

Ethylene Evolution by Tomatoes Stressed by Ammonium Nutrition

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Abstract. Studies of ethylene evolution by tomato (*Lycopersicon esculentum* Mill.) fruit were conducted with plants receiving $\text{NH}_4\text{-N}$ or $\text{NO}_3\text{-N}$ nutrition. Fruit of plants grown with $\text{NH}_4\text{-N}$ had a higher occurrence of blossom-end rot (BER), higher $\text{NH}_4\text{-N}$ concentrations, and higher ethylene evolution rates than fruit from plants grown with $\text{NO}_3\text{-N}$. Fruit of plants grown with $\text{NO}_3\text{-N}$ showed no enhancement in ethylene evolution with BER development. Fertilizing these plants with $\text{Ca}(\text{NO}_3)_2$ doubled the average Ca concentration of fruit and restricted BER development. Ammonium suppressed Ca accumulation in fruit relative to those grown with $\text{NO}_3\text{-N}$. Ethylene evolution increased as fruit from plants receiving $\text{NO}_3\text{-N}$ ripened, but without a concomitant increase in $\text{NH}_4\text{-N}$ concentrations in the fruit. Ammonium accumulation in fruit induced BER and enhanced ethylene evolution. These relationships were unique, for $\text{NH}_4\text{-N}$ accumulation did not seem to be a naturally occurring phenomenon in ripening fruit or in fruit that have BER arising from other causal factors.

Blossom-end rot (BER) of fruit is a physiological disorder that causes extensive losses of tomato production in fields or greenhouses. Blossom-end rot has been long recognized as Ca-deficiency disorder (Evans and Troxler, 1953; Geraldson, 1957; Maynard et al., 1957), which may be induced by drought (Stout, 1934), salinity (Robbins, 1937), K fertilization (Raleigh and Chucka, 1944), NH_4^+ fertilization (Spencer and Beckenbach, 1949), and low Ca supply (Lyon et al., 1942). The form of N fertilization in relation to BER has been investigated considerably because of the strong restrictive effects that NH_4^+ has on cation accumulation by plants (Barker et al., 1966; Pill et al., 1978; Wilcox et al., 1973).

In agreement with other researchers (Pill and Lambeth, 1980; Pill et al., 1978; Wilcox et al., 1973), we have noted a high incidence of BER on tomatoes grown with $\text{NH}_4\text{-N}$ and have observed also that BER-affected fruit ripen more rapidly than normal fruit (unpublished data). A significant correlation between incidence of BER and uniform ripening was noted among some tomato genotypes (Trinklein and Lambeth, 1976). The phenomenon of early ripening of BER-affected fruit may be controlled endogenously by Ca levels (Rigney and Wills, 1981; Wills et al., 1977) and ethylene production in the fruit (Hoffman and Yang, 1980). Ammonium nutrition suppresses Ca accumulation by plants (Greenleaf and Adams, 1969; Pill et al., 1978), perhaps resulting in restricted Ca levels in fruit and advanced ripening (Rigney and Wills, 1981; Wills et al., 1977). Ethylene evolution by tomato foliage is enhanced markedly by NH_4^+ toxicity (Corey et al., 1987). Perhaps the stress of NH_4^+ toxicity also enhances ethylene biosynthesis by fruit. The present research investigated the relationships among $\text{NH}_4\text{-N}$ nutrition, Ca accumulation, and ethylene production by fruit that were damaged by BER.

Materials and Methods

This research was conducted in the spring and summer seasons in the greenhouse and field in 1990. In one experiment started in April in the greenhouse, 'Heinz 1350' tomato plants were grown

