Characterization of an Ethylene Overproducing Mutant of Tomato (*Lycopersicon esculentum* Mill. Cultivar VFN8)

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ABSTRACT
Ethylene production rates and tissue ethylene concentrations were determined for the single-gene, Epinastic (*Epi*) tomato (*Lycopersicon esculentum* Mill.) mutant, and its parent, cv VFN8. The *Epi* phenotype was characterized by severe leaf epinasty, thickened stems and petioles, and a compact growth habit. In 4-day-old seedlings, ethylene production was significantly higher in *Epi* than in VFN8. Ethylene production rates also were higher for excised root, hypocotyl, cotyledon, and shoot tissue of 14-day-old *Epi* seedlings as compared with VFN8. The greatest difference in the ethylene production rate was observed in excised *Epi* shoot tissue, which was more than 2.5 times higher than in VFN8. Tissue ethylene concentrations of 19-, 25-, and 31-day-old *Epi* plants were 8, 172, and 307% higher than for VFN8, corresponding to increasing expression of the *Epi* phenotypic characteristics with age. The highest ethylene concentrations occurred in the shoot apex of both genotypes. Higher ethylene concentrations in *Epi* resulted from greater 1-aminocyclopropane-1-carboxylic acid content rather than increased ethylene-forming enzyme activity. The elevated ethylene levels in *Epi* did not result from increased auxin sensitivity. The sensitivity of root growth to inhibition by ethylene did not differ between VFN8 and *Epi*. Although elevated levels of ethylene in *Epi* plants apparently exacerbate its epinastic growth characteristics, other evidence indicates that this may not be the fundamental lesion. This mutant may provide a unique system for investigating the regulation of ethylene biosynthesis and the role of target cell types in plant development.

Single-gene plant mutants serve as powerful tools for investigating the biochemical, physiological, and morphological roles of hormones during plant growth and development (14, 17). Tomato mutants, in particular, are useful systems for examining the role of hormones during plant development. Over 800 monogenic mutants have been identified in tomato, and its strict diploid behavior and self-pollination ensure rapid expression of recessive mutants (18). Zobel (27) found an isogenic mutation from a normal tomato variety (*Lycopersicon esculentum* Mill. cv VFN8) having diageotropic growth characteristics. This single-gene mutant, *dgt*², exhibits a variety of pleiotropic morphological effects and is characterized by a horizontal growth habit of both roots and shoots, hypostatic, dark-green leaves and the absence of lateral roots (28). The phenotype of the *dgt* mutant can be at least partially reverted to normal by exposure to low concentrations of ethylene (28). Kelly and Bradford (12) have shown that the fundamental lesion of the *dgt* mutant may be an insensitivity to auxin.

Recently, another single-gene tomato mutant derived from the same parent line (VFN8) as *dgt* was found which is characterized by a contrasting developmental pattern, i.e. extreme leaf epinasty, thickened stems and petioles, an apparent reduction in anthocyanin production, a shortened and highly branched root system, and very erect growth. This *Epi* mutant, like *dgt*, sets fruit which ripen normally and have viable seed. Ursin (20) has presented a genetic analysis and morphological characterization of the *Epi* mutant. Treatment of normal tomato plants with exogenous ethylene induces leaf epinasty, stem thickening, and root branching, which are characteristics similar to those described for the *Epi* mutant. Thus, *Epi* might be hypothesized to be an ethylene overproducer or extremely sensitive to ethylene.

Although its phenotype suggests that ethylene may be the hormone responsible for the abnormal morphology of the *Epi* mutant, other hormones should not be overlooked. Zimmerman and Wilcoxen (26) were the first to report the stimulation of ethylene production by auxin in plant tissue, and increased ethylene production rates have been shown by the other researchers to result from elevated auxin levels (1). Burg and Burg (6) demonstrated that exogenous IAA stimulated ethylene production in excised pea tissue, resulting in tissue swelling and growth extension inhibition. Since IAA and ethylene stimulate many of the same physiological and morphological responses in plants, it seems reasonable to conclude that many of these responses might result from IAA-induced ethylene production. Auxin has been shown to regulate the rate of ethylene biosynthesis by inducing the synthesis of ACC synthase, which catalyzes the synthesis of the ethylene precursor, ACC (23–25). In contrast to the auxin-insensitive and ethylene-requiring *dgt* mutant (12, 28), the apparent ethylene overproduction by *Epi* could result from IAA overproduction or an increase in auxin sensitivity. Thus, the primary physiological lesion resulting from *Epi* gene mutation might be attributed to an alteration of the normal relationship between IAA and ethylene. This disruption in hormonal physiology could then result in the *Epi* phenotype. To test this hypothesis, we investigated the physiological roles of ethylene and IAA during the growth and development of the *Epi* mutant.

