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Elevated Atmospheric Ethylene and High Temperature Independently Inhibit Fruit Set But Not Vegetative Growth in Tomato

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Abstract. **Ethylene is an essential plant hormone at low concentrations. Concentrations in the field rarely exceed 5 nmol·mol^{-1} (0.005 ppm), but it can accumulate as a gas in closed, indoor environments. These elevated levels can reduce growth and yield. Temperature alters ethylene synthesis and has the potential to influence ethylene sensitivity of crop plants in sealed greenhouses and indoor environments. We studied ethylene sensitivity of tomatoes (*Solanum lycopersicum* L. cv. MicroTina) using a unique, 12-chamber system. Ethylene levels of 0, 20, and 40 nmol·mol^{-1} (parts per billion) were maintained throughout the life cycle, at an air temperature of 22 or 28 °C. Yield of red fruit was three times higher at 22 than at 28 °C. There was a steady decrease in yield with increasing ethylene concentration, but vegetative growth was reduced less than 10% in any treatment. The highest ethylene concentration reduced yield to 11% of the control at 22 °C and to 4% of the control at 28 °C; the intermediate ethylene level reduced yield to 51% of the control at 22 °C and 37% at 28 °C. Regardless of temperature, filtering of ethylene in indoor environments to below 20 nmol·mol^{-1} is necessary to achieve normal fruit set and yield in tomato.**

Ethylene is an endogenously synthesized plant hormone that influences growth and development at nanomolar (nmol·mol^{-1}; ppb) concentrations (Abeles et al. 1992). Atmospheric ethylene concentrations in field conditions seldom exceed 5 nmol·mol^{-1}. However, ethylene in closed environments can accumulate to more than 200 times ambient levels (Campbell et al. 2001). These elevated levels do not affect humans (Morgott 2015) but they can significantly alter plant growth and development.

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Ethylene regulates a wide range of developmental processes and serves an important role in abiotic and biotic stress responses (Dubois et al. 2018). Low levels of ethylene increase leaf area in some species (Fiorani et al. 2002; Lee and Reid 1997) and interact with other plant hormones to regulate seed dormancy and germination (Matilla 2000). The most well-known effect of ethylene is on leaf and flower and senescence (Abeles et al. 1992; Dubois et al. 2018; Iqbal et al. 2017). Ethylene-induced leaf senescence is an essential part of resource recycling in aged and stressed leaves (Iqbal et al. 2017).

Flower and fruit development is particularly sensitive to ethylene (An et al. 2020; Dar et al. 2021). In most plants, there is a transient increase in ethylene production (O'Neill 1997) and an upregulation of genes encoding ethylene-binding proteins following anthesis (Lashbrook et al. 1998; Porat et al. 1995). In tobacco (*Nicotiana tabacum* L.), ethylene signals anther dehiscence (Rieu et al. 2003) and microspore division in durum wheat (*Triticum durum* L.) (Sévenier and Coumans 1996). Pollination is signaled through an interorgan system involving transport of the ethylene-precursor 1-aminocyclopropane-1-carboxylic acid (ACC) to the flower corolla (O'Neill 1997; Porat et al. 1995; Woltering et al. 1995). ACC-oxidase (ACO) enzymatically converts ACC to ethylene, which causes the flower corolla to senesce and allows the fruit to develop (Stead 1992).

Elevated atmospheric ethylene can cause abnormal growth and reduce yield if it accumulates above threshold levels. Sensitivity to ethylene varies among and within species (Archambault et al. 2006; Klassen and Bugbee 2004; Onozaki et al. 2009). Most species begin to suffer yield reductions at 20 nmol·mol^{-1}, but sensitive species can be affected as low as 10 nmol·mol^{-1} (Klassen and Bugbee 2004). Ethylene-insensitive mutants have facilitated the identification of the genes that regulate ethylene synthesis and perception by plants (Gubrium et al. 2000; Stepanova and Ecker 2000). Such advances have the potential to reduce ethylene sensitivity in crop plants through classical breeding (Onozaki 2018) and genetic engineering (Czarny et al. 2006).

In closed environments, ethylene can quickly accumulate to more than 1000 nmol·mol^{-1} because of continuous production from healthy plants (Bingham et al. 2000; Campbell et al. 2001; Salisbury 1997; Wheeler et al. 1996). Closed greenhouses can reach ethylene concentrations of 100 nmol·mol^{-1} during periods of low ventilation (Blankenship and Kemble 1996; Gibson et al. 2000; Mortensen 1987). Ethylene on space shuttle flight STS-111 reached 130 nmol·mol^{-1} in transit from the International Space Station (ISS), attributable primarily to wet trash and off-gassing of materials (Perry and Peterson 2003). The air on the Mir Space Station has reached 1700 nmol·mol^{-1} ethylene (Campbell et al. 2001). Metropolitan areas have reported air with 700 nmol·mol^{-1} ethylene, primarily from automobile exhaust (Abeles et al. 1992).