in a soil-based medium [7 sandy loam : 3 peatmoss : 2 sand (b. volume) with 3 g limestone and 3 g ordinary superphosphate, 0N-8.8P-0K (per liter)] in 8.5-liter plastic nursery pots (21.5 × 21.5 cm). Ten plants in each of two nutritional regimes were grown in a completely random design. One regime provided N nutrition from daily applications of 100 ml 0.02 M $(\text{NH}_4)_2\text{SO}_4$ to impose NH_4^+ toxicity, as indicated by the development of BER and stem lesions (Maynard et al., 1966). Plants in the other regime were fertilized biweekly with 400 ml 20N-8.8P-16.6K fertilizer (urea ammonium phosphate, and potassium nitrate) supplying 200 mg N/liter; 26% of the initial supply of N from this fertilizer was a NO_3^- . Because of the inclusion of NO_3^- in the fertilizer and likelihood of nitrification in the medium, the plants were identified as $\text{NO}_3\text{-grown}$ plants. The latter regime produced plants with no toxicity or deficiency symptoms and no BER. The fruit harvested from this experiment were used to compare ethylene evolution and $\text{NH}_4\text{-N}$ accumulation by normal and BER-affected fruit from $\text{NH}_4\text{-stressed}$ plants and normal fruit from unstressed ($\text{NO}_3\text{-grown}$) plants. Green fruit were used in these comparisons. Preliminary fruit such as these generally have low ethylene evolution rate (Hoffman and Yang, 1980).

In another experiment started in March, 'Vendor' tomato plants were grown in a peatmoss-vermiculite-perlite medium (peat-lite) and fertilized with the same urea, ammonium phosphate, and potassium nitrate fertilizer. None of the 10 plants in this group showed any foliar toxicity or deficiency symptoms, but BER frequency was high among the fruit. After ethylene evolution was measured in fruit from this group of plants, half of the plants were fertilized with $\text{Ca}(\text{NO}_3)_2$ to provide 1 g Ca/pot (8.5-liter containers). Two weeks after fertilization, fruit were taken to determine Ca concentration.

In the field experiment started in May in a Hadley fine sand loam at South Deerfield, Mass., 'Heinz 1350' plants were fertilized only with 80 kg N/ha from NH_4NO_3 applied before planting. None of these plants showed foliar toxicity or deficiency symptoms, and none produced fruit with BER. Fruit from this experiment were used to determine ethylene evolution and $\text{NH}_4\text{-N}$ accumulation at different stages of ripening: green, 100% green breaker, <10% pink or red; turning, 10% to 30% tannish yellow pink, or red; ripe, >60% pink or red. These groupings were used because there were no differences in ethylene evolution between immature green or mature green fruit or among fruit ripened past the turning stage.

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In all experiments, ethylene was measured with whole fruit sealed in wide-mouth canning jars fitted with rubber septa in screw-top lids. Portions of the atmosphere in the jars were removed with a syringe to analyze ethylene evolution by gas chromatography (Corey et al., 1987). After ethylene evolution was determined, fruit were sectioned radially, and 10-g portions were saved for $\text{NH}_4\text{-N}$ analysis. The remaining portions of the fruit were weighed and dried to determine dry weights for calculating $\text{NH}_4\text{-N}$ on a dry-weight basis and for elemental analyses. Ammonium-N was determined volumetrically (Barker and Volk, 1964) on extracts made by homogenizing the 10 g of fruit in 50 ml of 1 M KCl + 0.02 M CuSO_4 and vacuum-filtering the homogenate. Fruit pH was determined electrometrically with a glass electrode and saturated calomel standard electrode on fruit juice extracted by mashing the fruit with a mortar and pestle and vacuum-filtering the resulting pulp. Calcium, Mg, and K concentrations were determined by atomic absorption spectrophotometry on 1 M HCl extracts of the dried fruit samples (Sahrawat, 1987). All determinations were made on at least duplicate samples of fruit taken on a given day, and replications were provided by repeating these determinations with new fruit on different days. Data were processed by analysis of variance (Steele and Torrie, 1980).

Results

Ethylene evolution and ammonium accumulation by fruit. Ethylene evolution and $\text{NH}_4\text{-N}$ accumulation are reported for green fruit with or without BER from plants receiving $\text{NH}_4\text{-N}$ nutrition and by unblemished fruit of 'Heinz 1350' plants receiving $\text{NO}_3\text{-N}$ nutrition (Fig. 1). Fruit with BER had the highest rates of ethylene evolution of the group. Fruit without BER from plants receiving $\text{NH}_4\text{-N}$ nutrition had much lower ethylene evolution but did not have $\text{NH}_4\text{-N}$ concentrations different from those of the fruit showing BER. On one occasion, $\text{NH}_4\text{-grown}$ fruit without BER at harvest developed BER after 24 h of storage at room temperature. None of the fruit from plants receiving $\text{NO}_3\text{-N}$ nutrition had BER, and all had low ethylene evolution rates and $\text{NH}_4\text{-N}$ accumulation

relative to the fruit from plants receiving $\text{NH}_4\text{-N}$ nutrition.

