

Effects of exposure in space on tomato seeds: Photosynthesis, biomass, and water relations of well-watered and drought-stressed plants

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Abstract

Tomato seeds exposed to space conditions for nearly six years on board the Long Duration Exposure Facility (LDEF) satellite were subsequently germinated and the resultant seedlings grown on earth under controlled conditions for analysis. Photosynthesis, biomass, and water relations were compared between mature plants grown from earth-based control seeds and space-exposed seeds under both well-watered and drought-stressed conditions. No consistent significant differences in photosynthesis and water relations were observed in the two sets of plants at any level of drought stress. Fruit production, however, though limited and variable, was significantly greater in plants grown from space-exposed seeds than in plants grown from earth-based seeds. Overall, exposure of seeds to space had only minor effects on the physiology and growth of plants grown from such seed.

Additional key words: cosmic radiation; internal CO₂ concentration; microgravity; net CO₂ exchange; osmotic potential; stomatal conductance; water potential.

Introduction

Plants subjected to the abnormal conditions of space are exposed to a variety of factors, *e.g.*, cosmic radiation, vacuum, temperature extremes, and microgravity, that may have a deleterious effect on their physiology, growth, and reproduction (Gaubin *et al.* 1983, Cowles *et al.* 1984, Volkmann *et al.* 1986, Halstead and Dutcher 1987, Krikorian and Levine 1991, Schaefer *et al.* 1993, Kuang *et al.* 1996, Tripathy *et al.* 1996). In particular, high-energy α -particles are probably responsible for many of the damaging effects. Although much previous work has focused on intact plants

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exposed to space (see above references), less is known about the effects of the harsh space environment on dormant seeds. Furthermore, results of germination studies using space-exposed seeds of several species are difficult to generalize; seed germination and seedling growth were stimulated in some studies, inhibited in others, or were simply unaffected (Saunders 1971, Anikceva *et al.* 1983, Gaubin *et al.* 1983, Brown and Chapman 1984, Cowles *et al.* 1984, Volkmann *et al.* 1986, Halstead and Dutcher 1987, Schaefer *et al.* 1993). Likewise, numerous studies of the effects of exposure of seeds to ionizing radiation in earth-based experiments report a variety of effects—both stimulatory and inhibitory—on the plants grown from these seeds (Miller and Miller 1987).

The "Space Exposed Experiment Developed for Students" (SEEDS) was a cooperative project of the National Aeronautics and Space Administration (NASA) Educational Affairs Division, NASA Langley Research Center (Washington, D.C.) and the *George W. Park Seed Company* (Greenwood, S.C.) in which 12.5 million tomato seeds were exposed to space conditions for almost six years, retrieved from space, then distributed to educational institutions throughout the United States for study (Grigsby *et al.* 1990, Melton 1991). The seeds were loaded on board the Long Duration Exposure Facility (LDEF), which was placed in orbit at 475 km on 7 April 1984 by the space shuttle *Challenger* (Mission 41-C). The tomato seeds, which were retrieved by the space shuttle *Columbia* (Mission STS-32) on 12 January 1990 (at the lower altitude of 342 km because of orbit decay), were exposed to space conditions longer than in any other previous NASA experiment involving the effects of space on biological tissue.

Basic germination and growth characteristics of the space-exposed tomato seeds have been examined in numerous studies (Melton 1991, Kahn and Stoffella 1996) but relatively little is known about the effects of space exposure on the subsequent physiology or degree of stress-tolerance of the plants grown from such seeds. The latter is particularly interesting in light of preliminary reports of premature chlorophyll development and increased drought-tolerance of plants grown from space-exposed seeds, relative to plants grown from earth-based seeds (Grigsby *et al.* 1990). Therefore, the objective of the current study was to examine the possibility of such effects by comparing photosynthetic gas exchange and water relations of mature plants grown from control and space-exposed seeds. Physiological characteristics were compared under both drought-stressed and well-watered conditions.

Materials and methods

Seed preparation: Space-exposed and control seeds were collected from *Lycopersicon esculentum* Mill. (cv. Rutgers California Supreme) plants during one growing season and were chosen from a seed lot with a high germination rate. Prior to flight, all seeds were tumbled in a spinning drum to remove pubescence, which reduced the volume and mass per seed allowing tighter packing. The controls were stored at *Park Seed Company* facilities at 101 kPa atmospheric pressure, 21 °C, and 20 % relative humidity (RH).

Twelve and one-half million seeds were packed in sets of four Dacron bags to provide four levels of radiation exposure in space. The four layers were then sealed into each of five Al canisters (each 1000 cm³ volume, sealed at 101 kPa atmospheric pressure and 20 % RH) designed to allow maximum high-energy particle penetration while in space. All seeds used in the current study were from canister number three.