Turbulent mixing with fresh air dilutes ethylene, and solar ultraviolet generates ozone, which oxidizes ethylene (Abeles et al. 1992). In controlled environment agriculture, air exchange with outside air and ultraviolet radiation can be low. For this reason, engineering solutions to scrub ethylene have been developed (Martínez-Romero et al. 2007). On the ISS, air-scrubbing technologies are designed to keep ethylene concentration below 50 nmol·mol^{-1} (Perry and Peterson 2003), but inhibition of pollination and seed set in sensitive species can occur as low as 10 nmol·mol^{-1} (Klassen and Bugbee 2002). Air purification equipment is expensive and requires significant energy, so environmental alternatives to reduce ethylene synthesis and sensitivity of plants warrants exploration.

Temperature significantly influences ethylene synthesis (Bours et al. 2013; Ciardi et al. 1997; Field 1981; Kazan 2015; Müller and Munné-Bosch 2015; Poór et al. 2022). Burg and Thimann (1959) reported that the rate of ethylene synthesis increased up to 30 °C in McIntosh apples and declined to near zero above 40 °C. ACO activity declined below 11 °C and above 37 °C due to perturbation of the membrane structure (Field 1985). Low temperature stress increases ethylene synthesis in chilling-sensitive plants (Wang 1989), and high temperature stress

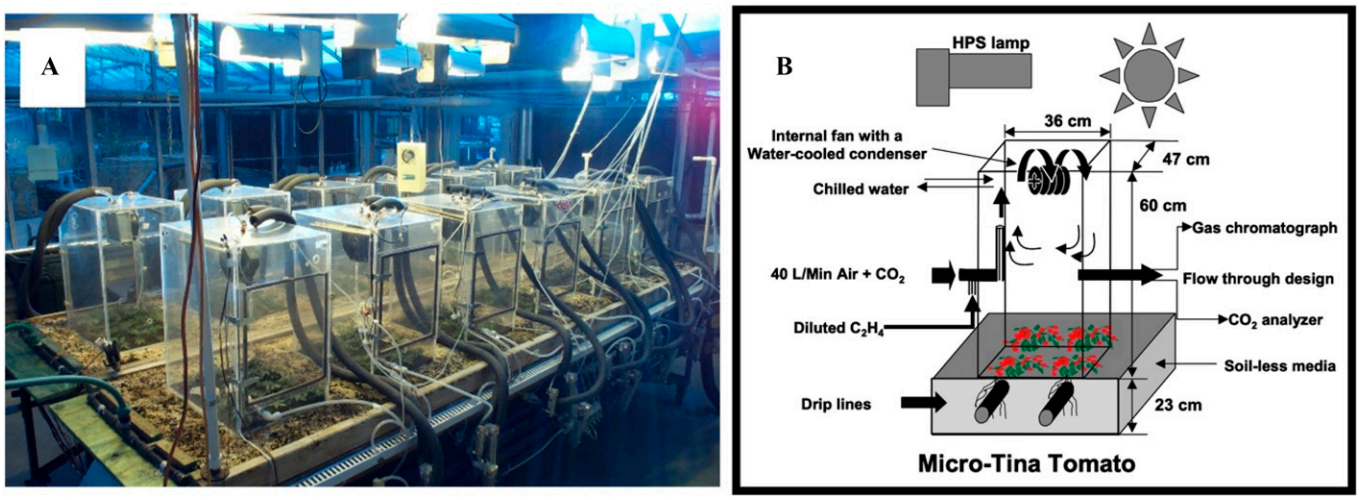

Fig. 1. (**A**) Twelve-chamber flow-through system. Temperature per chamber was regulated with heat elements and water-cooled heat exchangers supplied with water through insulated tubing. Air, ethylene, and CO_2 were supplied independently to each chamber. (**B**) Schematic diagram showing the air flow, temperature control, and root zone of one of 12 chambers in the greenhouse system.

caused kernel abortion in winter wheat (*Triticum aestivum* L.) (Hays et al. 2007). Kernel abortion did not occur in plants that were treated with the ethylene receptor inhibitor 1-methylcyclopropane (1-MCP) (Hays et al. 2007).

