Evaluating Ethylene Sensitivity and Exogenous Ethylene Impact on Early Growth of Grafted and Nongrafted Tomato Seedlings

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SUMMARY. Ethylene sensitivity of grafted and nongrafted tomato (*Solanum lycopersicum*) seedlings with three to four true leaves was examined. The concentration of exogenous ethylene that produced symptoms was between 1 and 10 $\mu\text{L}\cdot\text{L}^{-1}$ regardless of grafting. Symptoms of ethylene exposure included leaf epinasty, decreased maximal photochemical quantum yield of photosystem II (F_v/F_m), and increased plant height (nongrafted only). Grafted plants maintained higher F_v/F_m than nongrafted plants in response to higher ethylene concentrations. Ethylene-damaged plants showed comparable growth to the control plants 3 weeks after transplanting, but transplant quality was diminished as a result of ethylene exposure at high concentrations.

Grafted plants can provide resistance to soilborne diseases and abiotic stress, enhance plant vigor, and increase yields (Louws et al., 2010; Schwarz et al., 2010). The production of grafted tomato (*Solanum lycopersicum*) plants has increased in North America (Ertle, 2020). Grafted plants have greater value than nongrafted vegetable transplants; therefore, transplant quality needs to be maintained during the supply chain. One potential source of quality deterioration in commercial greenhouses, in storage facilities, and during shipping is exogenous and endogenous ethylene accumulation. Tomato is classified as highly sensitive to ethylene, but sensitivity can differ between cultivars and physiological stages (Edelman and

Jones, 2014). Dark-grown tomato seedlings exhibit the classic “triple response” when exposed to ethylene—including hypocotyl thickening, an exaggerated apical hook, and reduced hypocotyl elongation (Barry et al., 2001). The symptoms of ethylene damage on mature tomato plants can include flower senescence, bud and flower abscission, leaf chlorosis, and leaf epinasty (Edelman and Jones, 2014). Floral tissues are typically more sensitive to ethylene than vegetative tissue (Woltering, 1987). Leaf epinasty is the main symptom of ethylene exposure in vegetative tomato seedlings (4–5 weeks old) and is typically reversible after the plants are removed from the ethylene environment (Edelman and Jones, 2014). However, high concentrations of ethylene (10 $\mu\text{L}\cdot\text{L}^{-1}$) or long durations of ethylene exposure may also result in leaf abscission (Edelman and Jones, 2014; Woltering, 1987). In tomato transplants with visible first flowers, ethylene accumulation during

a simulated long-distance transportation reached $118 \pm 10 \text{ nmol}\cdot\text{mol}^{-1}$ ($0.118 \pm 0.01 \mu\text{L}\cdot\text{L}^{-1}$) when shipped at 19 °C. The ethylene accumulation resulted in flower abortion and abnormal first truss developments (Kubota and Kroggel, 2011). It is less clear how younger grafted tomato transplants without visible flowers will perform after extended exposure to ethylene, or whether there is any difference in ethylene sensitivity between grafted and nongrafted tomato seedlings. The objectives of this study were 1) to determine the ethylene sensitivity of grafted and nongrafted tomato seedlings, and 2) to determine whether a prolonged (4-d) ethylene exposure affects transplant quality and early growth after transplanting.

Materials and methods

Plant materials

Grafted and nongrafted tomato seedlings were grown in a greenhouse at the Kansas State University Olathe Horticulture Center (lat. 38.884347°N, long. 94.993426°W). ‘Cherokee Purple’ (Johnny’s Selected Seeds, Winslow, ME) was selected for the scion and ‘Maxifort’ was selected for the rootstock (DeRuijter Seeds, St. Louis, MO). During seedling growth, the greenhouse temperatures were maintained at $27 \pm 5^\circ\text{C}$ (day) and $17 \pm 2^\circ\text{C}$ (night). The seeds were sown in a germinating potting mix (Fafard Germinating Mix; Sun Gro Horticulture, Agawam, MA) in 12- × 12-inch trays. About 10 d later, the seedlings were transplanted into 50-cell propagation trays filled with potting mix (Professional Growing Mix, Sun Gro Horticulture). When both the rootstock and scion seedlings had similar stem widths (≈ 17 d later), the seedlings were splice/tube-grafted and healed according to Rivard and Louws (2011). The healing chambers were located in the greenhouse and were covered with polyethylene film and 55% shade cloth. The plants remained in the healing chambers for 10 d. After