The seeds were exposed to a gravitational force of 10⁻⁶ g and to various radiation levels while orbiting the earth in the LDEF satellite. Seeds in exposure level A received maximum doses (720 rad) of radiation while those in level D received the least amount of radiation (350 rad); intermediate levels of radiation received by the other layers were not measured. The temperature within each canister ranged from approximately -23 to +35 °C during the period of space exposure, depending on interception of solar radiation. The seeds were vacuum-packed in foil envelopes upon return to earth.

Plant growth: Seeds were received from NASA in 1990 and remained at room temperature in the sealed foil envelopes until use in 1992, whereupon they were placed in sterile Petri dishes on wet filter paper in a growth chamber under constant darkness with an alternating 13-h "day" at 30 °C air temperature and 50 % RH, and an 11-h "night" at 20 °C and 62 % RH. Germinated seeds were removed from Petri dishes and placed in standard greenhouse soil (7:2:1:1, v/v, mixture of clay loam, peat moss, Perlite, and vermiculite) when their root tips reached 1 cm in length. The soil flats with seedlings were provided a 13-h photoperiod of *ca.* 300 μmol m⁻² s⁻¹ photosynthetic photon flux density (PPFD) under the environmental conditions described above. All seedlings were watered once daily. Plants were fertilized (dilute solution of trace elements and 18 % of each of total N, P₂O₅, and K₂O) once each week after emerging from the soil. Seedlings 6 cm in height were planted into 15-cm diameter plastic pots using the same soil mix as above. Physiological measurements were made six weeks later. Because of the length of time required for all measurements, the entire experiment was performed twice (Group I: 7 February 1992-19 April 1992, and Group II: 12 May 1992-25 July 1992) to provide a larger sample size of plants at a similar age.

Photosynthetic rate was measured under the environmental conditions described above with a *LI-COR* (Lincoln, NE, USA) *LI-6000* Portable Photosynthesis System which utilizes an absolute infrared gas analyzer in a closed system with a 250 cm³ cuvette. Measurements were made using the youngest fully mature leaves at 0, 3.5, 7.0, and 10.5 h after watering in the morning. Plants from the different treatments were sampled in a staggered fashion in order to keep elapsed time between measurements constant among groups. After data collection, all leaf samples were dried at 65 °C for at least three days for inclusion in subsequent plant biomass determinations. For details regarding the use of the *LI-6000* system, see Martin *et al.* (1992).

Water relations characteristics: Water potential of another youngest mature leaf from each plant was estimated immediately after every photosynthetic measurement by measuring xylem tension with a *PMS Instruments* (Corvallis, OR) pressure chamber. The sample was then oven-dried for inclusion in biomass determinations.

Osmotic potential was determined using leaves collected from well-watered and drought-stressed plants 10.5 h after watering. The leaves were frozen at -65°C . Tissue sap was expressed from the thawed leaves with a vice, and osmotic potential was compared with standards using a *Wescor* (Logan, UT) *HR-33T* Dewpoint Microvolt Meter and *C-52* sample chamber. All leaf samples were oven-dried for inclusion in biomass determinations.

Growth: After all physiological measurements, each plant was separated into roots, leaves, stems, flowers, and fruits. Roots were carefully rinsed under water to remove as much soil as possible. All plant matter was then dried at 65°C for four weeks in a forced-air oven and then weighed. Total leaf biomass included leaves removed for the measurements described above.

Table 1. Mean values \pm standard deviation of leaf water potential and osmotic potential [-MPa] of plants grown in spring 1992 (Group I) from tomato seeds exposed to space ("Space") and from earth-based ("Earth") seeds. Plants were well-watered at zero hours, then increasingly drought-stressed at longer periods of time without water. Letters in parentheses represent level of exposure while in space. Numbers of plants at a given level of exposure while in space: Group I: A - 2, B - 4, C - 5, D - 7, earth - 7; Group II: A - 7, B - 6, C - 1, D - 6, earth - 6. Only values in the last row of Group I and next-to-last but one line of Group II were significantly different from the other ones ($p \leq 0.05$) according to the Mann-Whitney *U*-test comparing all plants grown from space-exposed seeds (all levels combined) with plants grown from earth-based seeds. In the last line for Group II different letters indicate significantly different means ($p \leq 0.05$) according to the comparison-of-means tests (values appear the same due to rounding).

