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Literature Study: Transport of water and solutes

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1. Introduction

Healthy growth and development of higher plants rely on an adequate availability and uptake of water and nutrients, as well as an efficient distribution of energy in the form of carbohydrates. Determination of the factors affecting the efficiency of processes that include absorption, transportation and distribution of these constituents in spaceflight is crucial for successful cultivation.

The long distance transport of water and solutes (mineral elements, organic acids, sugars and amino acids) takes place in the vascular systems (xylem and phloem), predominantly in the xylem. In general, solute flow in the xylem is unidirectional, while transport in the phloem is bidirectional (Marschner, 1995).

2. Scope of the Plant Sublevel

The following topics will be discussed:

- Water transport within the plant
- Mineral nutrition; uptake and transport of mineral nutrients
- Carbohydrate partitioning and translocation

Focus will be on potential effects of the physical factors **space radiation, varying gravity, magnetic field** and eventual **combined effects** of these factors.

For information on the particular conditions found on the Moon and Mars, see CEAS paper ”Literature Study of Higher Plants in Space for MELiSSA (LiRHiPliSME)- Input to MELiSSA Phase II project” (Kittang *et al.,* 2009).

The experimental effects are discussed under the assumption that here was an optimal control of temperature, light, pressure (1 atm), water and gas supply/composition; also optimal root support and availability of water and nutrients was assumed.

3. Transport within the plant

3.1 Water transport

For each gram of organic matter made by plants on Earth, approximately 500g of water is absorbed by the roots, transported through the plant body and lost to the atmosphere by evaporation from the plant surfaces in the transpiration process. The rate of water flux across the root (short-distance transport) and transport in the xylem vessels (long-distance transport) are determined by root pressure and transpiration (Taiz and Zeiger, 2002). As the permeability of plant membranes is much higher for water than for ions, the active uptake of ions and release into the xylem induce a passive net flux of water from the external solution into the root. This increase in hydrostatic pressure induces a mass flow of water and solutes in the xylem towards the shoot (root pressure). The major driving force for transpiration from leaves is the difference in water vapour concentration between leaf air spaces and the external air, which creates a negative pressure or tension in the xylem, thereby pulling the water towards the shoot (Taiz and Zeiger, 2002; Marschner, 1995). Water typically constitutes 80-95% of the mass of growing plant tissues, and even slight imbalances in the flow of water can cause water deficits and severe malfunctioning of many cellular processes (Taiz and Zeiger, 2002). As a solvent, water makes up the medium for movement of molecules within and between cells and greatly influences the structure of proteins, nucleic acids, polysaccharides, as well as other cell components. Another important role of water is dissipation of heat absorbed by irradiation. Balancing of the uptake and loss of water is a serious challenge for land plants, and even a greater challenge for plants in space.

Water uptake by roots involves a passive transfer of water along a water potential gradient from the soil into the root. Water taken up by the entire root system forms the transpiration stream and is driven somewhat by root pressure but primarily by water loss from leaves (transpiration). Water can enter the roots via root hairs and between epidermal cells. Once taken up through the roots, water is transported to stems and leaves through the xylem vessels. Water uptake patterns vary both diurnally, seasonally and with different stages of plant growth (Adiku, 2008). It has been shown in some cases that the plant can alter transpiration when nutrients or water is limiting, but whether the plant has any direct influence on or active mechanisms for water uptake requires further research (Adiku, 2008).

3.2 Plant nutrition

All aspects of plant growth depend on an adequate supply and uptake of nutrients. Only 19 elements are determined to be essential for plant growth. Hydrogen, oxygen and carbon are taken up through water and carbon dioxide, while the remaining 16 have to be taken up from the soil.

Essential elements are elements whose absence prevents a plant from completing its life cycle or that have a clear physiological role.

- Macronutrients

N, P, Ca, Mg, K, S, Si

- Micronutrients

Cl, Fe, B, Mn, Na, Zn, Cu, Ni, Mo

As opposed to water uptake, which is assumed to be passive along gradients in water potential, the uptake of nutrients is active and preferential. Research on plant nutrition has demonstrated that ion uptake in plants is

1. Selective; some ions are taken up preferentially while others are excluded.
2. Accumulative; the concentration of mineral nutrients can be much higher in the plant cell sap than in the external solution.
3. Genotypic; distinct differences in ion uptake characteristics exist among plant species.

The diversity of mechanisms involved in plant nutrition is described in Figure 1.