Although the effect of temperature on ethylene synthesis is well studied, few studies have evaluated how temperature affects ethylene sensitivity. Gubrium et al. (2000) observed a difference between the temperature responses of a transgenic ethylene-insensitive petunia (*Petunia ×hybrida* Vilm.) and wild-type petunia. Jones and Koen (1985) found that elevated temperatures increased mortality in apple flowers at petal-fall during Ethephon® thinning. In lettuce (*Lactuca sativa* L.), temperature had little influence on ethylene sensitivity (Mortensen 1989). Zimmerman et al. (1931) suggested that ethylene-induced leaf abscission in rose is minimized at low temperature.

We sought to determine the effect of ethylene on vegetative and reproductive growth of tomato (*Solanum lycopersicum* L.), and if sensitivity is altered by temperature. We hypothesized that ethylene sensitivity would be reduced at low temperature. Tomatoes were used in this research because their response to ethylene is well studied (Klee and Tieman 2002), ethylene-insensitive mutants have been developed (Wilkinson et al. 1997), and they are sensitive to low levels of ethylene commonly found on the ISS (Blankenship and Kemble 1996).

Materials and Methods

Plant material. Tomato plants (*Solanum lycopersicum* L. cv. MicroTina) were germinated in a peat:perlite (1:1) soilless media mixture supplemented with 2.4 $g \cdot L^{-1}$ dolomite 65 AG limestone to maintain pH at 5.5 to 6.5 throughout the trial. Seedlings emerged 3 d after planting (emergence = day 0). After emergence, the plants were watered to excess twice daily with a complete nutrient solution (Bugbee 2004; Langenfeld et al. 2022). The nutrient solution contained 7.0 mM N, 0.7 mM P, and 2.1 mM K supplied by Peters Professional® 20–10–20 (20N–4.4P–16.6K) powdered fertilizer (Scott-Sierra Horticultural Products Company, Marysville, OH, USA), 20 μM iron supplied by Nortrace® Ferión 138™ Fe-EDDHA (Nortrace, Ltd., Greeley, CO, USA), and 10 μM silica (Sodium-meta-Silicate 9-hydrate, crystal; Mallinkrodt Baker, Inc., Phillipsburg, NJ, USA).

Environmental conditions. The trial was conducted in a greenhouse using a unique, 12-chamber flow-through system (Fig. 1A and B), which has been described previously (Klassen and Bugbee 2002). Natural sunlight and supplemental high-pressure sodium (HPS) lighting provided a daily light integral (DLI) of 34 to 41 $mol \cdot m^{-2} \cdot d^{-1}$ in a 16-hour photoperiod measured above the chambers (model 190; LI-COR Inc., Lincoln, NE, USA). In addition, the transmission of photosynthetic photon flux density (PPFD) was monitored weekly with an Apogee Instruments, six-sensor light bar inside the chambers at canopy height (model SQ-306; Apogee Instruments Inc., Logan, UT, USA). Eight HPS lamps provided supplemental lighting of 20 $mol \cdot m^{-2} \cdot d^{-1}$, approximately half of the DLI. CO_2 was enriched to 1100 $\mu mol \cdot mol^{-1}$ (ppm) in all chambers and monitored continuously using an infrared gas analyzer (model 6251; LI-COR Inc.); sample tubes were inserted into the chambers near the intakes of the mixing fans.

Ten days after emergence, uniform plants were transplanted to acrylic Lucite™ chambers (36 × 47 × 60 cm; 0.17 m^2) at eight plants per chamber (47 plants/m^2). To minimize edge effects and side lighting, guard rows were planted between the chambers, and reflective Mylar® skirts were wrapped around the chambers. The temperature in all chambers was 28 °C until the appearance of the first floral buds on day 12. Temperature and ethylene treatments began on day 12 and were maintained through harvest on day 106.

Temperature monitoring and control. The day/night temperature was constant throughout the trial at either 22 or 28 °C. Chamber air temperatures were monitored using aspirated, type-E thermocouples. The temperature was within ± 0.2 °C among replicate chambers. Temperature control inside the chambers was facilitated by water-cooled heat exchangers and two, 50-W heating elements (Fig. 1A and B). Water at 4 °C, and air at 0.28 $m^3 \cdot min^{-1}$ (10 CFM) were supplied continuously through the heat-exchanger system to cool, homogenize, and dehumidify the air. Monitoring and control of temperature was facilitated using a CR10T datalogger, an AM416 relay multiplexer, and an SDM-CD16AC 16-channel AC/DC controller (Campbell Scientific, Inc., Logan, UT, USA).

Ethylene monitoring and control. Ethylene was measured once per hour in each chamber using a Shimadzu GC-17A (Shimadzu, Kyoto, Japan) gas chromatograph (GC) equipped with an 80/100 Porapak-Q column (Restek Corporation, Bellefonte, PA, USA).

