Plant Reproduction in Spaceflight Environments

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ABSTRACT

Because plant reproduction is a complex developmental process there are many possible sites of perturbation by the unusual environments of orbital spacecraft. Previous long-duration experiments on Soviet platforms shared features of slowed development through the vegetative stage of plant growth and aborted reproductive function. Our goal has been to understand how special features of the spaceflight environment impact physiological function and reproductive development. In a series of short-duration experiments in the Shuttle mid-deck we studied early reproductive development in *Arabidopsis thaliana*. Pollen and ovule development aborted at an early stage in the first experiment on STS-54 which utilized closed plant growth chambers. Post-flight analysis suggested that the plants may have been carbon dioxide limited. Subsequent experiments utilized carbon dioxide enrichment (on STS-51) and cabin air flow-through with an air exchange system (on STS-68). Both modifications allowed pollen and ovule development to occur normally on orbit, and full reproductive development up to the stage of an immature seed occurred on STS-68. However, analysis of plant roots from these experiments demonstrated a limitation in rootzone aeration in the spaceflight material that was not mitigated by these procedures.

In the future, additional resources (crew time, upgraded flight hardware, and special platforms) will invite more elaborate, long-duration experimentation. On the ISS, a variable speed centrifuge and upgraded plant habitats will permit detailed experiments on the role of gravity in shaping the plant micro-environment, and what influence this plays during reproduction.

INTRODUCTION

Historically, three broad goals have contributed to the presence of plants on orbital platforms: the use of plants as a psychological support for crew members; the desire to use plants in bioregenerative life support systems for long duration missions in the future; and the drive to understand the role of gravity in shaping basic life processes. Because of the extensive ground-based experiments dealing with gravity sensing and response mechanisms in plants, many previous spaceflight experiments have looked at the behavior of these gravity sensing systems (Johnson and Tibbitts 1968; Volkman et al. 1986). Currently interest is broadening to examine and understand changes in basic physiological functions of plants that may occur during microgravity, and how these may impact developmental processes such as growth and reproduction.

For over a decade, researchers have been unable to confirm any specific role for gravity in plant reproduction because of general problems in growing plants in microgravity. The plant growth over extended periods that is necessary for reproduction to occur was not possible, and plants frequently died in the transition from vegetative to reproductive stage (Halstead and Dutcher 1984, 1987; Nechitailo and Mashinsky 1993). *Arabidopsis thaliana* has been the most successfully studied species in this research area (Table I) because its compact size, low light requirement and short life cycle (Figure 1) make it amenable to experimentation in the small growth chambers that have been developed for use on orbital platforms (Krikorian and Levine 1991).

Several attempts to grow plants through a complete life cycle in space were unsuccessful because of delayed development (Kordyum et al. 1983; Mashinsky et al. 1994). Partial or total sterility of the reproductive material that eventually did develop has been observed in *Arabidopsis* (Kordyum et al. 1983; Merkys and Laurinavichius 1983). Even when *Arabidopsis* plants were pregrown to the flowering stage on earth and allowed to form seeds on orbit, only 55% were fertile (27% aborted; 18% had non-viable embryos) (Parfenov and Abramova 1981).

The only successful complete plant life cycle in microgravity to date was achieved in 1983 with *Arabidopsis thaliana* on board Salyut 7 in a miniature plant growth chamber called Phyton 3. The plants had grown from seed planted on orbit, and although development was delayed, they flowered and produced new seed. However, reports on the returned material described a large proportion of empty seed, and a high number of embryonic lethals in the seeds that were produced in space (Merkys and Laurinavicius 1983) relative to the ground controls. Currently an experiment in the Svet greenhouse on the Mir station shows promise that a full life cycle may have been completed in wheat as well (Salisbury et al., 1995).

These previous studies on plant reproduction in space have been summarized in Table I to highlight differences in plant material and ventilation capability of the plant growth hardware. [Sporadic flower formation also occurred in the PGU, equipped with an air exchange system, on STS-29 during an experiment designed to study spaceflight effects on chromosomes using aseptically cultivated plantlets of *Haplopappus gracilis* (Nutt.) (Levine et al. 1990).] Eight different types of flight hardware have been used to grow plants in space for studies on plant reproduction, and taking into account

Table I. Experiments on Plant Reproduction during Spaceflight.