MATERIALS AND METHODS

Plant Material. Tomato (*Lycopersicon esculentum* Mill.) seeds of *Epi*, its parent, cultivar VFN8, and cultivar VF36, were surface-sterilized for 45 min in 2% NaOCl solution (40% bleach). Seeds were then rinsed with 3 L of distilled water and sown as described in the following experiments.

Ethylene Determination. Ethylene production was determined for root, hypocotyl, cotyledon, and shoot tissue from 14-d-old

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² Abbreviations: *dgt*, *diageotropic*; *Epi*, *epinastic*; SAM, S-adenosylmethionine; ACC, 1-aminocyclopropane-1-carboxylic acid; EFE, ethylene-forming enzyme.
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Seeds and for intact, 4-d-old seedlings. Seeds of VFN8 and Epi were sown in flats containing Diamonio (Eagle-Picher Industries, Inc.) and then placed on a mist bench at 25°C. Five d after sowing, seedlings were transferred to a 27/20°C (day/night) greenhouse where they were fed half-strength Hoagland solution No. 2 (11). On d 14, uniform seedlings of both genotypes were selected and the root, hypocotyl, cotyledon, and shoot tissues were excised and placed into Erlenmeyer flasks containing 2% sucrose (w/v), 50 μg mL⁻¹ chloramphenicol and 50 mM MES (pH 6.1). Flasks were then purged with ethylene-free air and sealed. Ethylene was measured after 0.5 h by sampling 1 mL of gas from the headspace and injecting into a GC equipped with a photoionization detector (5). Ethylene was identified by co-chromatography with authentic ethylene and quantified by comparison of peak heights to those of standards. Each data point represents the mean of three replications with three to six tissue segments per replication.

For ethylene production by 4-d-old seedlings, surface-sterilized seeds were placed onto filter paper slanted in 18-mL vials containing 1 mL of 2.5 mM KH₂PO₄ (pH 6.0). Vials were then placed into 40-L aquaria and purged with ethylene-free air at a flow rate of 40 L h⁻¹. Room temperature was 27°C and the light intensity was 25 μE m⁻² s⁻¹. On d 4, vials were purged with ethylene-free air, capped with a rubber septum, and placed in the dark for 6 h. A 1-mL gas sample was withdrawn from the headspace and ethylene was measured by GC. Each data point represents the mean of 10 replications with three seedlings per replication. The experiment was repeated three times. The concentrations of O₂ and CO₂ were also measured and were considered optimal for ethylene production (data not shown).

**Internal Ethylene Determination.** Seeds were sown in a flat containing University of California mix (redwood bark:peat moss:sand, 1:1:1 v/v/v). The seeds were germinated on a mist bench and, after 5 d, were placed on a 27/21°C (day/night) greenhouse. On d 19, plants were transplanted to 15-cm plastic pots and maintained with half-strength Hoagland solution No. 2. At intervals, plants were removed from the greenhouse and transferred to the laboratory for ethylene analysis. Nineteen-d-old seedlings were excised above the soil surface, dipped into 0.1% Tween-20 (v/v), and immediately submerged under a stoppered-glass funnel filled with saturated ammonium sulfate solution in a polypropylene desiccator (3). The plants were subjected to a vacuum of 0.5 atm for approximately 30 s, after which the vacuum was removed and a 0.5 mL sample was withdrawn from the headspace and ethylene content measured by GC. For 25- and 31-d-old plants, plants were excised at the third leaf above the soil surface. Each data point represents the mean of 7 to 10 plants.

For measurement of ethylene concentrations of 90-d-old plants, plants were sectioned at the apex (including four youngest leaves) and then at each subsequent internode with the attached leaf. The data represent the ethylene concentration profile of one 90-d-old plant of each genotype. The experiment was repeated three times.