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Units

To convert U.S. to SI, multiply by	U.S. unit	SI unit	To convert SI to U.S., multiply by
0.3048	ft	m	3.2808
2.54	inch(es)	cm	0.3937
25.4	inch(es)	mm	0.0394
6.4516	inch ²	cm ²	0.1550
28.3495	oz	g	0.0353
1	ppm	$\mu\text{L}\cdot\text{L}^{-1}$	1
$(^\circ\text{F} - 32) \div 1.8$	$^\circ\text{F}$	$^\circ\text{C}$	$(^\circ\text{C} \times 1.8) + 32$

healing, the plants were returned to the greenhouse and grown for 1 week before beginning the experiment. Non-grafted 'Cherokee Purple' seeds were sown 2 weeks after the grafted plants. Both grafted and nongrafted plants had three to four true leaves at the start of the experiment. The plants were transferred to the Postharvest Physiology Laboratory at Kansas State University Olathe for the ethylene exposure treatments.

Expt. 1

EXOGENOUS ETHYLENE TREATMENT. The grafted and nongrafted plants were placed randomly in four separate Plexiglas chambers, with 25 grafted and 25 nongrafted plants in each chamber. The chambers were subjected to one of the following exogenous ethylene treatment concentrations: 0 (control), 0.1, 1, and 10 $\mu\text{L}\cdot\text{L}^{-1}$. The experimental design was most similar to a split-plot design, with ethylene treatment as the main effect and graft status of the plants as a subplot. The internal temperature in the chambers was $18.7 \pm 0.3^\circ\text{C}$ and the relative humidity ranged from 96% to 99%. The chambers remained on the laboratory bench and were exposed to a natural photoperiod near a window. The ethylene concentrations were confirmed two times each day with a gas chromatograph (8610C; SRI Instruments, Torrance, CA) equipped with a flame ionization detector and a 6-ft $\times$ 1/8-inch stainless steel packed column (HayeSep D column, SRI Instruments).

SYMPTOM EVALUATION. All measurements were made at day 0 immediately before the start of the experiment and once every 24 h during the 4-d treatment period (days 1–4). After the measurements were made, the plants were returned to the treatment chambers and re-injected with ethylene to satisfy the treatment concentrations. Plant height was recorded on 15 nongrafted and 15 grafted plants from each treatment group. The remaining 10 grafted and 10 nongrafted plants from each treatment chamber were used to monitor maximum quantum efficiency of photosystem II (F_v/F_m) and leaf epinasty. A handheld chlorophyll fluorometer equipped with leaf clips was used to measure F_v/F_m on a single leaf from each replicate plant (OS30p+; Opti-

Sciences, Hudson, NH). The leaves were dark-adapted for 30 min before measurement. Symptoms of leaf epinasty were quantified with a protractor by measuring the leaf angle where the adaxial side of the third true leaf met the main stem during the 4-d treatment period.

Expt. 2

SEEDLING GROWTH. The greenhouse experiment took place from 15 Apr. to 6 May. After the 4-d ethylene treatment, the plants were transported to the original greenhouse environment. Five days later, all plants were transplanted into nursery pots (6 inches in diameter $\times$ 5.6 inches in height) with potting mix (Professional Growing Mix). The plants were arranged in a completely randomized design on the greenhouse bench and were fertilized weekly with an application of water-soluble fertilizer using 15N–2.2P–12.5K (Jack's Professional LX; JR Peters, Allentown, PA). The greenhouse was maintained at $27 \pm 5^\circ\text{C}$ (day) and $17 \pm 2^\circ\text{C}$ (night). Six grafted and six nongrafted plants from each of the ethylene treatment groups were sampled destructively on the day of transplanting (day 0) and on days 7, 14, and 21. On each sampling day, stem length, total leaf area, and stem width were recorded. Stem length was measured from the soil surface to the apical meristem. The leaf area was measured with an area meter (LI-3100C; LI-COR, Lincoln, NE). The stem diameter measurements were taken 1 cm above the cotyledons using a digital caliper (Digital Fractional Caliper; Husky Tools, Atlanta, GA). The shoot and root tissue of each sampled plant was dried at 60°C in a laboratory oven for 48 h to evaluate dry biomass. Day 0 measurements were considered an evaluation of transplant quality and the subsequent sampling days (days 7, 14, and 21) were collected to monitor early growth.

