Shalhevet and Yaron, 1973) fruit fresh weight. Reduction in fruit fresh weight was not as great in the NaCl:$CaCl_2$ treatment as in the NaCl treatment, especially in 'Rutgers' fruit (Table 1). This differential effect suggests that Ca^{2+} partially counteracted the effect of NaCl on fruit growth, particularly for 'Rutgers' fruits. A similar amelioration by Ca^{2+} of the effects of NaCl on reduction of plant growth, and on necrosis of roots and shoots of bean plants, has been observed (Greenway and Munns, 1980).

Since ripening of *Nr* fruit is significantly slower than that of normal fruit, and since *nor* and *rin* fruit develop some yellow or red colour, respectively, around 65 days after anthesis (i.e. at the age of over-ripe 'Rutgers' fruit) (Tigchelaar et al., 1978), it seems reasonable to conclude that normal fruits precede those of the mutants in maturation and colour initiation. The first visible sign of ripening in *Nr* fruit was at the same time that *nor* fruit from saline treatments started to show some red colour development (Fig. 1). When *Nr* fruit had became totally yellow (i.e. 75 days after anthesis), red colour had started to develop in *rin*

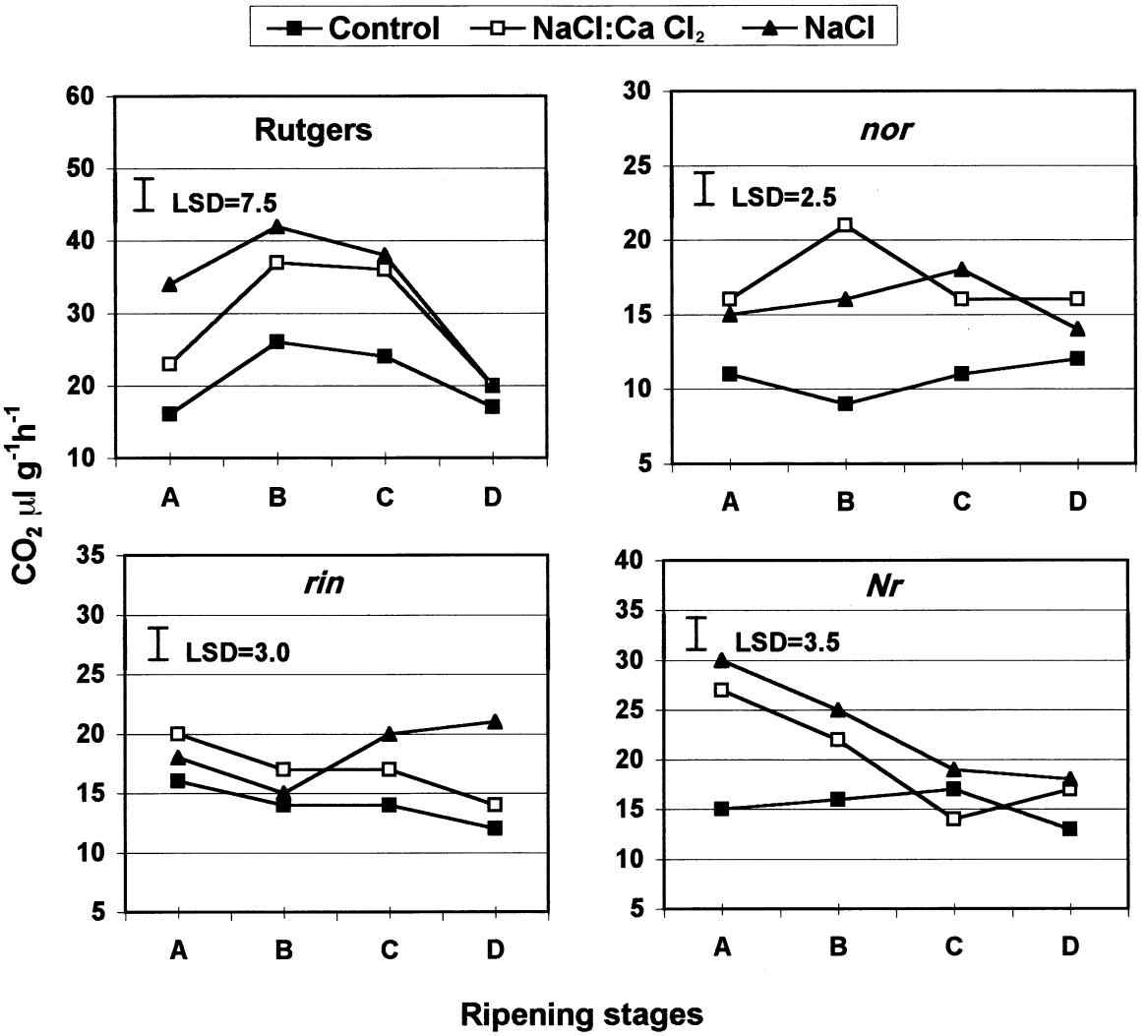

Fig. 2. Respiration levels, measured as CO_2 production, of tomato fruits growing in nutrient solution or supplemented with NaCl or NaCl:$CaCl_2$. Ripening stages are classified as previously described in Table 2 and each value is the mean of 25 fruits. The L.S.D. values are indicated as vertical bars at the 5% level.