Nutrient translocation in aerial plant parts

Long distance transport of elements from roots to shoots typically occurs in the nonliving xylem vessels and is thus driven by transpiration. Though transpiration stream is not essential for mineral transport, transpiration supports water uptake and transport, and some elements like calcium and boron are especially sensitive to the rate of transpiration (Salisbury and Ross, 1992). Indeed, several physiological disorders, such as the marginal apex necrosis of developing leaves in leafy crops like lettuce, occur when Ca become deficient due to reduced transpiration (Barta and Tibbit, 2000). Thus, a limitation of transpiration can result in a limited nutrient transport and a possible accumulation of

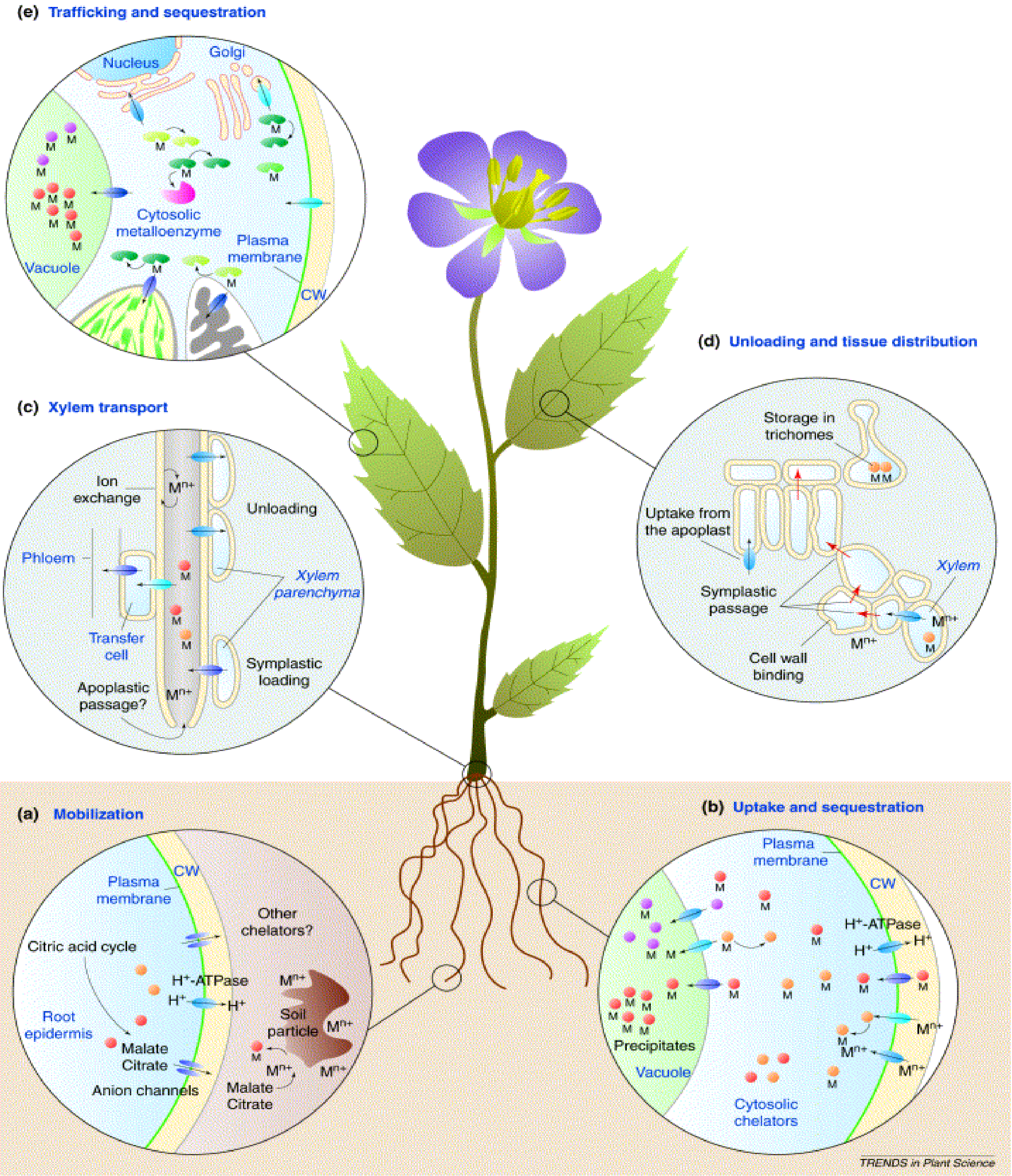

Figure 1. Mechanisms involved in plant nutrition (from Clemens *et al*., 2002)

nutrients in root cells and a limited nutrient uptake. Good correlation has been found between transpiration and nutrient uptake dynamics (Novak *et al.*, 2003).