Seeds	Reference	Plant	Chamber	Ventilation	Flowers
		Pre-grown Plants			
		Dicotyledons			
Arabidopsis	[1](Kosmos 1129)	open	+	+	Parfenov and Abramova 1981
	PGU/STS-54	closed	+	−	Kuang et al. 1995
	PGU/STS-51	closed+CO_2	+	−	Kuang et al. 1996a
	PGU/STS-68	active	+	+	Kuang et al. 1996b
		Monocotyledons			
Epidendrum	Malachite (Salyut 6)	open	−[2]	−	Nechitailo and Mashinsky 1993
		Seeds			
		Dicotyledons			
Arabidopsis	Svetoblok (Salyut 6)	closed	+	−	Kordyum et al. 1983
	Phyton (Salyut 7)	passive	+	+	Merkys and Laurinavicius 1983
Pisum	Oasis (Salyut 6)	open	−	−	Nechitailo and Mashinsky 1993
		Monocotyledons			
Triticum	Svetoblok M (Mir)	passive	+	−	Mashinsky et al. 1994
	Svet (Mir)	open w/fan	+	?[3]	Salisbury et al. 1995

These studies have utilized a variety of plant materials and growth chambers. The results of these experiments have been reviewed elsewhere (Halstead and Dutcher 1984; 1987; Musgrave et al. 1997; Nechitailo and Mashinsky 1993).
[1]plexiglas beaker containing moist soil
[2]plants were taken to the Salyut station in blossom but no more flowers were formed on orbit
[3]material is still on orbit

different configurations of hardware to provide variation in ventilation, the number rises to ten. Although vegetative development was generally delayed, flowering occurred in 80% of the hardware configurations. Seed production has occurred in space in only 30% of the spaceflight growth chamber types and with the exception of the experiment in the PGU described below, the seed production was diminished when compared to material on the ground. This means that in the majority of cases hardware that has been engineered to support plants during the reproductive stage of growth and does so in 1-*g* has not been successful in microgravity. Of the six experiments described in Table I using *Arabidopsis*, the three in which set seed occurred all had some type of ventilation with outside cabin air. Additional details on the hardware that has been used for experiments on plant reproduction may be found in a recent review by Porterfield et al. (1997).

REPRODUCTIVE DEVELOPMENT IN *ARABIDOPSIS* IN THE PGU

When we began to study spaceflight effects on reproductive development in *Arabidopsis*, we chose to work with pre-grown plants because of the large body of literature that indicated that vegetative development was often retarded during growth in microgravity. *Arabidopsis* takes about 45 days to complete a full life cycle. For experiments in the PGU, plants were pre-grown on an agarified nutrient medium that had been developed for use on Biosatellite (Brown et al. 1976) and were 13 days old at the time of launch. During the subsequent time on orbit, flower buds appeared and early events in reproductive development occurred (Figure 2A). In this system,