**Internal Ethylene, ACC, and EFE Determination of Twenty-eight-day-old Plants.** Internal ethylene and ACC concentrations and EFE activity were measured in 28-d-old plants. Internal ethylene concentration was determined as previously described. Each data point represents the mean of four replications with one sample per replication. For ACC, the apex plus four youngest leaves was excised, weighed, and frozen in liquid nitrogen. Extraction and measurement of ACC were as described by McKeon et al. (15) and Lizada and Yang (13), respectively. Each data point represents the mean of five replications. The activity of EFE was measured in excised tissue consisting of the apex plus four youngest leaves. The tissues were incubated in flasks containing 25 mL of 0.1, 1, or 5 mM ACC solution. At the end of 1 h, the flasks were placed into 0.5-L Mason jars, purged with ethylene-free air, and sealed. EFE activity was measured by the ability to convert exogenous ACC to ethylene in a 1-h period. Saturation of EFE was achieved with 1 mM ACC (data not shown). Each data point represents the mean of three replications. The experiment was repeated twice.

**IAA-Induced Ethylene Determination.** Seedlings were employed as described under "Ethylene Determination." Uniform 14-d-old seedlings of VFN8 and Epi were selected and their hypocotyls excised, weighed, and placed into 15-mL Erlenmeyer flasks containing 2% sucrose (w/v), 50 μg mL⁻¹ chloramphenicol, and 50 mM MES (pH 6.1). Flasks were then purged with ethylene-free air and sealed. At 2-h intervals, a 1 mL gas sample was withdrawn and analyzed for ethylene content by GC. Flasks were flushed again with ethylene-free air and sealed, and at intervals ethylene content was measured. The maximum IAA-induced ethylene production was determined to be at 8 h and was plotted versus the log of IAA concentration. Each data point represents the mean of four replications. The experiment was repeated three times. In the final experiment, IAA was added 4 h after excision to flasks containing hypocotyls of the three genotypes, VFN8, VF36, and Epi, to make final concentrations of 100 μM. Flasks were purged with ethylene-free air, sealed, and ethylene content was measured at 2 h intervals. Each data point represents the mean of five replications. The experiment was repeated twice.

**Root Elongation Assay.** Pregerminal seeds (for 2 d) of VFN8 and Epi were selected for uniformity (about 1 mm radial emergence) and were sown onto blotter paper in separate 11 × 11 × 3 cm plastic boxes containing 17 mL of 2.5 mM KH₂PO₄ (pH 6.0). The plastic boxes were placed in 40-L aquaria. The aquaria were covered with a sheet of glass, sealed with tape, and then either ethylene-free air or various concentrations of ethylene were introduced into the aquaria at a flow rate of 40 L h⁻¹. After 48 h, root length was measured and recorded as a percentage of the control genotype. Each data point represents the mean of 120 to 150 seedlings per ethylene concentration.

**RESULTS**

Differences in ethylene production rates between VFN8 and Epi were detected within 4 d after sowing, with Epi having higher rates than VFN8 (2.08 ± 0.08 and 1.38 ± 0.11 NL g⁻¹ h⁻¹, respectively [means ± 95% confidence intervals]). When ethylene production rates were measured for root, hypocotyl, cotyledon, and shoot tissue for 14-d-old VFN8 and Epi seedlings, significant differences in the ethylene production rates between the two genotypes were observed in shoot and root tissues. Ethylene production by shoot and root tissues of Epi were 122 and 67% higher, respectively, than the corresponding tissues of VFN8 (Fig. 1). Ethylene production rates for Epi cotyledon and hypocotyl tissue were also higher than for VFN8 by 17 and 10%, respectively, but the differences were not significant. Total rates of ethylene production were calculated based upon total ethylene produced (NL) and total tissue weight (g) (Fig. 1). Ethylene production rate of Epi was 62% higher than that of VFN8 within the first 0.5 h after excision (Fig. 1).