Whether or not transpiration affects uptake and translocation rates of nutrients depends predominately on the following factors:

- Plant age (developed leaves)
- Light or dark period (stomata opening)
- External concentration (translocation rates are usually more affected by transpiration than uptake rates)
- Type of mineral element
  - uncharged molecules are more affected than ions

An overview of the effect of transpiration on uptake and translocation of sodium and potassium in sugar beet plants is presented in Table 1. Numbers in the table show that potassium uptake and translocation rates do not depend on transpiration, while sodium uptake and translocation rates are affected by transpiration level.

Table 1. Effect of transpiration rate of sugar beet plants on uptake and translocation of potassium and sodium from different nutrient solutions (Marschner, 1995).

External concentration (nM)	**Potassium**		**Sodium**	
	Low transpiration	**High transpiration**	**Low transpiration**	**High transpiration**
Uptake rate (µmol per plant $(4h)^{-1}$)				
$1K^+ + 1Na^+$	4.6	4.9	8.4	11.2
$10K^+ + 10Na^+$	10.3	11.0	12.0	19.1
Translocation rate (µmol per plant $(4h)^{-1}$)				
$1K^+ + 1Na^+$	2.9	3.0	2.0	3.9
$10K^+ + 10Na^+$	6.5	7.0	3.4	8.1

Some inorganic solutes, including potassium, magnesium, phosphate and chloride, can also move in the phloem (Taiz and Zeiger, 2002). Transfer of solutes can also occur between the xylem and the phloem, and this transfer is important because xylem transport is directed mainly to the organs of highest transpiration, which are not necessarily the sites of highest nutrient demand (Marschner, 1995).

Nutrients with high phloem mobility include potassium, magnesium, phosphor and nitrogen, the latter as amino-N. Nutrients with low phloem mobility (mainly transported in the xylem) include calcium and manganese, while iron, zinc, copper, boron and molybdenum have intermediate phloem mobility (Marschner, 1995).

Nutrient uptake and transport in the root

Transport in roots can occur via three known mechanisms:

- Transport driven by concentration gradients, causing nutrient movement by diffusion and supported by electrochemical gradients (Hopman and Bristow, 2002)
- Mass transport of nutrients dissolved in water (advection). Computed from the product of nutrient concentration and water flux density.
- Active uptake through ion channels and transport proteins.

3.3 Carbohydrate partitioning and translocation

Translocation is the movement of photosynthates (sugars) through the phloem from the source, i.e. mature leaves to other plant parts, sinks, such as fruit, roots and immature leaves for growth or storage. Rate of translocation is dependent on the rate of photosynthesis and sink strength. When photosynthesis is decreased, it decreases the amount of photosynthate exported from leaves. However, plants are able to continue translocation even after photosynthesis has been strongly inhibited until a general stress response prevails.

Photosynthate allocation is the controlled distribution of fixed carbon quantities into various metabolic pathways. Fixed carbon can be stored (starch), metabolised within the cells of the source or immediately transported to sink tissues.

Photosynthate partitioning is the differential distribution of photosynthates in the whole plant. Partitioning determines the quantities of fixed carbon delivered to different sink tissues and therefore the pattern of growth. The growth must be balanced between shoot growth (photosynthetic productivity) and root growth (water and mineral uptake).

Photosynthate translocation, allocation and partitioning are areas of great interest because of their key role in crop productivity. Carbohydrate content in roots can correlate with the uptake of ions, e.g. reduced potassium uptake under the condition of limited carbohydrate supply from a source (leaves). Nitrogen uptake may also decrease with depletion of carbohydrate content (Taiz and Zeiger, 2002).

Early space experiments with plants often showed decreased amyloplast starch reserves, which is an indication of root exposure to a hypoxic environment (Porterfield, 2002).

4. Microgravity effects on transport of water and solutes

4.1 Factors affecting transpiration

Because of the transpiration-driven transport of water and solutes in the xylem, factors affecting transpiration have an effect on transport, too. Physical phenomena influenced by gravity that affect transpiration include buoyancy driven thermal convection (BDTC), boundary layer thickness, stomatal resistance (Porterfield, 2002) and atmospheric pressure (Rygalov *et al*., 2002).

Buoyancy Driven Thermal Convection

In the presence of gravity, buoyancy driven thermal convection (BDTC) induces mass movements and flow in the media surrounding the plant (Liao *et al.*, 2004). Unless there is some forced flow or movement in these gases and fluids, mass transport and exchange of small molecules as ions, gases and water between the plant tissues and the environment become diffusion limited. In space, due to the lack of BDTC, diffusion limits transport and gas exchange in higher plants. In this way, transpiration and water uptake can be restricted, and consequently uptake of nutrients via the transpiration stream is affected. Diffusion limitation occurs both in roots and aerial plant parts, but is generally higher in the aerial environment as the thermal conductivity and viscosity of the media are much lower (Porterfield, 2002).