'Vendor' tomatoes grown in peat-lite had high incidences of BER at the green, breaker, turning, and ripe development stages. Ethylene evolution by these fruit rose with increasing ripening stage, but there were no differences in ethylene evolution between fruit with and without BER (Fig. 2). Ammonium-N accumulation did not vary with BER condition of fruit, averaging 0.14 mg N/g fresh weight in fruit with BER and 0.18 mg N/g fresh weight in fruit without BER. These concentrations of $\text{NH}_4\text{-N}$ are about half of those occurring in fruit of plants grown with $\text{NH}_4\text{-N}$ (Fig. 1).

Ethylene evolution by 'Heinz 1350' tomatoes grown in the field with $\text{NO}_3\text{-N}$ increased with advancing ripening stage (Fig. 3). Ammonium-N concentrations did not vary with ripening stage, remaining at ≈ 0.15 mg N/g fresh weight, essentially the same as those in 'Vendor' tomatoes.

Calcium in fruit. Calcium concentrations were higher in 'Heinz 1350' fruit receiving $\text{NO}_3\text{-N}$ nutrition than in fruit of plants receiving $\text{NH}_4\text{-N}$ nutrition (Table 1). Calcium did not differ with respect to BER incidence on the $\text{NH}_4\text{-grown}$ fruit. Concentrations of Mg or K did not vary with fruit condition or nutritional status (Table 1). With 'Vendor', Ca concentrations differed slightly but significantly whether the fruit had BER or not (Table 2). Fertilization with Ca increased fruit Ca, with measurements taken 2.5 weeks after Ca fertilizer was applied. Blossom-end rot at this time was confined largely to ripe fruit, with very few green fruit having BER, a result indicating that fertilization had arrested BER development. Ripe fruit had higher Ca than green fruit, with the increases in fruit Ca being restricted to fruit from fertilized plants. Neither K nor Mg varied with BER status, with an average K concentration of 2.57% and an average Mg concentration of 0.16% on a dry-weight basis.

Fruit pH. The juice extracted from green 'Heinz 1350' fruit with $\text{NH}_4\text{-induced}$ BER was pH 5.5, which was higher than that (pH 4.5) from fruit of $\text{NO}_3\text{-grown}$ plants. Extracts from $\text{NH}_4\text{-grown}$ fruit without BER were pH 5.4. For ripening fruit with $\text{NH}_4\text{-induced}$ BER, juice pH was 4.8. Juice from ripening $\text{NO}_3\text{-grown}$ fruit was pH 4.4.