Statistical analysis

All data were analyzed using statistical software (SAS Studio 3.8; SAS Institute, Cary, NC). For the ethylene treatment experiment, F_v/F_m and leaf epinasty (leaf angle) were analyzed using the MIXED procedure with DDFM=KR in the MODEL statement and a repeated statement to account for repeated measures on the same plants. The fixed effects include

ethylene treatments, graft status, and an ethylene treatment $\times$ graft status interaction term. For plant height, grafted and nongrafted plants were analyzed separately for the fixed effect of ethylene treatment with repeated measures because the plants had significantly different heights at the start of the experiment. Mean separation was carried out using Bonferroni's test at $P \leq 0.05$.

For the greenhouse experiment, growth measurements were analyzed separately for each sampling day. Grafted and nongrafted plants were also analyzed separately because of significant differences in the plant morphology measurements at the start of the experiment. The data were submitted to the GLIMMIX procedure. The mean separation was carried out with Bonferroni's test at $P \leq 0.05$.

Results and discussion

Symptoms of epinasty occurred in grafted and nongrafted plants within 24 h (day 1) when treated with 1 and 10 $\mu\text{L}\cdot\text{L}^{-1}$ ethylene [$P \leq 0.0001$ (Fig. 1A)]. The degree of epinasty characterized the plants as being highly sensitive to ethylene (Edelman and Jones, 2014). The leaf angle after the first day of treatment was statistically similar between grafted and nongrafted plants and between the two ethylene concentrations levels (1 and 10 $\mu\text{L}\cdot\text{L}^{-1}$), with an average angle increase of 57% from the initial day 0 conditions. This indicates that the point of ethylene saturation likely occurs around 1 $\mu\text{L}\cdot\text{L}^{-1}$, because leaf epinasty was not significantly different at the higher concentration. The leaf angles were also similar between grafted and nongrafted plants on days 2 through 4 when treated at the two highest ethylene concentrations (Fig. 1A). Therefore, the graft status did not have a significant impact on this ethylene symptom. The plants treated with 0.1 $\mu\text{L}\cdot\text{L}^{-1}$ were not statistically different from the control treatment, indicating that the concentration required to produce symptoms is between 0.1 and 1 $\mu\text{L}\cdot\text{L}^{-1}$ (Fig. 1A).

A decrease in F_v/F_m can provide an early indication of plant stress from multiple abiotic stressors (Baker and Rosenqvist, 2004). Grafted and nongrafted plants treated with 1 and 10 $\mu\text{L}\cdot\text{L}^{-1}$ ethylene declined in F_v/F_m during the 4-d treatment, whereas those treated with 0.1 $\mu\text{L}\cdot\text{L}^{-1}$ ethylene

Fig. 1. (A) Leaf epinasty, (B) chlorophyll fluorescence [F_v/F_m], and (C) plant height of grafted and nongrafted tomato seedlings treated with 0 (control), 0.1, 1, and 10 $\mu\text{L}\cdot\text{L}^{-1}$ ethylene over a 4-d treatment period. For leaf epinasty, the leaf angle was the angle where the adaxial side of the third true leaf met the main stem. All points represent means of plant replicates for each parameter ($n = 10$ for leaf epinasty and chlorophyll fluorescence, $n = 15$ for plant height). Error bars represent the 95% confidence interval of the means at the $\alpha = 0.05$ significance level. For F_v/F_m , * = $P \leq 0.001$ of pairwise comparison between graft and nongrafted data points on a given day; 1 $\mu\text{L}\cdot\text{L}^{-1} = 1$ ppm, 1 cm = 0.3937 inch.

and the control remained constant (Fig. 1B). In nongrafted plants, F_v/F_m declined significantly ($P \leq 0.0001$) by day 2 of the ethylene treatment at the two highest concentrations. However, the grafted plants did not have significant reductions in leaf F_v/F_m values until day 4 of the ethylene treatment [$P \leq 0.0001$ (Fig. 1B)]. The total decline in F_v/F_m in nongrafted plants treated with 1 and 10 $\mu\text{L}\cdot\text{L}^{-1}$ at the end of the treatment period was 0.35,

whereas the decline in grafted plants was 0.14. This indicates the grafted plants may have improved tolerance to the exogenous ethylene treatments compared with the nongrafted plants. Tomato rootstocks could provide improved stress tolerance, which has been demonstrated in grafted plants subjected to heat stress (Rivero et al., 2003) and water stress (Suchoff et al., 2018). Also, it is well documented that plants preconditioned to stress can

have improved stress tolerance to secondary stress (Dong et al., 2013; Ghanbari and Sayyari, 2018; Zhang et al., 2018). For instance, tomato seedlings subjected to controlled drought stress had improved chilling tolerance, which was mediated by increased antioxidant enzyme activity, abscisic acid content, anthocyanin accumulation, potassium content, and proline content (Zhang et al., 2018). The grafted tomatoes in our experiment may have had better maintenance of photochemical efficiency during ethylene exposure as a result of the previous abiotic stress associated with grafting and wound healing.