Kitaya (2005) investigated effects of air velocities on photosynthesis, transpiration and water use efficiency of a plant canopy and plant leaves of cucumber seedlings. His studies showed that the transpiration rate of the canopy was increased 2.8 times by increasing the air velocity from 0.02 to 1.3 m s^{-1} (Kitaya, 2005). The increase in wind speed and transpiration, however, did not give an equivalent increase in photosynthesis and thus lowered the water use efficiency of the canopy (Kitaya, 2005).

Boundary layer thickness

At the leaf surface there is an unstirred boundary layer, limiting gas exchange to diffusion from the leaf. The size of this layer is increased with declining BDTC, and dominantly controlled by air velocity (Kitaya, 2005; Porterfield, 2002). In a closed system and reduced gravity environment, with decreased BDTC and air movement, boundary layer thickness is increased and consequently reduces transpiration, respiration and heat dissipation from the plant surface (Figure 2). In addition, various anatomical and

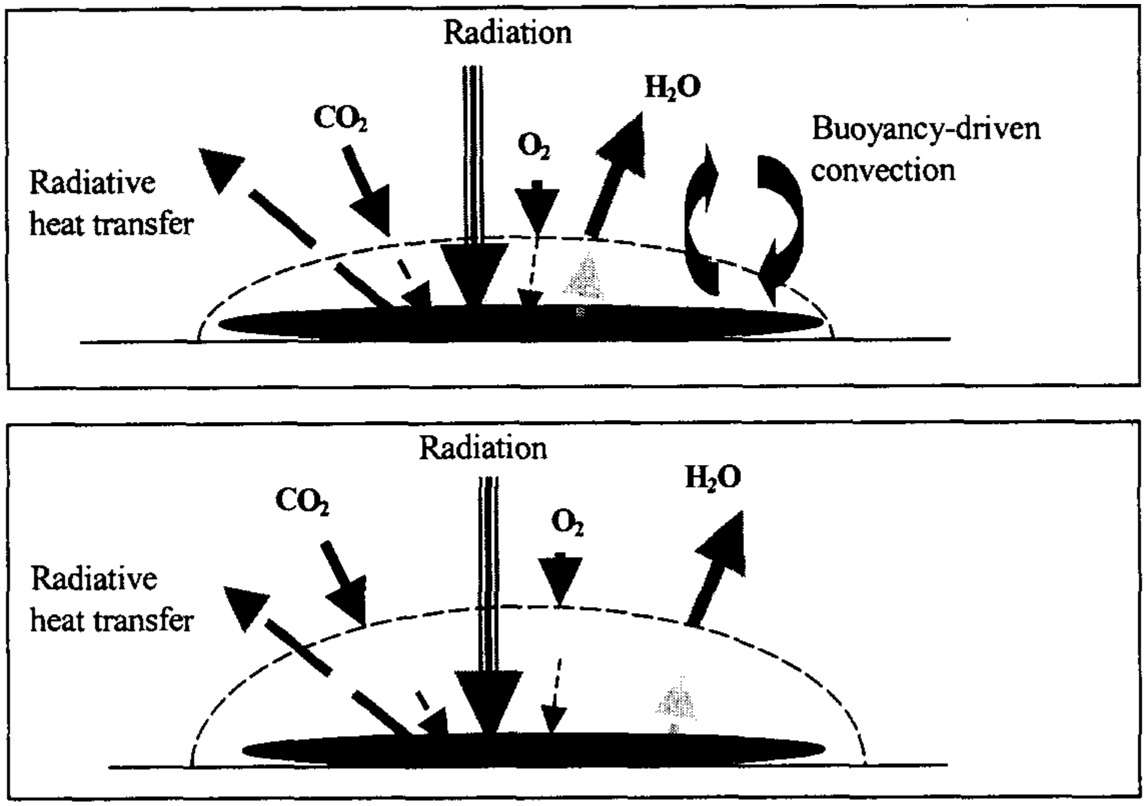

Figure 2. On Earth (l-g, top) boundary layers around plant organs are smaller than in microgravity (bottom) because of buoyancy-driven convective mixing. At 1g, the boundary layers are thin enough so that metabolic processes like respiration and transpiration are rarely diffusion-limited (Monje *et al.*, 2003).

morphological features, as for example hairs on the leaf surface, can influence the thickness of the boundary layer.

In a study performed by Kitaya *et al.* (2003), leaf temperatures were measured at different gravity levels and coupled to transpiration. The measurements were carried out at an air temperature of 25°, a relative humidity of 40% and an air velocity of 0.2 m s^{-1}. Their studies showed that mean leaf temperatures increased by 0.9-1.0°C by decreasing the gravity level from 1.0 to 0.01 g for 20 seconds (Kitaya *et al.,* 2003). The order of temperature increase in different leaves corresponded to the order of reduction in potential transpiration rates, so the increase in surface temperatures was attributed to suppressed convective heat transfer caused by reduced gravity resulting in decreased evapotranspiration (Kitaya *et al.,* 2003).