Clean air (less than 1 $nmol \cdot mol^{-1}$ ethylene) was supplied to each chamber at 40 $L \cdot min^{-1}$. Ethylene was rigorously maintained at 0, 20, or 40 $nmol \cdot mol^{-1}$ in individual chambers. To generate the low ethylene concentrations, pure ethylene was supplied at 45 kPa to a 15-cm-long section of 2-mm-thick silicone tubing enclosed in a PVC diluter capsule. The ethylene slowly diffused through the tubing wall and mixed with clean air that was independently supplied to the diluter. The diluted ethylene flowed from the diluter into a manifold where it was partitioned to the elevated ethylene chambers at the appropriate concentration through independent rotameters (Fig. 2). A similar approach has been described by Cushman and Tibbitts (1998).

Plant measurements. Overhead images were taken every third or fourth day from day 10 until canopy closure to quantify percent groundcover and rate of canopy closure as described by Klassen et al. (2003). Flower number was measured every third or fourth

day until day 35 and fruit numbers were measured through day 45 to characterize the impact of ethylene concentration on flower and fruit initiation. Flower and fruit counts were stopped on day 45 after fruit developed in all treatments due to time constraints. Pollination was facilitated by the fans used to homogenize the air. Plants were harvested on day 106 and final flower and fruit count measurements were made. All plant material was dried to a constant mass at 80 °C. Harvest index was calculated as the ratio of fruit fresh weight to total shoot fresh weight.

Statistical analysis. Three ethylene treatments (0, 20, and 40 nmol·mol^{-1}) and two temperature treatments (22 and 28 °C) were randomly assigned in a complete block design resulting in two replicate chambers of each of six treatments (Fig. 1A).

Statistical analyses were performed using the SAS® statistical analysis package (SAS Institute, Cary, NC, USA), Proc GLM procedure, Linear Analysis Model, Type III. One of the two replicate chambers at 40 nmol·mol^{-1} ethylene and 28 °C was removed from the analysis, because there was an aberrant, 3-day period of clean air following initialization of the first floral buds, which significantly increased yield.

Results

Vegetative growth. Ethylene minimally reduced vegetative growth, regardless of temperature (Table 1; Fig. 3). Increasing ethylene did not significantly affect the rate of canopy closure during vegetative growth (Table 1; data not shown). Percent groundcover through day 35 at 22 °C was 95% of the control at 20 nmol·mol^{-1} ethylene, and 91% of control at 40 nmol·mol^{-1} ethylene (data not shown). There was no significant interaction between temperature and ethylene on rate of canopy closure during vegetative growth (Table 1; data not shown).

Flower and fruit development. Increasing ethylene significantly decreased flower number ($P = 0.01$; Table 1, Fig. 4), whereas increasing temperature significantly increased flower number ($P = 0.03$; Table 1, Fig. 4). There was no interaction between ethylene and temperature on flower number ($P = 0.62$; Table 1). The first fruit in the 0 and 20 nmol·mol^{-1} treatments appeared on day 31 at 22 °C; at 28 °C, the first fruit appeared on day 23 (data not shown). Fruit did not develop until day 35 at either temperature in the 40 nmol·mol^{-1} treatments (data not shown).

Total fruit number at harvest significantly decreased with increasing ethylene ($P = 0.02$) and marginally decreased with increasing temperature ($P = 0.06$; Table 1, Fig. 5B), but there was no interaction between ethylene and temperature ($P = 0.49$; Table 1).

Red fruit number at harvest significantly decreased with increasing ethylene ($P < 0.001$) and temperature ($P = 0.04$; Table 1, Fig. 5A). At 22 °C, red fruit number declined to 47% and 14% of the control at 20 and 40 nmol·mol^{-1}, respectively (Fig. 5A). At 28 °C, red fruit numbers declined to 21% and 4% of the control at 20 and 40 nmol·mol^{-1}, respectively (Fig. 5A). There was no interaction between temperature and ethylene concentration on red fruit number ($P = 0.33$; Table 1).