The difference in seedling ethylene production between VFN8 and Epi corresponded with differences in phenotype as described by Ursin (20). While some characteristics are evident even in young seedlings, the Epi phenotype became more exaggerated during the course of growth and development. The vacuum extraction method (3) was employed to estimate ethylene concentrations in situ during development and to avoid potential problems associated with perturbation or wounding of the tissue. Harrison and Pickard (10) reported that upon horizontal place-
higher than VFN8. By d 25, the internal ethylene concentrations of VFN8 and Epi increased to 47 and 128 nL L⁻¹, respectively. During this 6-d period, the concentration of endogenous ethylene in Epi significantly increased almost fivefold, while that of VFN8 increased by less than twofold in the same time period (Fig. 2). Differences between the VFN8 and Epi phenotypes were also more evident. The Epi stem diameter increased, the petals were more reflexed, and the leaves were tightly curled. By d 31, the Epi ethylene concentration increased to 391 nL L⁻¹ compared with 96 mL L⁻¹ measured for VFN8 (Fig. 2). The ethylene concentration of Epi increased an additional threefold in the 6-d period, while in VFN8 the ethylene concentration doubled in the same time period. The marked increase in ethylene concentration of Epi corresponded to an increase in the exaggeration of the Epi phenotype. Epi had an extremely erect growth habit, thickened stems and petals, and severely curled leaves, as compared with VFN8 (Fig. 2).

In order to characterize differences in internal ethylene concentrations in various parts of 90-d-old VFN8 and Epi plants, leaves were excised and internal ethylene concentrations were measured at various positions along the stem. The highest concentrations of ethylene were measured in the leaves closest to the apex for both genotypes, and concentrations decreased basipetally (Fig. 3). Ethylene concentrations of Epi tissue were over 2- and 10-fold higher than for VFN8 in the apex and youngest expanded leaf. Ethylene concentrations were substantially higher in Epi than VFN8 at all positions except for the eighth leaf.

The higher concentrations of internal ethylene in Epi suggested that there was either a difference in the concentration of the precursor of ethylene, ACC, or a difference in EFE activity between VFN8 and Epi. The ethylene concentration of 28-d-old Epi plants was more than 5 times that of VFN8 (Table I). However, when the maximum EFE activities of both genotypes were compared by incubation in 5 mM ACC, no difference was observed. When tissues of the same age were assayed for ACC, Epi was found to have more than 6 times the ACC content of VFN8. Therefore, the high ethylene concentration in Epi tissue

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**Table I. Internal Ethylene Concentration, ACC Concentration, and EFE Activity of VFN8 and Epi**

Data are the means ± 95% confidence intervals of the means.

<table>
<thead>
<tr>
<th>Genotype</th>
<th>[C₂H₄]</th>
<th>[ACC]</th>
<th>EFE Activity</th>
</tr>
</thead>
<tbody>
<tr>
<td>VFN8</td>
<td>31 ± 5</td>
<td>0.48 ± 0.2</td>
<td>76.0 ± 10.8</td>
</tr>
<tr>
<td>Epi</td>
<td>162 ± 44</td>
<td>3.2 ± 0.7</td>
<td>77.9 ± 7.6</td>
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</tbody>
</table>

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**Fig. 1. Ethylene production rates by VFN8 and Epi root, hypocotyl, cotyledon, and shoot tissue 0.5 h after excision. Ethylene production by 14-d-old seedlings was calculated from total ethylene content (nL) and total tissue weight (g) in 0.5 h. Data are the means of three replications ± 95% confidence interval of each mean. There were three to six tissue segments per replicate.**

**Fig. 2. Phenotypic representations and internal ethylene concentrations of VFN8 and Epi plants 19, 25, and 31 d after sowing. Each data point represents the mean of 7 to 10 plants ± SE.**

**Fig. 3. Internal ethylene concentration profile of VFN8 and Epi plants 90 d after sowing. Representative profiles of one plant of VFN8 and Epi are shown.**
was a result of a high ACC content and could not be attributed to differences in EFE activity.