Annual average airflow values on Earth range from 1-7 m s^{-1}, depending on geographical situation (Porterfield, 2002). Plants grown in closed chambers typically experience airflows below 0.5 m s^{-1}, and the biophysical limitations in physiological transport resulting from a diffusion limited boundary layer could be significant (Porterfield, 2002). In an experiment to assess microgravity effects on plant boundary layers, Stutte and Monje (2004) measured the boundary layer as temperature differences in wicks at various wind speeds. They concluded that the boundary layer is greater under 0g conditions than either 1g or 2g conditions, and that the effects of air velocity on boundary layer were less in 0g than 1g for both wet and dry surfaces. The observed effects of 0g, however, could be mitigated by air velocitiesfor wheat seedlings higher than 0.4 m s^{-1} (Stutte and Monje, 2004). For larger leaves of cucumber Kitaya (2005) reported a steadily increasing transpiration rate in leaves with increasing wind velocities from 0.02 to 1.3 m s^{-1} under 1g conditions (see Figure 3). The effects of air velocity were more significant in a plant canopy than in a single leaf, because of the reduction of air velocity inside a canopy (Kitaya, 2005). Also Porterfield (2002) concluded that boundary layers are stable even in a significant airflow.

Information about 0-g effects on boundary layer development of monocot and dicot leaves from Stutte and Monje is going to be published. For equations and details in calculation of boundary layer thickness in relation to airflow and leaf area see Porterfield (2002).

Stomatal resistance

In the absence of a boundary layer, when wind velocity is high, the factor controlling water loss from the leaf is primarily stomatal resistance. Stomatal opening is controlled by hormones produced in plant roots, and affected by a number of environmental factors as temperature, humidity, atmospheric CO_2, light intensity and photoperiod (Webb, 2003, Kitaya, 2005, Roelfselma & Hendrich, 2005, Casson & Gray, 2008). At this point, information regarding the effect of microgravity on stomatal resistance seems to be very limited.

Kirkham (2008) attempted to measure stomatal resistance and leaf temperature in simulated microgravity with wheat plants grown in horizontal tubes. Some of the horizontal grown plants showed high stomatal resistance (>50 s cm^{-2}), but the study was of limited value due to poor root establishment and wilting of plants grown horizontally (Kirkham, 2008). Studies on plant stand gas exchange indicate that stomatal resistance is not altered under microgravity conditions (Monje *et al.*, 2005). More details on plant gas exchange can be found in TN 97.08 (WP 250).