fruit from the NaCl-treated plants (Fig. 1). Because of these differences, fruit were harvested at physiologically equal ages and not on the basis of days after anthesis.

Salinity treatment appeared to have no significant effect on the significant reduction in firmness that occurred during 'Rutgers' and *Nr* fruit ripening (Table 2). Fruit firmness in these two lines was more related to fruit ripening than saline treatments. In *nor* and *rin* lines, however, saline treatments significantly reduced fruit firmness over the control whether ripening was induced or not. It has previously been reported that Ca^{2+} levels in *rin* fruit were significantly reduced when plants were grown with both NaCl and $CaCl_2$ in the nutrient solution (Atta-Aly, 1988). This was especially obvious when the EC of the saline solution was higher than 5.5 mmohs cm^{-1}. Since Ca^{2+} is a major component of the fruit cell wall, salinity treatments may produce softer *rin* fruit because of the reduced Ca^{2+} content in the fruit. Softer fruit may due also to reduced water content in fruit

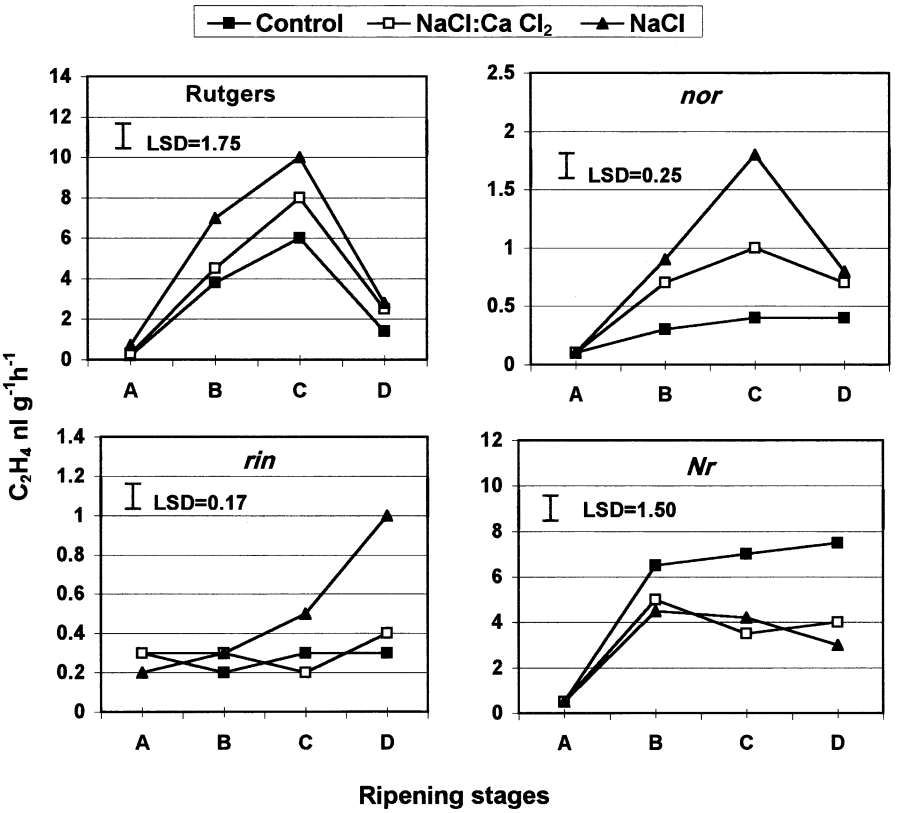

Fig. 3. Ethylene production of tomato fruits growing in nutrient solution or supplemented with NaCl or NaCl:$CaCl_2$. Ripening stages are classified as previously described in Table 2 and each value is the mean of 25 fruits. The L.S.D. values are indicated as vertical bars at the 5% level.

produced under saline conditions (Sharaf and Hobson, 1986).