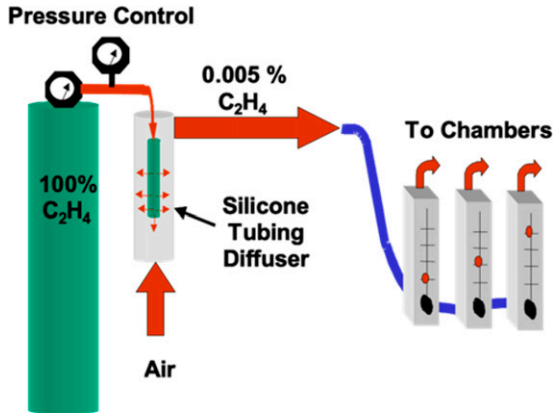

Fig. 2. Schematic diagram of the unique ethylene diluter system. Pure ethylene was supplied to the silicone tubing diluter. The ethylene slowly diffused through the 2-mm-thick tube and mixed with house air that was independently supplied to the diluter. The diluted ethylene flowed from the diluter into a rotameter manifold where it was partitioned to each chamber at the appropriate concentration. A similar approach was used by Cushman and Tibbitts (1998).

Yield. Total fruit mass (kg·m^{-2}) declined with increasing ethylene ($P = 0.003$) and temperature ($P < 0.001$), but there was no interaction between ethylene and temperature on total fruit mass ($P = 0.11$; Table 1, Fig. 5D).

Red fruit mass (kg·m^{-2}) declined with increasing ethylene ($P = 0.004$) and temperature ($P = 0.003$; Table 1, Fig. 5C). There was an interaction between ethylene and temperature ($P = 0.05$; Table 1), but this effect was small compared with the main effects. At 22 °C, red fruit mass declined to 51% and 11% of the control at 20 and 40 nmol·mol^{-1}, respectively (Fig. 5C). At 28 °C, red fruit mass declined to 37% and 4% of the control at 20 and 40 nmol·mol^{-1}, respectively (Fig. 5C). Red fruit mass was three times higher at 22 °C than 28 °C at all ethylene concentrations (Fig. 5C).

Fruit size (g per fruit) significantly decreased with increasing temperature ($P = 0.01$; Table 1, Fig. 5E and F), but there was no effect of ethylene ($P = 0.24$) or interaction between ethylene and temperature ($P = 0.51$; Table 1). Fruit size was approximately 65% lower at 28 °C than at 22 °C (Fig. 5E and F).

Harvest index, the ratio of fresh fruit mass to total fresh shoot mass, significantly decreased with increasing ethylene ($P = 0.03$) and temperature ($P = 0.002$), but there was no interaction between ethylene and temperature ($P = 0.61$; Table 1, Fig. 6).

Discussion

In this study, 20 and 40 nmol·mol^{-1} ethylene had a minimal effect on vegetative growth of tomato. This is consistent with the results of Blankenship and Kemble (1996) who reported a minimal effect of ethylene on plant height in tomato. In Super Dwarf rice, a similarly minimal effect on vegetative biomass was observed up to 1000 nmol·mol^{-1} ethylene (Klassen and Bugbee 2002).

Table 1. Probability (P) values for the effects of ethylene and temperature on tomato growth and development. Vegetative growth was unaffected by either ethylene or temperature. Reproductive development was significantly affected by both ethylene and temperature at 0 to 40 nmol·mol^{-1} ethylene and 22 and 28 °C. There was an interaction between temperature and ethylene on red fruit yield, but this effect was small compared with the main effects.

Stage	Parameters	Ethylene	Temperature	Ethylene by temp
Growth	Percent ground cover	0.36	0.65	0.63
	Vegetative fresh weight	0.63	0.06	0.79
	Vegetative percent dry mass	0.29	0.19	0.89
Development	Flower number	0.01[i]	0.03[i]	0.62
Yield	Red fruit number	<0.001[i]	0.04[i]	0.33
	Total fruit number	0.02[i]	0.06	0.49
	Red number (percent of total)	0.18	0.04[i]	0.18
	Red fruit fresh weight	0.004[i]	0.003[i]	0.05[i]
	Total fruit fresh weight	0.003[i]	<0.001[i]	0.11
	Red mass (percent of total)	0.14	0.13	0.19
	Red fruit percent dry mass	0.67	0.24	0.91
	Total fruit percent dry mass	0.32	0.29	0.16
	Red fresh weight per fruit	0.24	0.01[i]	0.55
	Total fresh weight per fruit	0.60	0.01[i]	0.51
	Harvest index	0.03[i]	0.002[i]	0.61

[i] $P < 0.05$.