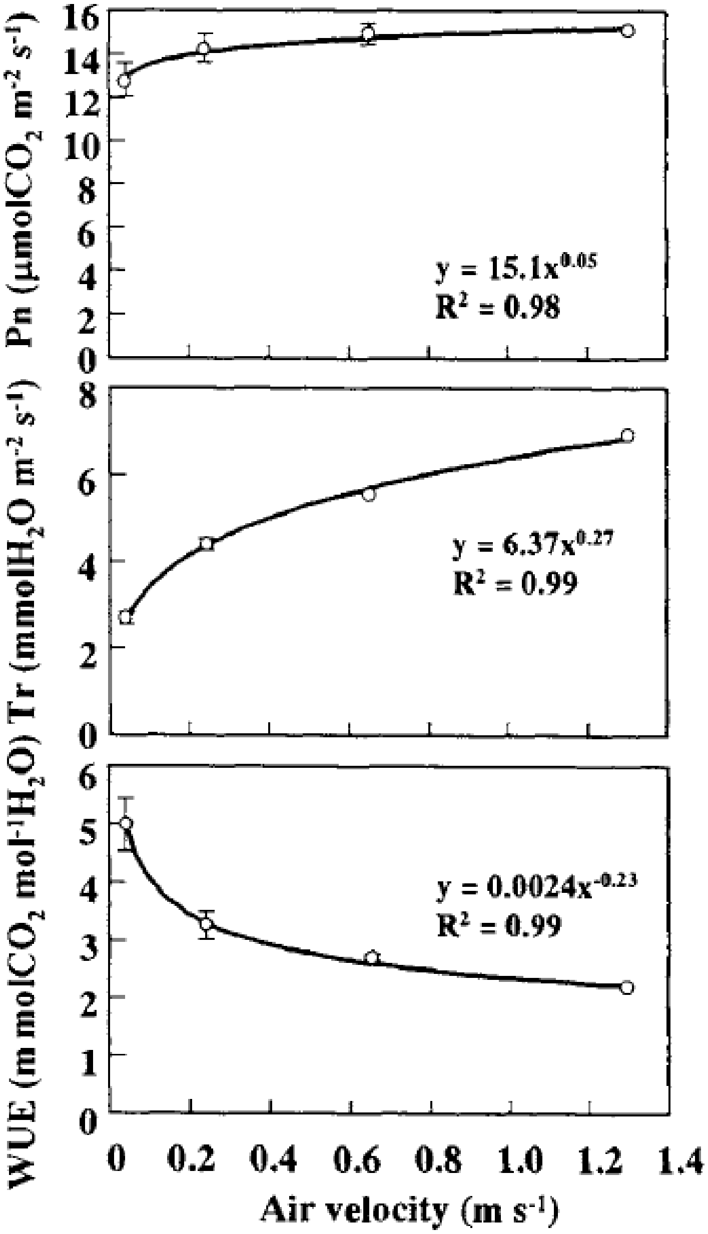

Figure 3. Effects of air velocity on photosynthesis (Pn), transpiration (Tr) and water use efficiency (WUE) of a cucumber seedling canopy (from Kitaya, 2005). The air velocity was measured 50mm above the canopy.

Unusual stomatal phenomena have also been observed at super-elevated CO_2 conditions (e.g. ≥ 5000 μmol mol^{-1}), which are common in space craft environment. Namely, stomatal resistance can actually decrease at super-elevated CO_2, and stomata can remain open at night (Wheeler *et al.*, 1999). The mechanisms behind this apparent reversal of the normal CO_2 effect on stomata is still unknown.

Diffusion

Diffusion is based on random Brownian motions of molecules, and is not gravity dependent. However, as gravity affects BDTC and consequently boundary layer thickness, gravity may have secondary effects on diffusion. Diffusion becomes the main limiting factor for gas exchange under reduced gravity conditions.

4.2 Oxygen transport

As mentioned previously, the mass flow of air and oxygen in and out of the root zone can be affected by changes in barometric pressure, temperature differences in the soil, wind, and penetration of water down into the soil (Porterfield, 2002). Larger boundary layers also form in the shoot-to-root zone when convective mixing is no longer present in microgravity (Figure 4). This essentially caps off the root zone from oxygen re-supply from the air above due to lacking turbulence. Re-supply of oxygen consumed by plant roots in microgravity would occur only through diffusion processes and roots become hypoxic (Monje *et al.*, 2003). A number of experiments have noted physiological changes in microgravity exposed roots that are consistent with hypoxia in the root zone (Liao *et al.,* 2004; Porterfield, 2002). Liao *et al.* (2004) made direct physical measurements of microgravity induced changes (inhibition) in oxygen bioavailability in a root matrix. They developed a root oxygen bioavailability sensor (ROB), simulating the relative oxygen consumption of a growing root tip. The ROB sensor was designed to measure oxygen bioavailability as opposed to concentration; the absolute oxygen concentration is not changed by microgravity (parabolic flight, see Table 3). Their results indicate that induction of alcohol dehydrogenase (ADH) in spaceflight is not part of a non-specific stress response, but is caused by spaceflight hypoxia triggered by microgravity induced biophysical limitations (Liao *et al.,* 2004). Other studies also support the theory that metabolic changes in plant roots in microgravity are caused by hypoxia associated with reduced oxygen availability in microgravity (Stout *et al.,* 2001; Porterfield *et al.*, 1997a, b; Paul *et al.,* 2001). In an experiment including a more detailed analysis of metabolism of spaceflight exposed roots, Stout *et al.* (2001) investigated plant responses at different stages of development. Mature and flower bearing plants showed a 489% increase in ADH activity, and younger more immature plants a 47% increase in ADH activity.