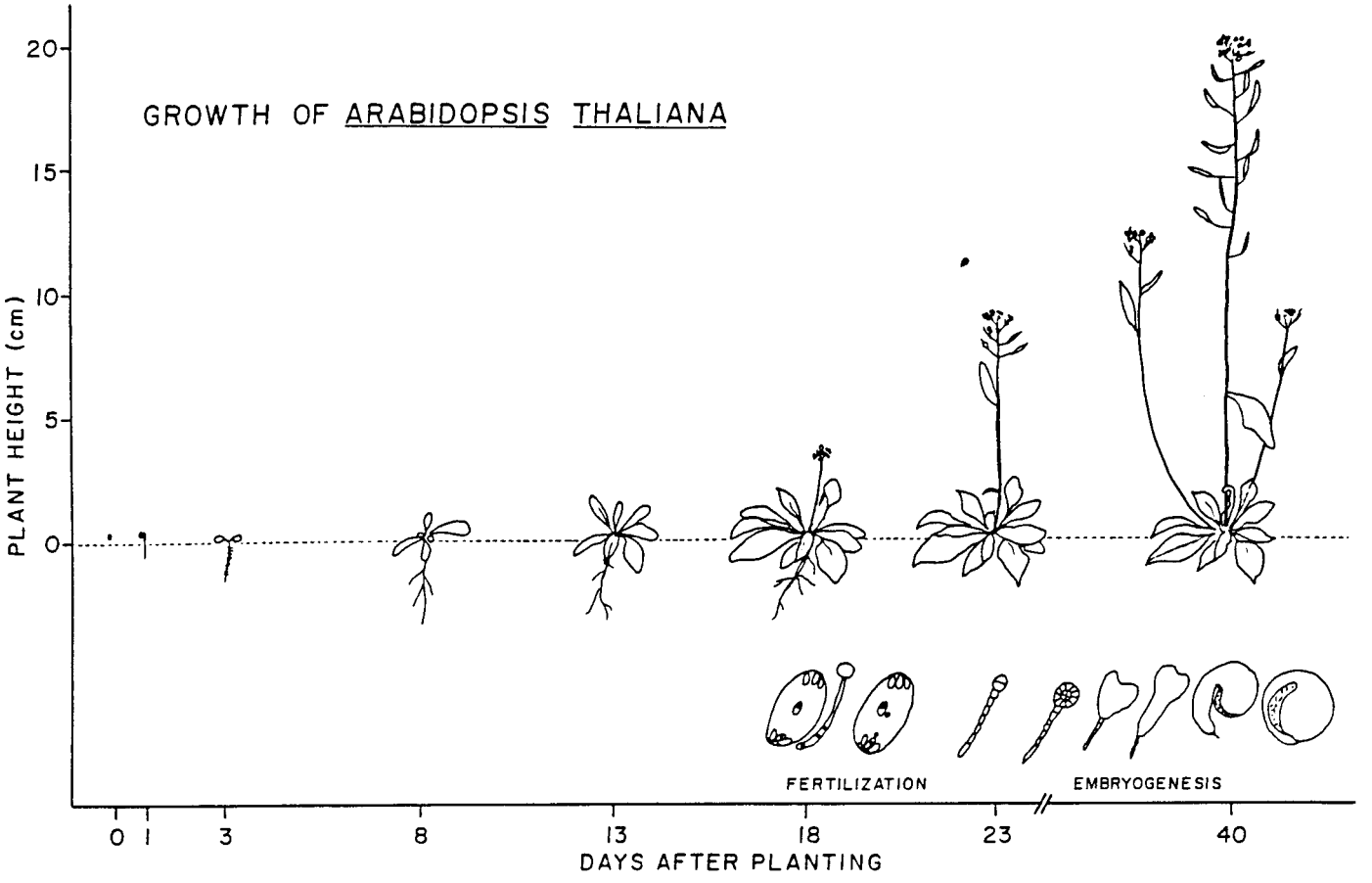

Figure 1. Life Cycle of *Arabidopsis thaliana*. *Inset diagrams (not to scale) show events occurring inside the embryo sac during the time period indicated: growth of pollen tube into the embryo sac to effect fertilization, events in early embryogenesis and maturation.*

even during short duration shuttle flights it is possible to study spaceflight effects on the complex processes of mitosis, meiosis, cell division, tip growth of cells, tissue differentiation and organ formation (Figure 1, inset).

In our three experiments with the PGU, plants developed at the same rate in spaceflight and ground control, and initiated the same number of flowers. Approximately 500 flowers were available from each experiment (Musgrave et al., 1997). The differences in success of subsequent reproductive development in microgravity were related to variations in the gas phase of the plant growth hardware as described below.

In Chromex-03 on STS-54, growth chambers were closed, and reproductive development aborted at an early stage in both the male and female tissues of the spaceflight material. Pistils were collapsed and the ovules inside were empty. No viable pollen was observed using a functional test (Heslop-Harrison et al. 1984), and young microspores were deformed and empty (Kuang et al., 1995). Analysis of foliage indicated that the spaceflight material had significantly lower carbohydrate levels than the ground controls (Brown et al., 1993). Flowering and seed production are known to be hindered by insufficient carbon reserves in the plant. Thus we hypothesized that the failure in reproductive development in this case was attributable to some limitation on the whole plant physiological performance rather than on the reproductive apparatus *per se*.

Supplementation of the gas phase of the closed plant growth chambers with high carbon dioxide (8,000 ppm) in Chromex-04 (STS-51) overcame this early abortion, and material developed normally (Figure 2) up through the stage of mature pollen and embryo sacs. Pollen was viable and well-formed, although a film-like substance inside the tapetum appeared to restrict the release of pollen from the anthers (Kuang et al. 1996a). Fertilization did not occur in this material and scanning EM analysis of stigmatic surfaces postflight revealed that no pollen had been transferred from the anthers to the stigmatic papillae (Figure 2C).