Rates of ethylene production induced by 100 μM IAA were measured for excised hypocotyls of VFN8, Epi, and another normal tomato genotype, cultivar VF36. Ethylene production rates by the three genotypes were maximal 8 h after excision (4 h after IAA addition; Fig. 4). VF36 had a higher maximal ethylene production rate than either VFN8 or Epi, although the ethylene production rate of Epi was significantly higher than that of VFN8. In order to determine whether Epi was more sensitive to IAA in stimulating ethylene production, excised hypocotyls from 14-d-old VFN8 and Epi seedlings were treated with various concentrations of IAA and ethylene production was measured. Ethylene production rate reached a plateau in VFN8 hypocotyls at 10 μM, whereas ethylene production in Epi hypocotyls increased linearly from 1 to 100 μM IAA (Fig. 5). These results suggest that the difference in maximal ethylene production rates between VFN8 and Epi (Fig. 4) resulted from Epi having a higher maximal response to IAA, rather than Epi being more sensitive to IAA.

Intact seedlings were exposed to ethylene to distinguish possible differences in ethylene sensitivity between VFN8 and Epi. This system avoided some of the wounding artifacts that are associated with explant preparation (2). After 2 d of exposure to ethylene, percent root length inhibition increased with increasing exogenous ethylene concentrations (Fig. 6). The ethylene concentration required to achieve a 50% reduction in root length was slightly lower for VFN8 (0.33 μL L⁻¹) than for Epi (0.45 μL L⁻¹; Fig. 6, inset). Thus, the results of this assay suggest that the Epi mutant was not more sensitive to ethylene than was VFN8. Similar results were observed for ethylene growth inhibition of dark-grown hypocotyls (8).

**DISCUSSION**

Our results show that Epi has significantly higher levels of internal ethylene than its parent, cv VFN8. Measurable differences in the ethylene production rate existed between genotypes early during seedling growth. Ethylene production rates by 4- and 14-d-old VFN8 seedlings were well within the range of production rates, 0.5 to 2 nL g⁻¹ h⁻¹, reported for vegetative tissue (4). In contrast, ethylene production rates of 4- and 14-d-old seedlings of Epi exceeded this range, perhaps accounting for the phenotypic differences found in young seedlings of the two genotypes. Ursin (20) characterized the phenotype of Epi seedlings as having reduced root and hypocotyl lengths, increased lateral root branching, reduced anthocyanin and reflexed cotyledons, as compared to VFN8. Root lengths of 4-d-old Epi seedlings employed in the ethylene sensitivity assay were always 40 to 60% less than the root lengths of VFN8 (Fig. 6).

The tissue ethylene concentrations of both genotypes increased during growth and development. The smallest difference in internal ethylene concentrations between the two genotypes was observed at 19 d after sowing. A possible reason for such a small difference might be that the ethylene concentrations were near the limits of detection. However, at 25 and 31 d, the percent increase and absolute ethylene concentrations were significantly higher in Epi and coincided with the exaggeration of the Epi phenotype (Fig. 2). The highest tissue ethylene concentrations

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**FIG. 4.** Rate of ethylene production by excised hypocotyls of VFN8, VF36, and Epi after treatment with 100 μM IAA. Arrow indicates time of IAA application. Each point represents the mean of five replications with 10 hypocotyls per replication. Bars indicate the 95% confidence interval of each mean. A representative experiment is presented.

**FIG. 5.** Rate of ethylene production by excised hypocotyls of VFN8 and Epi after treatment with the indicated IAA concentration. Values are the rates between 6 and 8 h after addition of IAA, when ethylene production was maximal. Each data point represents the mean of four replications with 10 hypocotyls per replication. Bars indicate the 95% confidence interval of each mean. A representative experiment is presented.

**FIG. 6.** Root lengths of 2-d-old seedlings of VFN8 and Epi after treatment for 2 d with the indicated concentration of ethylene. Inset, Reciprocal plot of percent root elongation inhibition and ethylene concentration. Each point represents the mean of 120 to 150 seedlings ± 95% confidence interval of the mean. Control (untreated) root lengths of a representative experiment were 30.8 ± 0.7 (se) mm for VFN8 and 20.4 ± 0.8 (se) mm for Epi.
were found near the shoot apices of mature plants and decreased basipetally. This agrees well with other reports (4) that have shown that the most prolific sites of ethylene production are in the meristematic and nodal regions of plants.