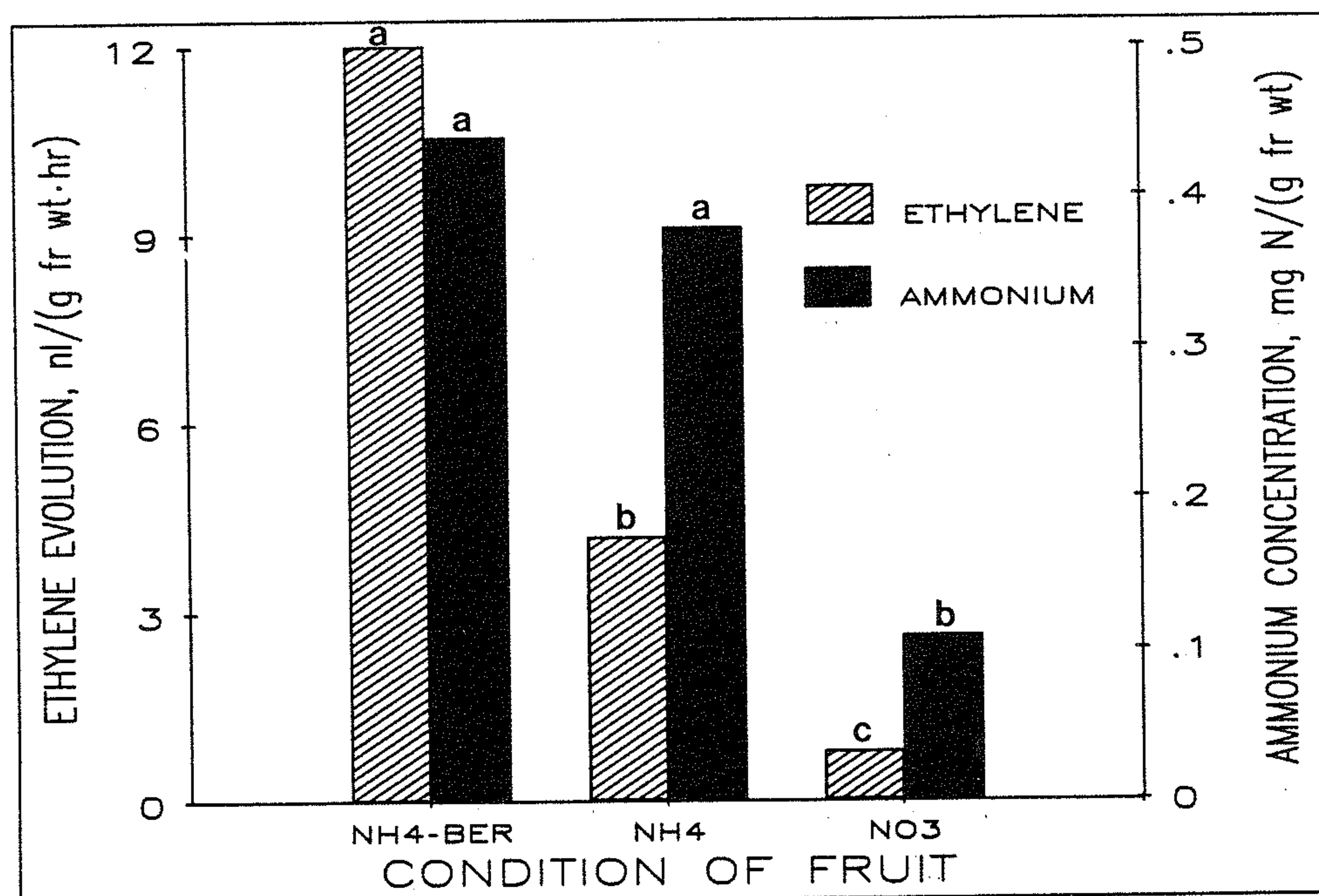


Fig. 1. Ethylene evolution and $\text{NH}_4\text{-N}$ concentrations in green 'Heinz 1350' tomatoes with $\text{NH}_4\text{-N}$ with or without blossom-end rot (BER), and with $\text{NO}_3\text{-N}$. Letters over bars indicate significant difference by Duncan's multiple range test among means for ethylene evolution or $\text{NH}_4\text{-N}$ concentration.