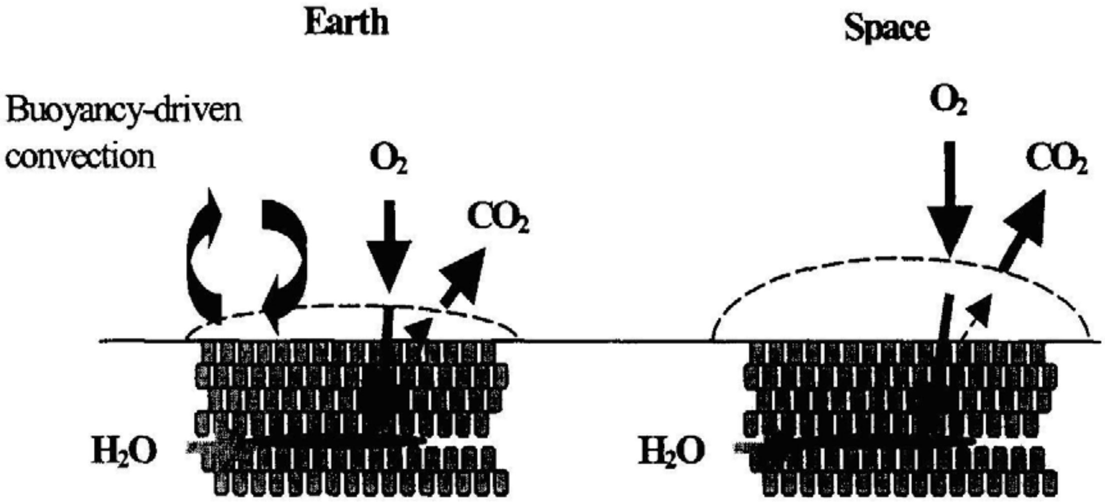

Figure 4. The lack of buoyancy driven convection in microgravity essentially caps off the root zone from 0_2 re-supply as boundary layers increase compared to 1g (Monje *et al.*, 2003).

Presumably these differences are due to a more developed root system and higher energy demands among the older plants (Stout *et al.,* 2001).

Porterfield *et al.* (2000) measured the availability of oxygen in the root zone by examining the changes in alcohol dehydrogenase (ADH) activity within the root tissue. ADH activity is a sensitive biochemical indicator of hypoxic conditions in plants. In both dwarf wheat and *Brassica rapa,* ADH activity increased significantly as a result of exposure to the spaceflight environment. These results show how important gravity-mediated physical processes are for the maintenance of normal physiological function in plants. Specifically, these results give strong evidence for that the spaceflight environment may cause a given rooting matrix to provide a lower level of root oxygenation relative to its performance on Earth (Porterfield *et al.*, 2000).

Nutrient uptake in roots can also depend on aerobic metabolism, and ion absorption can decrease as oxygen around the roots decreases. Several spaceflight studies have suggested that changes in water and gas distribution are limiting oxygen availability to the roots of space-grown plants. Plant responses to root zone hypoxia include accelerated synthesis of glycolysis and fermentative enzymes, notably alcohol dehydrogenase (Porterfield *et al.*, 2000; Stout *et al.*, 2001; Porterfield, 2002).

4.3 Space flight experiments

Russian experiments on the Salute and Mir station showed impaired plant growth in space compared to laboratory controls (Aliyev *et al.*, 1985). Chemical analyses of retrieved plant material (pea and wheat), along with clinostat experiments, link the stunted growth to nutritional issues. Flight control plants had far lower nitrogen and higher potassium levels in both stems and roots compared with ground controls. Furthermore, the levels of nitrogen and phosphorous were considerably elevated compared to aerial plant parts grown in the absence of gravity. Electrostimulation of root had significant effects on nutrient redistribution in the plants, especially the in-flight plants, and seemed to help the plant to overcome some of the micro-g induced adverse effects on nutrient uptake (Nechitailo and Gordeev, 2001). However, these results are not in accordance with studies performed by Heyenga *et al.* (2000), who compared the uptake radio nuclides calcium-45 and iron-59 between ground and flight plant material (*Catharanthus roseus)* and saw little difference, thus the work of Heyenga *et al.* (2000) indicated that the mechanisms for nutrient uptake in plants continue to function under micro-g conditions.

Levine and Krikorian (2008) found that spaceflight exposure resulted in an elevated uptake of potassium. This could have been due to either increased quantity of root tissue or a microgravity related change in uptake kinetics (Levine and Krikorian, 2008).

In a study assessing the portion of free and membrane bound calcium in plants exposed to micro-g (experiments on board the Salyut 6 orbiting station) Ca^{2+} levels in pea root cells were elevated compared to ground controls (Belyavskaya, 1996).

The space flight experiments involving plant nutritional aspects are summarised in Table 2.