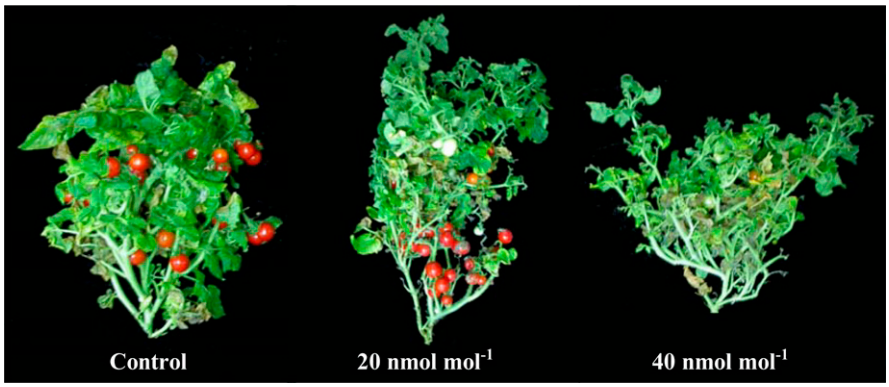

Fig. 3. Representative plants from the three ethylene treatments at 22 °C at harvest on day 106. The control plants were symmetrical with larger leaves and more numerous fruit. The 20 nmol·mol^{-1} plants were asymmetric with longer branches and small leaves. The 40 nmol·mol^{-1} plants were small and symmetrical with many short branches and small leaves. Fresh leaf mass per plant was unaffected by ethylene (P = 0.63).

Interestingly, minimal epinasty was observed in any treatment. Epinasty has the potential to indirectly reduce growth by reducing photon capture, but this was not observed in this study. Epinasty in potato occurred at 50 nmol·mol^{-1} ethylene (Wheeler et al. 2005). It is possible that 40 nmol·mol^{-1} was below the epinastic threshold in this variety.

Although there was no effect of ethylene up to 40 nmol·mol^{-1} on vegetative growth, increasing ethylene significantly reduced flower development and fruit yield. This is consistent with others who have evaluated the effect of increasing ethylene concentration on fruit yield (Blankenship and Kemble 1996; Klassen and Bugbee 2002, 2004) and provides new insight into the effect of ethylene on growth and development at different temperatures. Blankenship and Kemble (1996) found that yield of Red Robin tomatoes grown at 20/18 °C (day/night) decreased to 82% and 15% of the control at 10 and 50 nmol·mol^{-1} ethylene, respectively. Continuous exposure to 100 nmol·mol^{-1} ethylene completely inhibited fruit set (Blankenship and Kemble 1996). Results from this study suggest a similar yield reduction would occur across a range of temperatures commonly used in controlled environment agriculture.

Our results are also consistent with studies that have demonstrated yield reductions in other seed crops. Yield of wheat (*Triticum aestivum* L. cv. USU-Apogee) and rice (*Oryza sativa* L. cv Super Dwarf) decreased to 64% and 37% of the control when exposed to 50 nmol·mol^{-1} ethylene (Klassen and Bugbee 2002). This suggests a common response to elevated ethylene among seed and fruit crops.

Vegetative crops such as lettuce and radish tend to be less sensitive to elevated ethylene than flower, fruit, and seed crops (Klassen and Bugbee 2004). The exact stage during floral development (e.g., microspore division, stigma growth) that is most ethylene sensitive warrants further investigation. Most studies to date have evaluated the response of crops to chronic ethylene exposure (Blankenship and Kemble 1996; Campbell et al. 2001; Cushman and Tibbitts 1998; Klassen and Bugbee 2002, 2004; Mortensen 1989). Identifying the critical period around anthesis may help limit the amount of time scrubbing systems must keep ethylene concentrations below a threshold level of 10 to 20 nmol·mol^{-1} on the ISS. This also has implications for crop production where intentional manipulation of sex expression (Martínez and Jamilena 2021; Yamasaki et al. 2005) or inhibition of seed or fruit set is desirable (Galoch 1978).

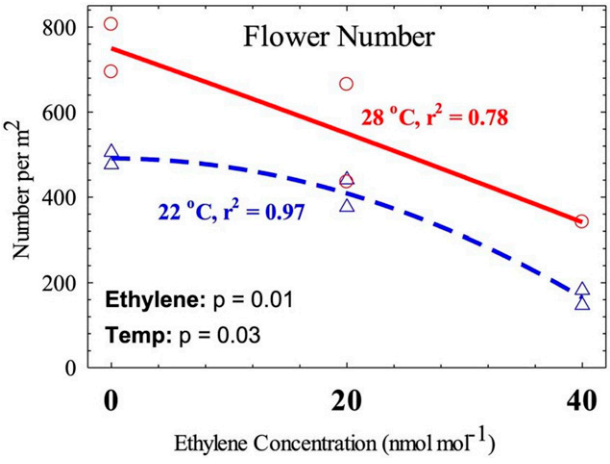

Fig. 4. Effect of ethylene and temperature on flower number on day 31. The number of flowers significantly decreased with increasing ethylene (P = 0.01) and significantly increased with increasing temperature (P = 0.03). There was no significant interaction between ethylene and temperature (P = 0.62).