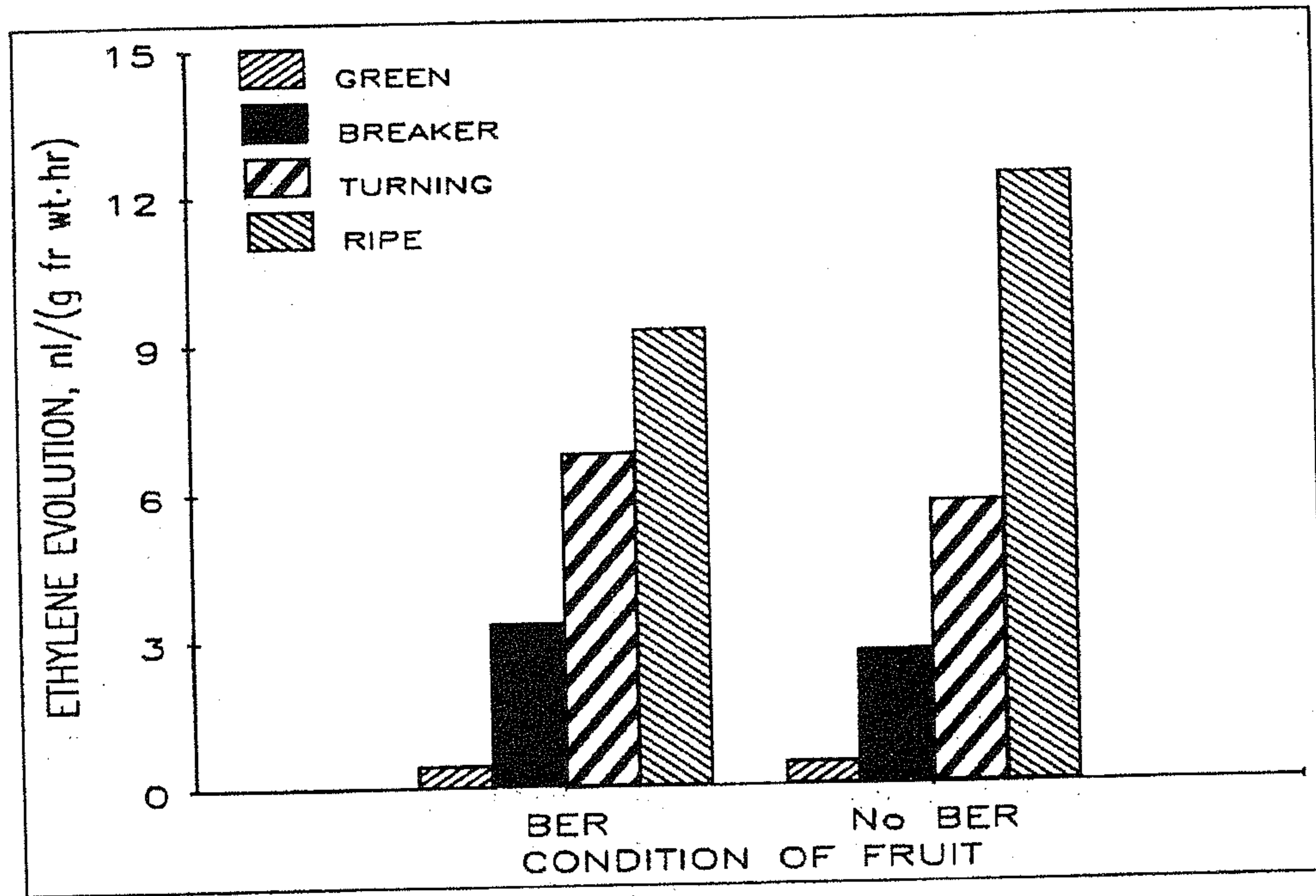


Fig. 2. Ethylene evolution of 'Vendor' tomatoes at different ripeness stages with or without blossom-end rot (BER). Results of analysis of variance: BER, nonsignificant; ripeness, significant ($P \leq 0.01$); BER \times ripeness, nonsignificant.