Grafted plants did not change significantly in plant height across the 4-d treatment (Fig. 1C). All nongrafted plants increased significantly in plant height from day 0 to day 4 [$P \leq 0.0001$ (Fig. 1C)]. The increase in plant height was 8.2%, 10.9%, 22.1%, and 24.6% for treatments of 0, 0.1, 1, and 10 $\mu\text{L}\cdot\text{L}^{-1}$ ethylene. Stem elongation is a common plant response to low irradiance, and this is likely the reason for stem elongation in the nongrafted plants (Kurepin and Pharis, 2014). However, the nongrafted plants treated with 1 and 10 $\mu\text{L}\cdot\text{L}^{-1}$ exogenous ethylene had significantly greater plant heights by day 4 compared with the control ($P \leq 0.05$ and $P \leq 0.0001$, respectively). Exogenous ethylene typically results in the cessation of stem elongation (Abeles et al., 1992), but in our study we saw contrary results among the nongrafted tomatoes. Plants in flooded conditions exhibit ethylene-mediated shoot elongation as an adaption response, and treatment of plants at saturating ethylene concentrations can mimic this response (Jackson, 2008). Stem elongation of tomato seedlings is a negative quality trait because growers prefer compact transplants with thick stems (Lee et al., 2010).

Within 24 h of being removed from the ethylene treatment, leaf necrosis of the two oldest leaves and abscission of cotyledons occurred in both grafted and nongrafted plants treated with 1 and 10 $\mu\text{L}\cdot\text{L}^{-1}$ ethylene. All symptoms of leaf epinasty improved in the upper canopy within 24 h. The plants with ethylene damage were of poorer quality at the time of transplanting, as observed by significantly lower leaf area, greater plant height, and

Table 1. Plant growth measurements of grafted and nongrafted tomato seedlings after 4 d of exogenously applied ethylene at the concentrations of 0 (control), 0.1, 1, and 10 $\mu\text{L}\cdot\text{L}^{-1}$. Each value represents the mean of measurements obtained from six grafted and six nongrafted plants at the time of transplanting in a greenhouse (day 0) and after 7, 14, and 21 d of growth.

Plant measurements ^z	Grafted					Nongrafted				
	Ethylene (μL·L ⁻¹) ^z				P value ^y	Ethylene (μL·L ⁻¹)				P value
	0	0.1	1	10		0	0.1	1	10	
Day 0 ^x										
Leaf area (cm ²)	42.53 a ^w	46.84 a	21.62 b	21.05 b	<0.0001	50.82 a	59.11 b	16.50 c	17.50 c	<0.0001
Stem (mm)	2.90	2.97	3.00	3.09	NS	3.21	3.27	3.28	3.45	NS
Plant height (cm)	9.70 b	9.32 b	10.12 b	11.13 a	<0.0001	7.87 ab	7.70 b	8.35 ab	8.83 a	0.0273
Shoot biomass (g)	0.18	0.17	0.15	0.13	NS	0.23 ab	0.29 a	0.20 b	0.19 b	0.0002
Root biomass (g)	0.06	0.06	0.06	0.06	NS	0.09	0.11	0.09	0.08	NS
Day 7										
Leaf area (cm ²)	114.01	102.10	103.57	90.31	NS	133.62	151.48	116.67	107.08	NS
Stem (mm)	4.36	4.11	4.18	4.16	NS	4.92 a	4.82 a	4.61 ab	4.28 b	0.001
Plant height (cm)	11.17	11.25	11.28	11.45	NS	9.70	9.98	10.67	10.52	NS
Shoot biomass (g)	0.43 a	0.42 ab	0.37 ab	0.33 b	0.0143	0.55 b	0.63 a	0.46 c	0.43 c	<0.0001
Root biomass (g)	0.10	0.08	0.07	0.11	NS	0.17 ab	0.19 a	0.13 bc	0.11 c	0.0007
Day 14										
Leaf area (cm ²)	319.91 b	463.94 a	312.55 b	423.69 a	<0.0001	377.66 ab	454.59 a	336.21 b	461.95 a	0.0010
Stem (mm)	6.35	6.47	6.58	6.61	NS	6.85 a	6.52 a	5.16 b	6.03 a	<0.0001
Plant height (cm)	15.67	16.77	16.40	16.84	NS	16.53	16.25	16.53	16.35	NS
Shoot biomass (g)	1.97 a	1.92 a	1.62 b	1.55 b	0.0003	2.09 a	2.13 a	1.67 b	1.84 b	<0.0001
Root biomass (g)	0.33 b	0.44 a	0.27 b	0.33 b	0.0005	0.53 b	0.69 a	0.45 b	0.50 b	<0.0001
Day 21										
Leaf area (cm ²)	667.73 b	792.25 ab	681.48 b	887.15 a	0.0054	771.25	877.97	839.99	859.65	NS
Stem (mm)	6.51 bc	7.6 ab	6.0 c	7.71 a	0.0003	7.66 a	7.17 ab	6.52 b	6.84 ab	0.0427
Plant height (cm)	25.78 ab	23.18 b	28.6 a	23.32 b	0.0001	26.93	24.75	26.3	25.85	NS
Shoot biomass (g)	5.08	5.75	4.84	5.73	NS	5.21	5.9	5.17	5.47	NS
Root biomass (g)	0.62	0.59	0.52	0.59	NS	0.77	0.81	0.71	0.69	NS