The rate-limiting step in the formation of ethylene in plant tissue is the conversion of SAM to ACC (21). This conclusion is based on evidence that the enzyme which converts ACC to ethylene is largely constitutive in most plant tissue except for preclimacteric fruit and flower tissue (22). The higher concentration of ethylene in Epi than in VF8 results from increased ACC concentration or EFE activity. When 20-d-old VF8 and Epi excised shoots were assayed for ACC content and EFE activity, the results clearly indicated that elevated ACC levels are responsible for the increase in ethylene concentration of Epi tissue rather than altered EFE activity (Table I). Therefore, we present evidence for a single-gene mutant of tomato that produces elevated levels of ethylene resulting from greater ACC content. To our knowledge, this is the first such tomato mutant to be reported.

Since endogenous IAA is thought to regulate endogenous ethylene production in vegetative plant tissue, the dose-response curve for IAA-induced ethylene was determined using excised VF8 and Epi hypocotyls. The results indicate that while Epi hypocotyls may have greater ethylene production capacity at high auxin levels, the sensitivity to lower, more physiological concentrations of IAA differs little between VF8 and Epi. In addition, the results obtained from the IAA-induced ethylene production study of VF8, VF36 and Epi indicated that VF36 had a much higher ethylene production rate than VF8 and Epi, yet its phenotype is normal. These results, along with the evidence that internal ethylene concentrations of 60-d-old Epi plants exceeded those of VF36 (data not shown), cast further doubt on the significance of IAA in inducing higher ethylene production rates by Epi compared with VF8. However, these results do not preclude the possibility of differences in endogenous IAA content between genotypes. Inasmuch as IAA-induced ethylene production has been reported to control apical dominance (7), perhaps the phenotype of Epi can be explained by a higher level of IAA in the Epi shoot apex. However, the IAA content of 7-d-old, dark-grown VF8 and Epi seedlings did not differ (9).

It is possible that the Epi phenotype results from increased sensitivity to ethylene. However, when intact seedlings were exposed to various concentrations of ethylene, root growth inhibition in Epi was not more sensitive to exogenous ethylene than in VF8, for the difference in the concentrations of ethylene resulting in half-maximal biological activity was slight (Fig. 6, inset). Ursin (20) also found no difference in ethylene sensitivity between VF8 and Epi using a petiole epinasty assay. The ethylene binding site found in vivo in tobacco leaves has a high affinity and specificity for ethylene and exhibits saturation kinetics for a biological response (19). The average ethylene concentration for both genotypes that would be required to occupy one-half of the binding sites would be 0.39 μL L⁻¹. The highest ethylene concentration measured in VF8 tissue was 0.096 μL L⁻¹, considerably below the value of 0.39 μL L⁻¹ required for half-maximal binding. In comparison, the highest ethylene concentration measured in Epi tissue was 0.39 μL L⁻¹, a concentration that would result in half-maximal binding. Therefore, it is not surprising that the Epi phenotype displays a variety of characteristics which can be induced in normal plants by elevated ethylene levels.

If elevated ethylene concentrations were the sole cause of the Epi phenotype, then blocking ethylene synthesis action should restore the normal growth pattern. However, treatment of dark-grown Epi seedlings with ethylene biosynthetic and action inhibitors failed to normalize the Epi phenotype, even though application of ethylene to VF8 seedlings resulted in a phenocopy of the Epi morphology (8). Growing Epi plants in nutrient solution supplemented with silver thiosulfate, a translocatable ethylene action inhibitor, only reduced the severity of the Epi characteristics without fundamentally altering them (8). Thus, while the elevated tissue ethylene concentrations reported here undoubtedly exacerbate the epinastic and other growth characteristics of the Epi mutant, particularly in older plants, they may not represent the fundamental lesion. Ursin (20) found that IAA-induced petiole epinasty in VF8 is strictly dependent upon stimulation of ethylene production, while in Epi, IAA will still induce partial epinasty even when ethylene production is completely blocked. This author suggested that the Epi mutation may have altered the mechanism by which target cells (16) discriminate between auxin and ethylene in the regulation of cell expansion. As a result, Epi cells respond to auxin alone as if both auxin and ethylene were present, leading to the abnormal phenotypic characteristics. The reason for the elevated ethylene synthesis rates in Epi plants remains unknown, but they would tend to reinforce this "constitutive" ethylene response (Fig. 2). Hence, this mutant provides a unique system for investigating the regulation of ethylene biosynthesis and the role of target cell types in plant growth and development.

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