The increase in ethylene production by fruit of each of the four lines was accompanied by an increase in red colour development, with the exception of *Nr* fruit which showed extensive yellow colour development (Figs. 1 and 3). Since ethylene production by *Nr* and 'Rutgers' fruit was similar (Fig. 3), the *Nr* mutation may be related more to insensitivity to ethylene. It has also been reported that the *Nr* mutation influences the level of ethylene-inducible gene expression and is linked to the ETR1 (ethylene-response mutant) gene (Yen et al., 1995). On the other hand, the 50% reduction in ethylene production reported by Tigchelaar et al. (1978) for *Nr* fruit compared to normal fruit may have resulted from comparing the fruits on the basis of days after anthesis rather than precise physiological stages. In *nor* and *rin* fruits, the NaCl treatment stimulated both ethylene production and red colour development (Figs. 1 and 3). Ethylene treatment alone has no effect on the ripening of *nor* fruit (Adato and McGlasson, 1977). This may indicate that the NaCl treatment partially overcame fruit resistance to ethylene action in *nor* fruit. In *rin* fruit, however, ethylene treatment stimulated red colour development and besides these saline treatments, only wounding has been reported to induce ethylene production in *rin* fruit (Frenkel and Garrison, 1976). NaCl treatment, therefore, may partially overcome inhibition of ethylene synthesis in *rin* fruit. Mizrahi et al. (1982) reported that NaCl treatment did not stimulate *rin* fruit ripening. Ripening stimulation observed in *rin* fruit of NaCl-treated plants (Figs. 1 and 3) may be due to

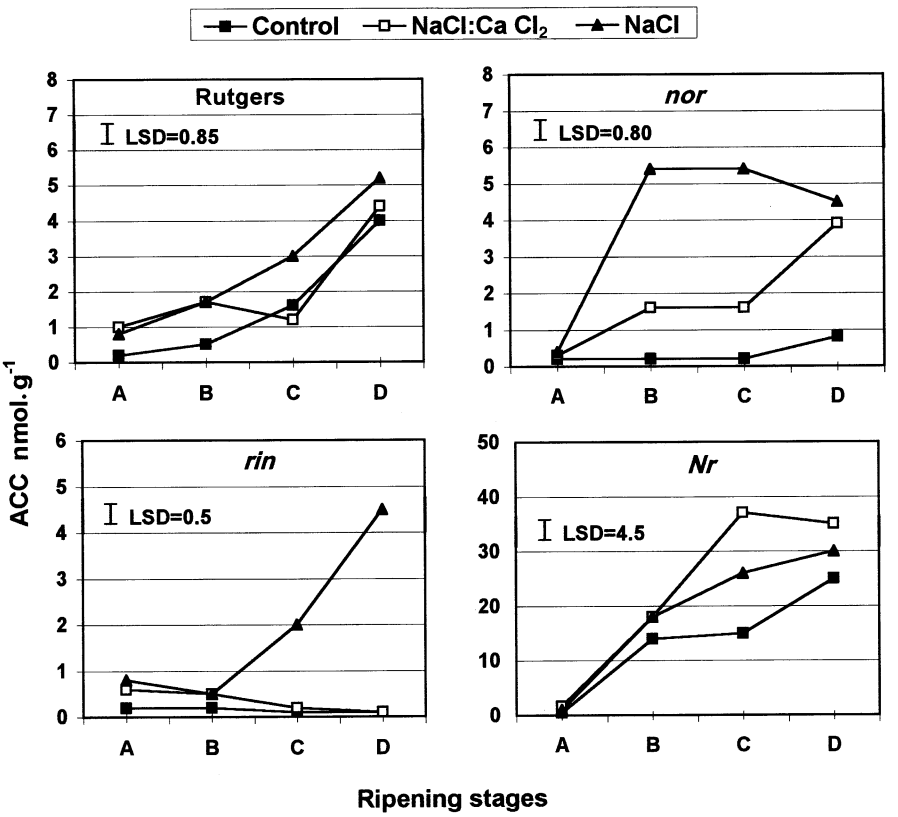

Fig. 4. The ACC contents in tomato fruits growing in nutrient solution or supplemented with NaCl or NaCl:$CaCl_2$. Ripening stages are classified as previously described in Table 2 and each value is the means of 25 fruits. The L.S.D. values are indicated as vertical bars at the 5% level.