There is the potential for other environmental factors to affect ethylene sensitivity. PPFD altered ethylene synthesis and sensitivity in some species (Beßler et al. 1998; Kao and Yang 1982), but not others (Romagnano and Bugbee 2013). Modification of phytochrome activity with red and far-red photons (Vangronsveld et al. 1988) and temperature (Bours et al. 2013) affected ethylene synthesis and sensitivity through transcriptional control of genes that regulate synthesis and perception (Foo et al. 2006). Root-zone hypoxia increases ethylene synthesis in waterlogged plants (Drew 1997), leading to aerenchyma formation and internode elongation in rice (*Oryza sativa* L.) (Gibbs and Greenway 2003).

Temperature had a significant effect on flower development, fruit set, and fruit yield. Plants at 28 °C produced more flowers, that developed faster than at 22 °C, but these flowers failed to set fruit. Pollination of tomato occurs at night, and high night temperatures have been shown to reduce tomato pollen viability (Peet and Bartholemew 1996). In this study, the day/night temperature was constant. It is possible that a lower night temperature could have improved fruit set in the 28 °C treatment. Alternatively, the increase in flower number may have caused carbohydrate limitations and increased abortion of flowers (Lauxmann et al. 2016), leading to a lower fruit yield. Reducing temperature has been shown to minimize the abortion of reproductive structures (Heuvelink et al. 2020). Low auxin transport in response to high temperature has been shown to induce fruit abscission in pepper (Huberman et al. 1997). Thus, interactions with other phytohormones may alter ethylene responses in response to temperature.

CO_2 reduces ethylene sensitivity at extremely high concentrations (10%; 1 × 10^7 μmol·mol^{-1}; Burg and Burg, 1967), but Klassen and Bugbee (2002) found that CO_2 up to 5000 μmol·mol^{-1} (0.5%) did not affect ethylene sensitivity in wheat (*Triticum aestivum* L.). Greenhouses and closed environments are typically enriched to 800 to 1200 μmol·mol^{-1} and rarely reach concentrations above 2000 μmol·mol^{-1}. Astronauts on the ISS exposed to CO_2 concentrations above ~3000 μmol·mol^{-1} have an increased risk of headaches and other health problems (Law et al. 2014).

Elevated CO_2 (1100 μmol·mol^{-1}) was used in this study to increase fruit set and minimize carbohydrate limitations. Elevated CO_2 minimizes abortion of reproductive structures (Heuvelink et al. 2020), increases yield (Mamatha et al. 2014), and increases the optimal temperature for plant growth (Berry and Bjorkman 1980; Sage and Kubien 2007). At ambient CO_2, the optimal temperature for tomato yield is between 21 and 24 °C