	Potential	Water	Space				Earth	Space
		stress [h]	(A)	(B)	(C)	(D)		(A→D)
Group I	water	0	0.4 \pm 0.1	0.6 \pm 0.2	0.6 \pm 0.2	0.6 \pm 0.1	0.7 \pm 0.2	0.6 \pm 0.2
		3.5	0.7 \pm 0.0	0.7 \pm 0.2	0.7 \pm 0.1	0.7 \pm 0.1	0.7 \pm 0.1	0.7 \pm 0.1
		7.0	0.7 \pm 0.1	0.9 \pm 0.1	0.9 \pm 0.2	0.8 \pm 0.1	0.8 \pm 0.1	0.8 \pm 0.1
		10.5	1.1 \pm 0.1	1.0 \pm 0.1	1.0 \pm 0.1	0.8 \pm 0.2	1.0 \pm 0.3	0.8 \pm 0.2
	osmotic	0	0.6 \pm 0.0	0.8 \pm 0.0	0.7 \pm 0.1	0.7 \pm 0.1	0.8 \pm 0.2	0.7 \pm 0.1
		10.5	0.8 \pm 0.0	0.8 \pm 0.1	0.7 \pm 0.0	1.6 \pm 2.3	0.8 \pm 0.1	0.7 \pm 0.1
Group II	water	0	0.5 \pm 0.1	0.5 \pm 0.1	0.6	0.6 \pm 0.1	0.6 \pm 0.1	0.5 \pm 0.1
		3.5	0.6 \pm 0.0	0.7 \pm 0.1	0.8	0.7 \pm 0.1	0.8 \pm 0.2	0.7 \pm 0.1
		7.0	0.7 \pm 0.1	0.8 \pm 0.1	0.9	0.8 \pm 0.2	0.9 \pm 0.3	0.7 \pm 0.2
		10.5	0.7 \pm 0.1	0.9 \pm 0.3	1.4	0.9 \pm 0.3	1.0 \pm 0.3	0.8 \pm 0.3
	osmotic	0	0.8 \pm 0.1	0.8 \pm 0.2	0.9	0.9 \pm 0.1	0.9 \pm 0.1	0.9 \pm 0.1
		10.5	0.8 \pm 0.1a	0.8 \pm 0.1b	1.0	0.8 \pm 0.0ab	0.9 \pm 0.1ab	0.8 \pm 0.1ab

Statistical analysis: Nonparametric statistics were utilized because the low sample sizes made results of normality tests difficult to interpret. The means from each space-exposure layer, as well as the control means, were compared with a Kruskal-Wallis test; if significant differences were indicated, the Dunn's Procedure was used to determine which means were significantly different. The Mann-Whitney *U*-test was used to compare the overall means of all space-exposed and earth-based data.

Significant differences in all tests were inferred only when $p \leq 0.05$. Statistical procedures followed Sokal and Rohlf (1981) and Rosner (1990).

Results and discussion

In April 1983, a preliminary experiment on board a space shuttle determined that launch and entry gravitational forces had no consistent effects on tomato seed germination or fruit production of the resultant plants (Grigsby *et al.* 1990, Melton 1991, also see Kahn and Stoffella 1996). These results imply that potential launch

Table 2. Means \pm standard deviations of net CO_2 exchange, P_N [$\mu\text{mol m}^{-2} \text{s}^{-1}$], stomatal conductance, g_s [$\mu\text{mol m}^{-2} \text{s}^{-1}$], and internal CO_2 concentration, C_i [$\mu\text{mol m}^{-3}$] of leaves of plants grown in spring 1992 (Group I) and in summer 1992 (Group II) from tomato seeds exposed to space ("Space") and from earth-based ("Earth") seeds. Plants were well-watered at zero hours, then increasingly drought-stressed at longer periods of time without water. For numbers of plants at a given exposure level while in space see Table 1. All differences between results were insignificant according to the Mann-Whitney *U*-test and comparison-of-means test (see legend to Table 1).