^z1 $\mu\text{L}\cdot\text{L}^{-1}$ = 1 ppm, 1 cm^2 = 0.1550 inch^2 , 1 mm = 0.0394 inch, 1 cm = 0.3937 inch, 1 g = 0.0353 oz.

^yP value of the analysis of variance F test.

^xDay 0 is the day of transplanting and represents the quality of seedlings at the time of transplanting.

^wWithin a row, values followed by the same letter are not significantly different according to a Bonferroni adjustment at the $\alpha = 0.05$ significance level.

^{NS}Not significant at an $\alpha = 0.05$ significance level.

lower shoot biomass (nongrafted only) compared with the control plants (Table 1). Stem diameter and root biomass were not affected by ethylene treatment on day 0, but the stem diameter of nongrafted plants treated with 1 and 10 $\mu\text{L}\cdot\text{L}^{-1}$ remained lower than control plants for the subsequent three sampling periods (Table 1). Shoot biomass also remained lower than the control for grafted and nongrafted plants that experienced ethylene damage for the first 2 weeks of growth, which was likely a result of lower leaf necrosis in the ethylene-damaged plants. By day 21, shoot biomass for grafted and nongrafted plants was comparable across all treatments. Interestingly, the leaf area of grafted and nongrafted plants treated with 0.1 and 10 $\mu\text{L}\cdot\text{L}^{-1}$ ethylene exceeded the control plants and those treated with 1 $\mu\text{L}\cdot\text{L}^{-1}$ on day 14 (Table 1). This trend continued for grafted plants only on day 21. It is

unclear why the ethylene concentrations of 0.1 and 10 $\mu\text{L}\cdot\text{L}^{-1}$ increased the leaf area 2 weeks after the exposure period, because ethylene typically inhibits leaf expansion (Abeles et al., 1992).

On day 7, the root biomass of the nongrafted plants treated with 10 $\mu\text{L}\cdot\text{L}^{-1}$ ethylene was 35% lower than the control plants ($P \leq 0.001$), indicating that the highest concentration of ethylene may have inhibited early root growth (Table 1). Inhibition in root growth is a common symptom of ethylene in dark-grown arabidopsis (*Arabidopsis thaliana*) seedlings (Stepanova et al., 2007), which has also been demonstrated in tomato (Negi et al., 2010). By day 14, there was no suppression in root biomass of the nongrafted plants treated with 10 $\mu\text{L}\cdot\text{L}^{-1}$ ethylene. The plants grafted to the interspecific rootstock did not have any significant

reductions in root biomass as a result of the high-concentration ethylene treatments, which could suggest the root system was less sensitive to this ethylene response.

Although all ethylene-treated plants survived and early growth was not affected severely, plants treated with 1 and 10 $\mu\text{L}\cdot\text{L}^{-1}$ ethylene had poorer overall visual quality because of lower leaf necrosis. Propagators of high-quality grafted tomato seedlings should take precautions to prevent extended ethylene exposure or the promotion of endogenous ethylene in greenhouse operations and in the postproduction supply chain. To our knowledge, this is the first experiment to examine the difference in ethylene sensitivity between grafted and nongrafted plants. These preliminary results suggest that grafted seedlings differ in response to exogenous ethylene compared with nongrafted plants, as indicated by better

maintenance of F_v/F_m , and unaltered plant height. Further research needs to be conducted to confirm these results and understand the mechanisms of altered ethylene responses.

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