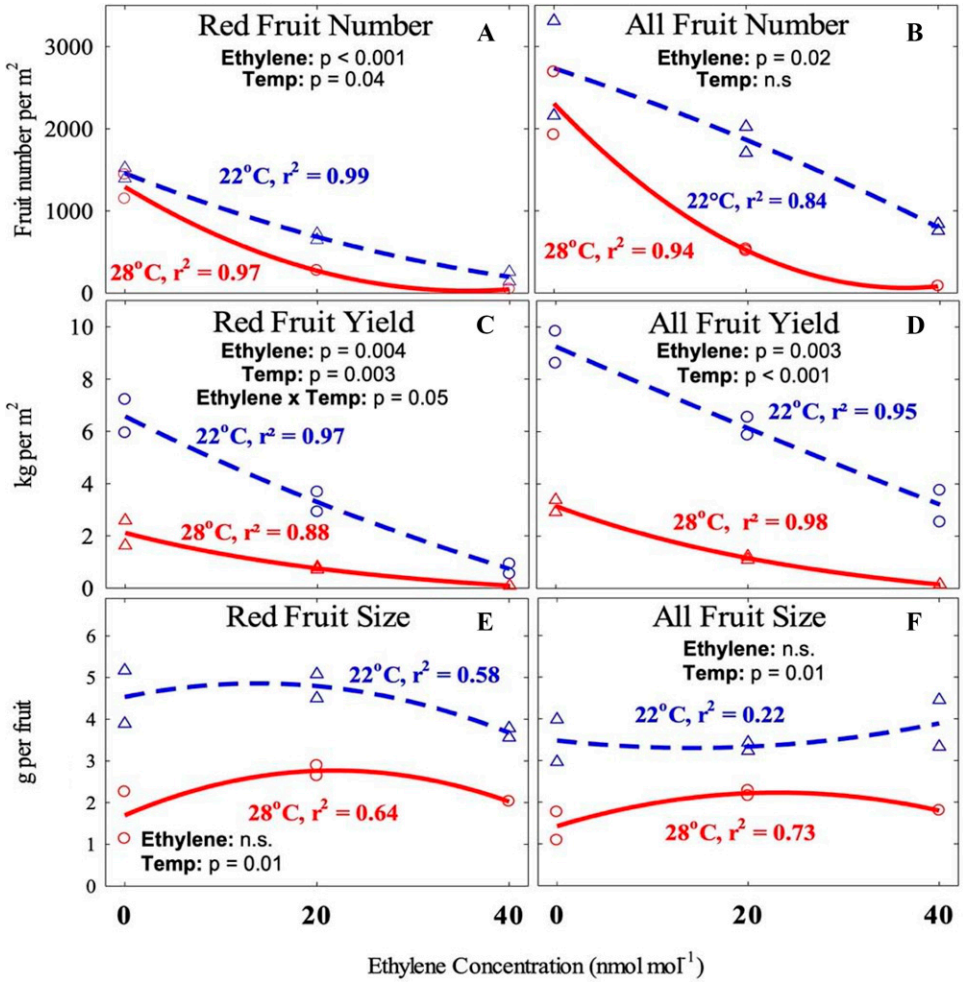

Fig. 5. Effect of ethylene and temperature on (**A** and **B**) fruit number, (**C** and **D**) fruit yield, and (**E** and **F**) fruit size at harvest on day 106. (**A**) Red fruit number at harvest declined with increasing ethylene ($P < 0.001$) and temperature ($P = 0.04$). There was no significant interaction between ethylene and temperature ($P = 0.33$). (**B**) Total fruit number at harvest declined with increasing ethylene ($P = 0.02$) and marginally decreased with increasing temperature ($P = 0.06$). There was no interaction between ethylene and temperature ($P = 0.49$). (**C**) Red fruit yield at harvest significantly decreased with increasing ethylene ($P = 0.004$) and increasing temperature ($P = 0.003$). There was a small but statistically significant interaction between ethylene and temperature ($P = 0.05$). (**D**) Total fruit yield significantly increased with increasing ethylene ($P = 0.003$) and increasing temperature ($P < 0.001$) but there was no interaction between ethylene and temperature ($P = 0.11$). (**E**) There was no significant effect of ethylene on red fruit size ($P = 0.24$) but increasing temperature significantly decreased fresh weight per red fruit ($P = 0.01$). There was no interaction between ethylene and temperature ($P = 0.55$). (**F**) All fruit size was unaffected by ethylene ($P = 0.60$), but increasing temperature significantly decreased fresh weight per fruit ($P = 0.01$). There was no interaction between ethylene and temperature ($P = 0.51$).

(Sato et al. 2000). Temperature differences of only a few degrees outside this range can decrease fruit production (Adams et al. 2001). The optimal temperature is expected to increase ~3°C at elevated CO_2 (Berry and Bjorkman 1980). The temperatures in our study were slightly below optimal (22 °C) and slightly above optimal (28 °C) at elevated CO_2.

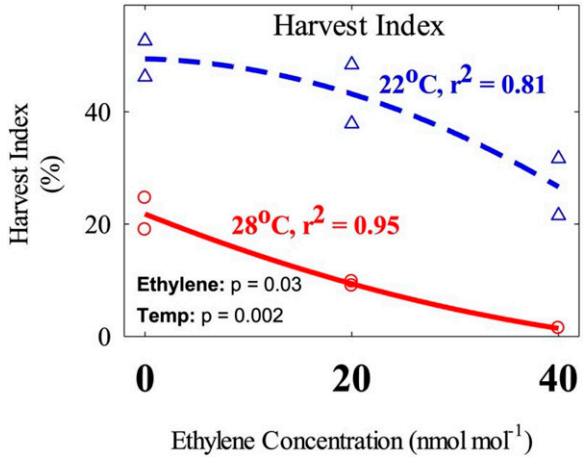

Fig. 6. Effect of ethylene and temperature on harvest index, calculated as the ratio of fresh fruit mass to total fresh shoot mass. Harvest index decreased with increasing ethylene ($P = 0.03$) and increasing temperature ($P = 0.002$), but there was no significant ethylene by temperature interaction ($P = 0.61$).

Conclusion

Fruit set relative to the control was inhibited at all ethylene concentrations up to 40 nmol·mol^{-1} at 22 and 28 °C. This indicates that ethylene inhibits floral development and fruit set independent of temperature. The decrease in fruit number with an increase in temperature suggests that reducing temperature may not reduce ethylene sensitivity but may increase yield of MicroTina tomatoes in high ethylene environments.

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