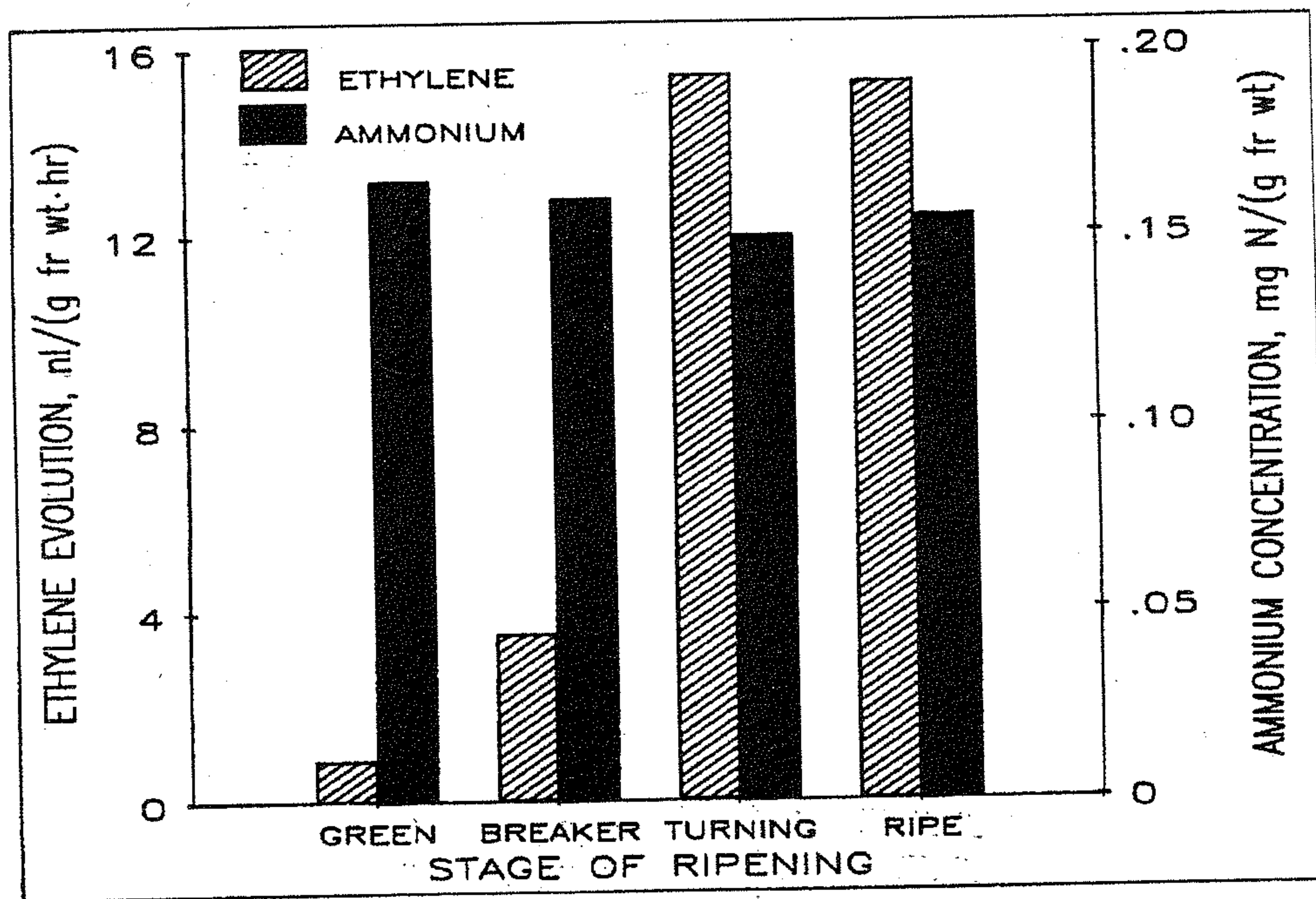


Fig. 3. Ethylene evolution and $\text{NH}_4\text{-N}$ concentrations in 'Heinz 1350' tomatoes at different ripeness stages. Results of analysis of variance: ethylene, significant increase with ripening ($P \leq 0.01$); $\text{NH}_4\text{-N}$, no change with ripening.

Table 1. Elemental composition of 'Heinz 1350' tomatoes with or without blossom-end rot (BER) from plants grown on $\text{NH}_4\text{-N}$ or $\text{NO}_3\text{-N}$ nutrition.

Condition of fruit		Concn (mg·kg ⁻¹ dry wt)		
N source	BER ²	Ca	Mg	K
NH_4	BER	390 a	1141 a	26,062 a
NH_4	No BER	382 a	1106 a	25,280 a
NO_3	No BER	682 b	1209 a	25,502 a

²Condition at harvest. None of the $\text{NO}_3\text{-N}$ -grown tomatoes had BER. Mean separation within columns by LSD at $P \leq 0.01$.

Discussion

Plants stressed by $\text{NH}_4\text{-N}$ nutrition produced fruit with high incidences of BER. These fruit accumulated higher $\text{NH}_4\text{-N}$ concentrations, had higher ethylene evolution rates when green, and had lower Ca concentrations than unblemished fruit from plants receiving $\text{NO}_3\text{-N}$ nutrition. The accumulation of $\text{NH}_4\text{-N}$ was a unique characteristic of fruit from plants grown on $\text{NH}_4\text{-N}$, neither normally ripening fruit nor BER fruit of plants receiving $\text{NO}_3\text{-N}$ showed enhanced $\text{NH}_4\text{-N}$ levels. Stresses such as NH_4 toxicity (Corey et al., 1987), certain nutrient deficiencies (Fer

Table 2. Concentrations of Ca in ripe or green 'Vendor' tomatoes with or without blossom-end rot (BER) and before or after Ca fertilization.