	Water stress [h] (A)	Space (B)	(C)	(D)	Earth	Space (A >D)		
Group I	P_N	0	8.5 \pm 0.2	7.5 \pm 1.4	7.9 \pm 2.9	7.3 \pm 2.2	7.3 \pm 2.7	7.7 \pm 2.1
		3.5	8.9 \pm 0.1	7.6 \pm 0.9	6.2 \pm 3.1	6.6 \pm 1.9	6.4 \pm 2.3	7.0 \pm 2.1
		7.0	7.0 \pm 4.3	0.9 \pm 0.5	3.2 \pm 2.4	4.5 \pm 1.6	2.8 \pm 2.6	3.6 \pm 2.6
		10.5	3.6 \pm 2.3	1.2 \pm 0.8	1.0 \pm 1.3	2.0 \pm 1.6	1.7 \pm 1.5	1.7 \pm 1.6
	g_s	0	0.33 \pm 0.20	0.31 \pm 0.15	0.28 \pm 0.08	0.46 \pm 0.21	0.39 \pm 0.13	0.36 \pm 0.17
		3.5	0.39 \pm 0.20	0.35 \pm 0.10	0.30 \pm 0.17	0.36 \pm 0.16	0.37 \pm 0.07	0.34 \pm 0.14
		7.0	0.10 \pm 0.10	0.11 \pm 0.15	0.09 \pm 0.08	0.19 \pm 0.13	0.10 \pm 0.10	0.14 \pm 0.12
		10.5	0.06 \pm 0.10	0.03 \pm 0.01	0.03 \pm 0.00	0.04 \pm 0.02	0.03 \pm 0.01	0.04 \pm 0.02
	C_i	0	13.7 \pm 0.4	14.7 \pm 0.6	14.9 \pm 1.6	14.6 \pm 1.0	14.6 \pm 1.4	14.6 \pm 1.1
		3.5	14.3 \pm 0.9	14.1 \pm 0.6	13.8 \pm 1.4	13.5 \pm 1.0	13.7 \pm 1.2	13.8 \pm 1.0
		7.0	12.1 \pm 1.3	13.9 \pm 1.1	12.7 \pm 0.8	12.8 \pm 1.2	13.0 \pm 1.6	12.9 \pm 1.1
		10.5	13.5 \pm 1.0	13.3 \pm 2.1	13.5 \pm 3.8	12.1 \pm 2.9	13.0 \pm 2.4	12.9 \pm 2.8
Group II	P_N	0	4.7 \pm 1.2	5.3 \pm 1.6	3.9	5.3 \pm 1.1	5.4 \pm 1.0	5.0 \pm 1.3
		3.5	6.0 \pm 1.0	5.0 \pm 1.7	2.5	5.5 \pm 2.1	4.3 \pm 1.6	5.2 \pm 1.7
		7.0	4.0 \pm 2.2	3.5 \pm 2.1	2.9	3.4 \pm 1.7	3.5 \pm 2.7	3.6 \pm 1.8
		10.5	3.7 \pm 1.6	3.7 \pm 2.1	-0.1	2.2 \pm 0.9	1.6 \pm 1.5	3.1 \pm 1.8
	g_s	0	0.15 \pm 0.09	0.25 \pm 0.15	0.12	0.21 \pm 0.16	0.17 \pm 0.04	0.20 \pm 0.13
		3.5	0.24 \pm 0.01	0.31 \pm 0.23	0.08	0.28 \pm 0.14	0.24 \pm 0.17	0.27 \pm 0.16
		7.0	0.18 \pm 0.16	0.26 \pm 0.31	0.06	0.16 \pm 0.13	0.14 \pm 0.13	0.19 \pm 0.20
		10.5	0.10 \pm 0.07	0.11 \pm 0.10	0.02	0.05 \pm 0.01	0.05 \pm 0.02	0.08 \pm 0.07
	C_i	0	12.8 \pm 1.8	13.0 \pm 0.9	11.8	13.6 \pm 1.0	13.8 \pm 0.9	13.0 \pm 1.3
		3.5	12.7 \pm 1.2	13.2 \pm 1.2	11.8	13.3 \pm 0.8	12.8 \pm 1.7	13.0 \pm 1.1
		7.0	12.1 \pm 1.5	12.5 \pm 1.6	11.2	12.2 \pm 2.1	13.0 \pm 1.3	12.2 \pm 1.6
		10.5	11.4 \pm 1.6	11.5 \pm 1.9	14.2	11.6 \pm 1.1	13.3 \pm 1.6	11.6 \pm 1.6

and entry stresses did not adversely affect seed germination and subsequent growth of the plants. Given these findings, the assumption is made that the earth-based seeds are adequate controls for the experimental seeds, which were exposed to space radiation, vacuum, and weightlessness. On the other hand, inconsistencies in temperatures between the space-exposed seeds and earth-based controls were unavoidable.

Because plants in the first growth period (Group I) were significantly larger than those in the second period (Group II), it was not possible to pool the two sets of values. As a result, sample sizes were smaller than desired. Reasons for the discrepancy in plant size in the two sets of plants are unclear; however, a slight change in the potting mix (more clay and less sand) during the second growth period reduced drainage of the soil and may have reduced plant growth.