In Chromex-05 on STS-68, an air exchange system provided a flow of filtered cabin air through the plant growth chambers, and development proceeded normally on orbit through the stage of immature seeds (Figure 3). These seeds have been found to be comparable to those produced in the ground control material in their

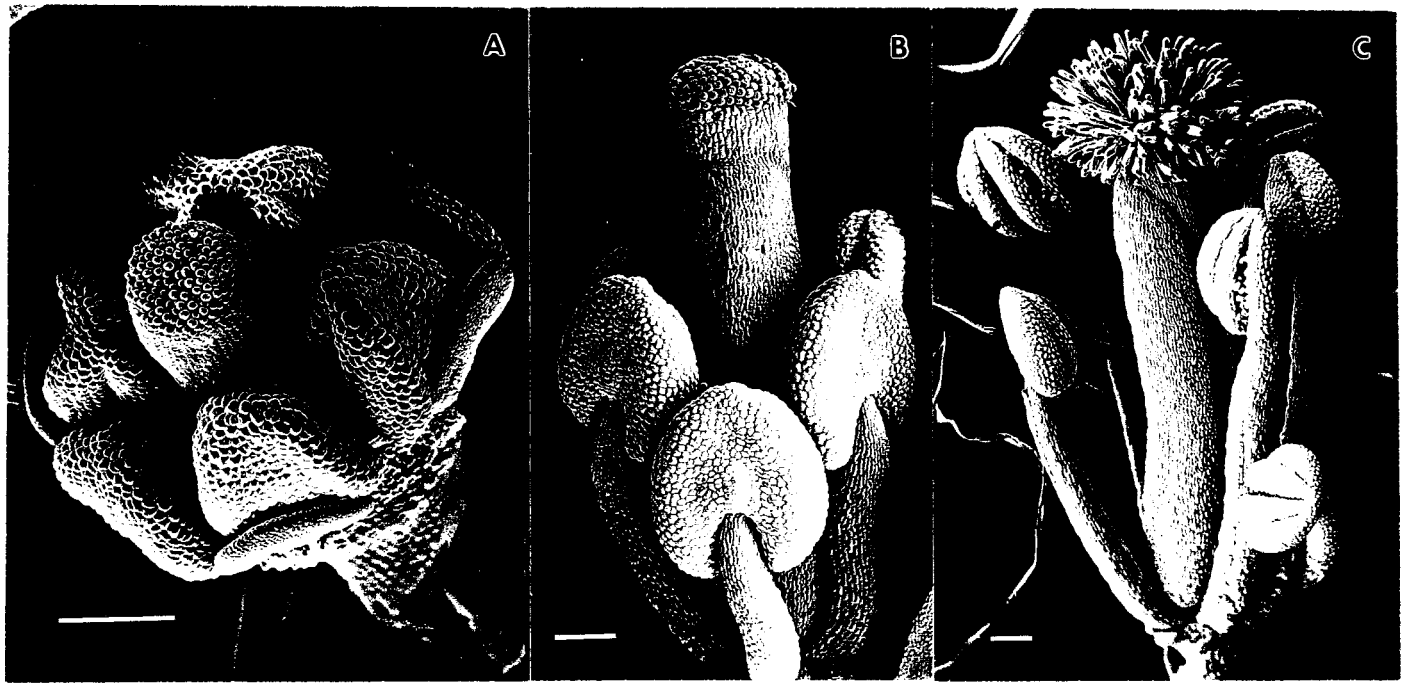

Figure 2 (A,B,C). Early Reproductive Development in *Arabidopsis thaliana*. *Development was successful when plants were provided with supplemental carbon dioxide in closed plant growth chambers or with a continuous supply of air flowing through the chambers. A. developing anthers and pistil in a 0.5 mm bud (sepals have been removed); B. further maturation of the male and female reproductive tissues from a 1.5 mm bud (petals and sepals have been removed); C. anthers have dehisced, and pollen grains are visible in this opening flower (petals and sepals have been removed). Stigmatic papillae are ready to receive the pollen. SEMs by Dr. Sharon W. Matthews, Louisiana State University. Bar = 100 microns.*

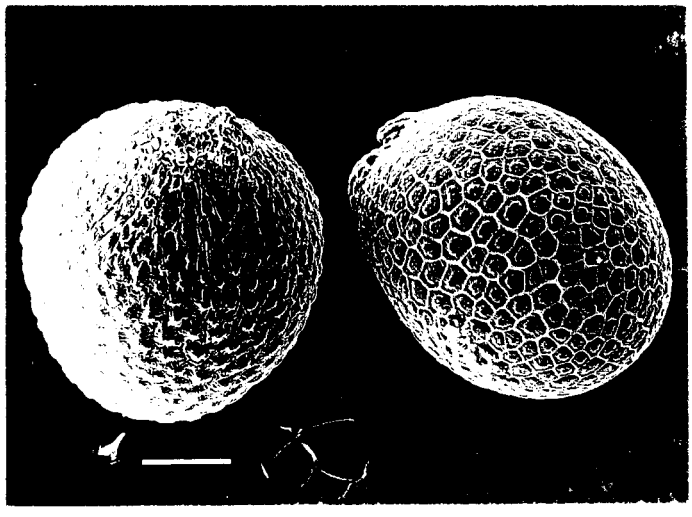

Figure 3. SEM of developing seeds of *Arabidopsis thaliana* dissected from a 7 mm silique from the Chromex-05 experiment on STS-68. *Photo by Dr. Sharon W. Matthews, Louisiana State University. Bar = 100 microns.*