Condition of fruit and means	Ca concn (mg·kg ⁻¹ dry wt)				
	Before fertilization		After fertilization		Mean
	Green	Ripe	Green	Ripe	
BER	625	563	1075	1503	957
No BER	694	669	1162	1663	1089*
Mean (ripeness × fertilization)	660 a ^z	616 a	1118 b	1583 c	
Mean (fertilization)	669		1377**		

^zMean separation within the ripeness × fertilization interaction by LSD at $P \leq 0.01$. BER condition × fertilization × ripeness interaction was nonsignificant.

**Significant by F test at $P \leq 0.05$ or 0.01, respectively.

and Barker, 1992a), and salinity (Feng and Barker, 1992b) lead to NH₄-N accumulation in tomato foliage. Ammonium-N accumulation seems to be followed by ethylene evolution (Barker and Corey, 1991; Feng and Barker, 1993). With plants grown with NH₄-N, we noted that NH₄-N accumulated in fruit without BER and that ethylene evolution was lower from these fruit than from those with BER. These observations and BER development during storage of harvested, green, NH₄-grown fruit suggest that NH₄-N accumulation precedes BER development and ethylene biosynthesis. Perhaps, in parallel with the physiology of foliage, NH₄-N accumulation in green fruit initiates injury and processes that lead to ethylene evolution (Barker and Corey, 1991).

The finding of lower total Ca concentrations in NH₄-grown fruit agrees with results in which NH₄-N nutrition or depressed Ca levels were related to enhanced BER incidence (Greenleaf and Adams, 1969; Pill et al., 1978). Fruit with BER from plants grown with NH₄-N had about half the Ca concentration of unblemished fruit from plants grown with NO₃-N. With plants on NO₃-N nutrition, differences in fruit Ca concentrations were small but significant between BER and normal fruit. Although it is understood clearly (Geraldson, 1957; Maynard et al., 1957) that BER is a result of Ca deficiency, attempts to demonstrate that fact through fruit analyses have not always been successful (Murray et al., 1972; Pill and Lambeth, 1980). Differences in Ca distribution (Pill and Lambeth, 1980) or relationships of Ca with K and Mg in fruit (Murray et al., 1972) have been offered as explanations for the lack of correlation between BER and total fruit Ca. We did not measure Ca partitioning in fruit, but observed no special relationships among Ca, K, and Mg in fruit with BER, regardless of source of N nutrition.

Some similarities between the physiological responses of NH₄-stressed fruit and bruised or diseased fruit are apparent. Bruised mature-green fruit ripened quickly and had higher ethylene evolution rates and lower titratable acidity than unblemished fruit (MacLeod et al., 1976). Ripe fruit infected with *Alternaria tenuis* or anthracnose (*Colletotrichum coccodes*) had higher pH and lower titratable acidity than uninfected fruit (Sapers et al., 1978). Ammonium accumulation was not measured in the previous studies; however, NH₄⁺ has been shown to accumulate in disease-infected leaves and to be a causal agent in the injury resulting from the infections (Bashan et al., 1980; Lovrekovich et al., 1970). The deleterious effects of bruising and disease infection may have been due to NH₄⁺ accumulation induced by these injuries.

The increased ethylene evolution rates and apparently increased ripening rates by green fruit from plants grown with NH₄-N seem to be the result of stresses imparted by NH₄-N accumulation in the fruit. Our results show that NH₄-N accumulation was confined to NH₄-grown plants, was not associated with

normal fruit ripening, and did not occur in fruit with BER induced by factors other than NH₄-N nutrition. The results also suggest that restricted Ca accumulation by fruit of plants grown with NH₄-N was associated with BER development.