Table 3. Means \pm standard deviations of biomass of plants grown in spring (Group I) and summer (Group II) 1992 from tomato seeds exposed to space ("Space") and from earth-based ("Earth") seeds. Plants were separated into roots, leaves, stems, flowers, and fruits for biomass determination. Letters in parentheses represent degree of exposure while in space. All results of Mann-Whitney U-tests comparing all plants grown from space-exposed seeds (all levels combined) with plants grown from earth-based seeds were significant at $p \leq 0.05$, with the exception of values for stems in Group I and for roots and leaves in Group II. Results of comparison-of-means tests comparing each mean with one another (excluding the combined mean) are marked with letters; different letters indicate significantly different means ($p \leq 0.05$).

	Space (A)	(B)	(C)	(D)	Earth	Space (A > D)	
Group I	Plant no. 2	4	5	7	7	18	
	Root	74.9 \pm 18.3	95.9 \pm 23.6a	52.6 \pm 25.1abc	59.9 \pm 25.9bc	38.4 \pm 31.8c	59.7 \pm 31.5abc
	Leaf	34.9 \pm 1.3	33.4 \pm 2.7	29.3 \pm 4.4	25.4 \pm 6.5	22.3 \pm 6.3	27.3 \pm 6.8
	Stem	17.9 \pm 3.7	17.4 \pm 3.4	16.3 \pm 4.8	15.1 \pm 4.3	11.0 \pm 4.1	14.7 \pm 4.6
	Flower	0.4 \pm 0.1	0.4 \pm 0.2	0.3 \pm 0.3	0.3 \pm 0.1	0.2 \pm 0.2	0.3 \pm 0.2
	Fruit	6.5 \pm 8.8	1.3 \pm 1.0	2.7 \pm 3.1	4.9 \pm 4.2	1.4 \pm 2.2	3.0 \pm 3.8
Group II	Plant no. 7	6	6	6	6	20	
	Root	12.9 \pm 7.3ad	12.5 \pm 7.5d	25.2	18.6 \pm 12.0bdc	34.7 \pm 9.4c	19.7 \pm 12.3abcd
	Leaf	23.9 \pm 8.9	20.7 \pm 7.9	19.0	24.1 \pm 7.0	33.7 \pm 8.1	25.3 \pm 8.9
	Stem	11.0 \pm 3.6	8.1 \pm 4.9	8.4	10.7 \pm 2.2	13.0 \pm 3.4	10.6 \pm 3.8
	Flower	0.6 \pm 0.3	0.5 \pm 0.2	0.3	0.6 \pm 0.2	0.6 \pm 0.1	0.5 \pm 0.2
	Fruit	1.4 \pm 1.3	1.3 \pm 1.9	3.2	3.2 \pm 5.5	0.7 \pm 0.9	1.7 \pm 2.9

The water potential and osmotic potential values verify that the plants were progressively more drought-stressed at 3.5, 7.0, and 10.5 h after watering (Table 1). Turgor potential had decreased to zero, or nearly so, by the last measurements. No evidence for osmotic adjustment was observed. Gas exchange values collected during this period of drought stress indicated typical photosynthetic declines in response to drought within each group of plants (Table 2).

With few exceptions, under well-watered conditions, and at all times after watering, photosynthetic gas exchange parameters, water relations, and biomass (Table 3) of plants grown from space-exposed seeds, regardless of layer, *i.e.*, level of

exposure to space radiation, were not significantly different from values of plants grown from seeds that remained on earth. Although significant differences were observed in stem biomass between space-exposed and control plants in Group II, no significant differences were observed in Group I (Table 3). In addition, leaf biomass exhibited differences in Group I but not in Group II, as did osmotic potentials of the drought-stressed plants. Because of the small sample sizes and the inconsistencies between groups, the results are of questionable biological significance. On the other hand, a consistent effect of space-exposure of the seeds was observed in fruit biomass. In both Groups I and II, plants grown from space-exposed seeds produced significantly more fruit biomass than plants grown from earth-based seeds (Table 3). Fruit production was extremely low over the experimental period, however, and variability among plants within the same experimental group was high. Furthermore, Kahn and Stoffella (1996) found no effect of space exposure of these seeds on fruit production of the subsequently grown tomato plants. Thus, it seems unlikely that space exposure results in increased fruit production.

In summary, exposure of tomato seeds to space for nearly six years had no apparent effect on photosynthesis, water relations, and biomass of plants grown from such seeds, regardless of the water status of the plants. The results may, on the other hand, indicate a potential increase in fruit production associated with space exposure of the seeds. These studies could have important implications for future space missions that rely on plants grown from seed flown in space.

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