morphology and size (Kuang et al. 1996b). The oldest seeds from these plants contained completely developed embryos with seed coats. Tissue development included radicle, hypocotyl, meristematic apical tissue, and differentiated cotyledons. Protoderm, procambium, and primary ground tissue had differentiated in these embryos. Starch and protein reserves were deposited in the embryos during tissue differentiation in a manner quantitatively and qualitatively similar to the ground control (Kuang et al., 1996b). This is the first instance in which seed development in microgravity has been found to be completely comparable to that in ground controls.

THE PLANT MICROENVIRONMENT IN MICROGRAVITY

This opportunity to perform a series of spaceflight experiments and change variables incrementally as one would in a laboratory experiment has provided us with unique insight into the importance of metabolic components of the gas phase for normal reproductive development. In our first experiment with closed plant growth chambers in the PGU the abortion of reproductive development was analogous to that in a previous report using Svetoblok (Kordyum et al., 1983). However when we used closed chambers supplemented with high carbon

dioxide, pollen and embryo sacs were indistinguishable from the ground control. The obstacle to seed formation in this experiment was apparently lack of pollen release from the anthers. The results have been especially intriguing because they imply the existence of stagnant air zones in microgravity that lead to a shortage of carbon dioxide and excess of water vapor around the plant. Deficiency in carbon dioxide resupply would limit photosynthesis and subsequently result in the reduction in carbon reserves that was observed in the spaceflight material in STS-54 (Brown et al. 1993). Flow through of cabin air was necessary to permit the full reproductive sequence to occur on orbit on STS-68 while both of the previously tried hardware configurations using closed chambers were sufficient to support reproductive development in 1-*g*.

As more experiments are conducted in microgravity, the body of circumstantial evidence is building that growth hardware is not providing the intended environment for plants when used in a microgravity setting. This has been investigated quantitatively for the parameter of the ability of growth media to supply oxygen to root systems. Using alcohol dehydrogenase activity as an indicator of the extent of root hypoxia, our laboratory has shown that the agarified plant growth medium used to grow *Arabidopsis* in STS-54 and STS-68 provided 28% less oxygen to plant roots in microgravity than in 1-*g* (Porterfield et al. 1995). Researchers working with porous substrates in the Svet greenhouse on Mir space station have estimated that the amount of water held in microgravity when a substrate is saturated is 2.5X that in 1-*g* because pore spaces can continue to fill with water in microgravity (Bingham et al. 1996). Refurbishment of the Svet hardware to include moisture sensors distributed throughout the granular matrix of the root module has made possible better control of rootzone moisture (Bingham et al. 1995) and is probably the main reason why Svet is now able to grow plants successfully over long durations. The ability to monitor and control the plant microenvironment in microgravity is crucial to the success and validity of future spaceflight experiments with plants.

Toward this end we have recently begun to investigate the gaseous microenvironment inside developing reproductive structures in *Arabidopsis*. Previous work had indicated that low oxygen availability would completely eliminate seed development. For crop species such as soybean and sorghum, this occurs at 5% oxygen, however our lab has determined that a lower oxygen concentration (2.5%) is required to eliminate seed production in *Arabidopsis* (Crispi et al. 1997), perhaps due to differences in size and diffusion distance in the species. *In ovulo* oxygen concentrations are known to be lower than prevailing oxygen because of the respiratory demands of the developing embryo and the oxygen resupply rate (Hess and Carman 1993). In *Arabidopsis* we used oxygen microelectrodes to measure oxygen content of the gas

Table II. Oxygen concentrations at the surface and inside the locule of *Arabidopsis* siliques in the dark or light (4.27 W cm^{-2}).