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Developmental Light Level Affects Growth, Morphology, and Leaf Physiology of Young Carambola Trees

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Abstract. Growth and leaf physiology responses of container-grown 'Arkin' carambola (*Averrhoa carambola* L.) trees to long-term exposure of ≈25%, ≈50%, or 100% sunlight were studied in four experiments in Guam and Florida. Shading increased rachis length and leaflet area, and decreased leaflet thickness. Shaded trees also had a more horizontal branch orientation. Shading reduced dark respiration (R_d) and light compensation and saturation points but increased chlorophyll concentration and N-use efficiency. Light-saturated net CO₂ assimilation (A) was not affected by developmental light level. Trees in full sun had smaller total leaf area, canopy diameter, and shoot : root ratio and exhibited leaflet movement to avoid direct solar radiation. Also, trees grown in 100% sunlight had a more vertical branch orientation and greater stomatal density than shaded trees. The ratio of variable to maximum fluorescence (F_v/F_m) declined during midday in 100% sunlight trees. This pattern was accompanied by a midday suppression of A in 100% sunlight-grown trees in Guam. 'Arkin' carambola trees exposed to ≈25%, ≈50%, or 100% sunlight for up to 39 weeks exhibited physiological and morphological adaptations that resulted in similar growth. These results indicate that carambola efficiently adapts to different developmental light intensities.

Plants adapt to different irradiance levels by anatomical, morphological, and/or physiological changes that allow the maintenance of a positive carbon balance in a wide range of light environments (Bjorkman, 1981; Fitter and May, 1981; Kramer and Kozlowski, 1979). Low irradiance generally leads to larger leaves with reduced thickness, stomatal density, and conductive tissue per unit leaf area. Canopy responses to low light include increased internode length and reduced leaf area index. Plants also exhibit numerous physiological adaptations to low irradiance, including increased quantum yield and reduced R_d , light compensation and saturation points.

Campbell et al. (1985) suggested that shading of carambola trees results in reduced fruit production and recommended planting trees in sites exposed to full sun. However, in several areas, including Australia (Watson et al., 1988) and Florida (Crane, 1992), carambola trees are grown under shade coverings for insect or wind control. Furthermore, pruning of mature carambola trees is necessary for tree size control or to prevent overcrowding (Campbell et al., 1985; Crane, 1992), but little is known about optimum canopy size or the relationship of canopy size to natural shading and yield.

The rapidly increasing commercial production of carambola has resulted in the industry developing in advance of adequate research. Thus, a better understanding of the light-acclimation process of trees may lead to improved management practices under various conditions. The objectives of this study were to determine the influence of light level during plant development on growth,

morphology, and leaf physiology of carambola trees and to classify carambola with respect to shade tolerance.

Materials and Methods

Three separate experiments were conducted on the island of Guam (lat. 13°N). Twelve quonset-style structures with a height of ≈1.5 m were constructed outdoors on top of raised benches to provide 24%, 47%, or 100% of ambient light conditions (four structures per transmittance level). Shading was achieved by covering the structures with neutral-woven polyethylene fabric, and sunlight transmittance was measured using a quantum sensor (model LI-190 SA; LI-COR, Lincoln, Neb.) oriented perpendicular to the solar beam. The full sun structures were left uncovered. The fabric on shaded structures extended to the bench top on the east and west sides of each structure, but the bottom halves of the north and south sides were left open to facilitate air flow. Numerous measurements indicated that no differences existed in ambient temperature among the structures. Thus, four replications of each light intensity were arranged in a completely randomized design.

Experiment 1. Carambola seedlings growing in 2.6-liter containers were grafted with 'Arkin' budwood in May 1991 and grown in an open-sided fiberglass structure (≈50% light transmittance) until the beginning of the experiment. The container medium consisted of 2 peat : 1 perlite : 1 sand (by volume). Trees were fertilized with a nutrient solution containing 7.5 mM N, made with HydroSol (W.R. Grace & Co., Fogelsville, Pa.) and calcium nitrate. Each tree received 125 ml solution per week, and was watered to container capacity every 2 days.

Twenty-four uniform trees with a mean height of 33 cm were moved to the experimental area on 27 Sept. 1991. Two trees were placed in each structure, and irrigation and fertilization were continued as previously described.

Canopy and leaf growth characteristics were determined after

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