the higher NaCl concentrations used, or to the longer exposure time of plants to NaCl treatments. Unlike the NaCl treatment, the NaCl:$CaCl_2$ treatment did not induce ripening in *rin* fruit (Figs. 1 and 3). This may due to the presence of high Ca^{2+} levels in the saline solutions or to higher levels of salt or water stress from using Ca^{2+}-free salts. It is well known that Ca^{2+} can counteract ethylene action (Wills and Tirmazi, 1979) and is displaced by Na^{+} in plant cell membranes under saline growing conditions (Cramer et al., 1985). Adding Ca^{2+} to the saline solution may arrest such displacement and consequently inhibit fruit response to C_2H_4. Furthermore, the lack of C_2H_4 production in *rin* fruits was overcome only with the NaCl treatment (Fig. 3). Infiltrating normal fruit with Ca^{2+} inhibits ripening and ethylene production by tomato fruit (Wills and Tirmazi, 1979). In addition, ethylene exposure was unable to reverse the inhibitory effect of Ca^{2+} treatment on the ripening of normal fruit. Atta-Aly (1988) found that feeding detached fruit with the cationic chelator ethylenediamintetraacetic acid (EDTA) through the pedicel stimulated ethylene production and ripening of *rin* and *nor* fruits, and this may indicate that Ca^{2+} may play a vital role in fruit ripening and a specific role in the non-ripening mutant's mode of action.

Both saline treatments significantly increased respiration of mature-green *nor* fruit over the control (Fig. 2) and stimulated fruit ripening, while neither saline treatment was able to increase the respiration of mature-green *rin* fruit and only the NaCl treatment stimulated *rin* fruit ripening. These data strongly suggest that *nor* fruits are

more responsive to salt-induced ripening than are *rin* fruits.

Levels of ACC in fruit of each of the four lines followed the same pattern as ethylene production, with the exception of over-ripe 'Rutgers' fruit in which ethylene production declined while ACC levels continued to increase. A reduced level of ethylene production in over-ripe fruit is accompanied by decreased EFE (ethylene forming enzyme) activity, with ACC accumulation (Hoffman and Yang, 1980). At the over-ripe stage, it appears that the conversion of ACC to ethylene by EFE became the rate-limiting step in ethylene production. Over-ripe 'Rutgers' fruit showed a significant decrease in ethylene production during the time when ACC levels significantly increased (Figs. 1 and 3).

As ripening was stimulated in *nor* fruit by both saline treatments, and in *rin* by the NaCl treatment, ACC levels significantly increased over those of the control fruit (Fig. 4). At the same time, ethylene produced by *rin* and *nor* fruit of the NaCl treatment or of both saline treatments, respectively, was significantly lower than that of red-ripe 'Rutgers' fruit. These data may indicate that ACC conversion to ethylene (i.e. EFE activity) was lower in the mutants than in 'Rutgers', and this could be the reason behind ACC accumulation. In *Nr* fruit, however, while ethylene production significantly increased with the first sign of fruit ripening to the same level as that produced by red-ripe 'Rutgers' fruit, a significant reduction occurred under both saline conditions, especially after the fruit became yellow (i.e. 75 and 90 days after anthesis). Measuring ACC levels in *Nr* fruits, therefore, may explain the unexpected ethylene reduction found with saline treatments. Data presented in Fig. 4, however, showed that ACC levels increased in *Nr* fruits above that in the control under both saline treatments. Furthermore, ACC levels in *Nr* fruit were 5-fold greater than that in over-ripe 'Rutgers' fruit, which may suggest higher ACC synthase activity in *Nr* than in 'Rutgers' fruit. Unlike 'Rutgers' fruit, *Nr* fruit did not show a decrease in ethylene production at the final stage of ripening, indicating a constant rate of ACC conversion to ethylene under normal conditions. Under saline conditions, however, the increased levels of ACC in *Nr* fruit were accompanied by ethylene reduction. It seems, therefore, that EFE in *Nr* fruit is more sensitive to salinity than ACC synthase.

It can be concluded that the *Nr* mutation only inhibited ripening development by inhibiting ethylene action and not autocatalytic ethylene biosynthesis. In *rin* and *nor* fruit, however, the mutation inhibited both red colour development and ethylene biosynthesis. NaCl treatment, however, partially overcame the *nor* and *rin* mutations and induced both ethylene biosynthesis and fruit red colour development.

Acknowledgements

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