	Oxygen concentration (%)	
Location	Dark	Light
Silique surface	20.8±0.3	20.5±0.2
Inside locule of silique	6.8±2.1	12.8±1.4

Mean values ± SD.

inside of developing siliques (Table II). In the dark, oxygen content inside the silique was less than a third of the external concentration. In the light, oxygen content within the small green silique is almost two-thirds the ambient level due to photosynthetic contributions of oxygen to the locule space. How will microgravity features such as lack of convective air movement and increased water-holding capacities of matrices affect such delicately balanced microenvironments inside the plant? The challenge of providing appropriate levels of oxygen and carbon dioxide to plant tissues in microgravity is a difficult one. Even more enigmatic, however, is the problem of conducting a meaningful ground control for microgravity experiments when the physical environment around the plant changes in ways that cannot be mimicked in 1-*g*. These questions must be addressed if we hope to be able to carry out experimentation on the gravity dependent processes going on inside cells (Todd 1989).

PROSPECTS FOR FUTURE EXPERIMENTS ON ISS

Currently joint US-Russian experiments on full plant life cycles in space are underway on the Mir space station using the upgraded Svet greenhouse (Salisbury et al. 1995). On the ISS, newly designed plant habitats will be available for stationary use or rotating in the Centrifuge Facility to provide variable *g*-levels to plants on orbit. Each plant habitat will occupy about twice the volume of the PGU and will provide enhanced capabilities for plant research in addition to greater numbers of independent units that can be used simultaneously on or off the centrifuge (Table III).

Although the original goal of having the habitat centrifuge on ISS was to provide a 1-*g* centrifuge control for spaceflight experiments, thereby distinguishing between microgravity and other spaceflight effects, a far more important scientific contribution of this facility will be found in elucidating microgravity effects on plant microenvironment through studies at fractional *g*-levels. An excellent use for the onboard centrifuge will be to use

Table III. Comparison of attributes of the PGU flight hardware that was used to conduct the experiments on plant reproduction reviewed here, and plant growth hardware that will be available in the future on ISS.

Characteristic	PGU[1]	ISS Plant Growth Hardware
gravity level	no inflight control possible	0 - 2.0 *g* (on 2.5 m centrifuge)
habitats on orbit	1	up to 8
subchambers	6 (or 5 with AES)	1 large to 6 small
specimen size	21 cm total height, root + shoot	38 cm total height, root + shoot
lighting	fluorescent 30-75 μmol/m^2/sec	fluorescent 180-600 μmol/m^2/sec, or LED 0-1000 μmol/m^2/sec
nutrient delivery	selectable[2]; foam, agar	selectable[3]; MPNE, Astroculture, Feed-On-Demand
temperature	heating (2°C above ambient and up)	cooling and heating (20-30°C)
atmosphere	gas sampling ports allow sampling replacement possible with AES	monitoring of CO_2 and humidity CO_2 control (300-2000 $\pm$ 50 ppm) humidity control (60-90 $\pm$5%) ethylene degradation unit ($<$ 5 ppb)
image recording	only pre- and post-flight	video imaging *in situ*
sample accessibility	only pre- and post-flight	subchambers easily opened on orbit

[1]as used for Chromex-03, Chromex-04 and Chromex-05 on STS-54, STS-51 and STS-68
[2]for examples see Cowles et al. 1984; Levine and Krikorian 1992; Porterfield et al. 1995
[3]for examples see Dreschel et al. 1994; Morrow et al. 1995; Levine et al. 1995

a battery of sensors to determine the gravity response curve for the various physical features that define the plant microenvironment. Coupled with "reporter" information such as the ADH experiment described earlier in which a physiological function of the plant tells us about the actual environmental conditions being experienced at fractional *g*-levels, these data will go far in clarifying whether metabolic changes occurring in microgravity are in fact consequences of an altered plant microenvironment. These studies at fractional *g*-levels will also have applicability to the biological life support research aimed at developing methodology for plant growth on planetary and lunar surfaces (Olson et al. 1988).

In addition, because the growth space within the chambers is greater and has more flexibility in control level for light, humidity, carbon dioxide and nutrient delivery technologies, more species should be able to be accommodated, allowing us to expand the list of plant materials in Table I. The long-duration capabilities of these habitats will allow multiple generations of plant growth, and a crucial question to be answered in this venue is how spaceflight and microgravity in particular may impinge on the genome over time (Krikorian, 1997). The advent of the new facilities on ISS will usher in a new way of doing experiments about spaceflight effects on plant reproduction in which the possibility for iterative work will free us from having to draw conclusions based on differences from ground controls. Instead, a body of experimentation on the ISS should grow to be self-referencing as results from changes in parameters on orbit permit us to understand plant microenvironments in microgravity.

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