Table 2. Spaceflight experiments involving plant nutrition aspects

Organism	Method, Mission/vehicle, Duration	Scope	Results	Reference
Madagascar periwinkle (*Catharanthus roseus*)	The Plant Generic Bioprocessing Apparatus (PGBA) onboard the Shuttle mission STS-94 in July 1997 (16 days)	Determination of plant nutrient uptake and distribution in space flight conditions using isotopes.	The observed response between space flight and ground control material appeared comparable	Heyenga *et al.*, 2000
Pea *(Pisum sativum),* wheat *(Triticum aestivum)*	Combination flight (Salute and Mir station, 25 days) and clinostat experiments.	To check if electrostimulation can help plants to overcome micro-g induced adverse effects on nutrient uptake.	Flight plants had lower N and K then ground controls. Electrostimulation improved significantly nutrient redistribution in the plants, especially the in-flight plants.	Nechitailo and Gordeev, 2001
Haplopappus gracilis, Hemerocallis cv. Autumn Blaze	CHROMEX-01 Shuttle mission STS-29 in March 1989 (5 days)	Changes in plant medium composition after a spaceflight experiment	A two-fold reduction of the final concentration of potassium in the flight medium.	Levine and Krikorian, 2008
Pea (*Pisum sativum,* cv. Uladovsky)	Salyut 6	To assess the portion of free and membrane bound Ca in plants exposed to microgravity.	Ca levels in pea root cells were elevated compared to ground control.	Belyav-skaya, 1996
Brassica *(Brassica rapa* L.*)*	Shuttle mission STS-87 (16 days) Mir space station in 1997	To examine microgravity-induced root zone hypoxia in shoots and roots	ADH (alcohol dehydrogenase) activity was increased in the spaceflight roots	Stout *et al.*, 2001

Organism	**Method, Mission/vehicle, Duration**	**Scope**	**Results**	**Reference**
Dwarf wheat *(Triticum aestivum* L. cv. Yecora Rojo) *Brassica rapa* L. (cv. CrGC#l-33)	Astroculture^{TM}-04 STS-63 in January of 1995 (8 days)	To measure the availability of oxygen in the root zone.	ADH activity increased 248% to 304% in dwarf wheat when compared with the ground controls and *Brassica* showed increases between 334% and 579% when compared with day zero controls. No differences were found in ADH localization in the dwarf wheat flight or ground tissues.	Porterfield *et al.*, 2000

4.4 Simulated microgravity

Results from simulated microgravity (clinostat) and parabolic flight experiments involving plant nutritional aspects are summarised in Table 3. The results presented have been discussed in Section 4.1 (Stomatal resistance) and Section 4.2 (Oxygen transport).

Table 3. Simulated and real (parabolic flight) microgravity experiments involving plant nutrition aspects.

Organism	**Method, Mission/vehicle, duration**	**Scope**	**Results**	**Reference**
Arabidopsis thaliana	Parabolic flight KC 135 Clinostat Flooding with nutrient solution to submerge the roots	To determine if physical changes in gravity-mediated oxygen transport can be directly measured. To test whether disruption of gravisensing can induce a non-specific ADH response.	The oxygen bioavailability for roots decreased with gravity. The water logging treatment induced ADH activity while clinostat treatment showed no response.	Liao *et al.*, 2004
Triticum aestivum L. cv. “Jagger”	Wheat plants were grown in horizontally oriented tubes	To determine the effect of gravity on plant water uptake and stomatal resistance.	Stomatal resistance was higher in plants grown horizontally (>50 s cm^{-1}) than vertically (<30 s cm^{-1})	Kirkham, 2008

5. Radiation and magnetic field effects

No relevant articles were found about either the radiation or geomagnetic shielding effect on transport of water and solutes in plants. However, there were changes observed in microlocalization of some minerals in rice (*Oryza sativa* L.) embryoes when caryopses received a high irradiation dose (1000 Gy). Changes were also found in the micro-localization of S, K, Mg, P and Ca in aleuron level, endosperm and embryo after 201 days, 457 days and 2107 days flight onboard Salyut 7. Interpretation of these results is difficult because of the lack of real control samples (Bayonove *et al.*, 1994). Cytochemical studies have demonstrated the disruption in Ca^{2+} balance under geomagnetic shielding, which affected the ultrastructure of pea root cells (Belyavskaya, 2001).

6. Conclusions and future work

The work presented leads to the following conclusions:

- Results available are very limited and inconclusive
- Transport of some nutrients is impaired by secondary effects of gravity (lack of buoyancy driven thermal convection and factors affecting transpiration)
- Root zone hypoxia impairs root growth and nutrient uptake
- Transport of water and solutes is crucial for successful plant growth in microgravity

As the transport of water and solutes is one of the basic plant physiological processes, it is necessary to investigate how it will be affected by conditions that can be found on the Moon and Mars.

Experiments *on the ground* should focus on:

Uptake of water and important nutrients in simulated microgravity;
Radiation (UV-B, UV-C, gamma, proton and neutron) effect on water and nutrient uptake and translocation;
Water and nutrient uptake under geomagnetic shielding.

Experiments *in space* should cover:
Water and nutrient uptake in fractional gravity;
Effects of space radiation in low Earth orbit and beyond on water and nutrient uptake and translocation.

7. References

1 Aliev, A. A., Abilov, Z. K., Mashinskii, A. L., Ganieva, R. A., Ragimova, G. K. & Alekperov, U. K. Ultrastructural and some physiological features of the photosynthetic apparatus of garden peas cultivated aboard the orbital station Salyut-7 over a period of 29 days. *Izvestiya Akademii Nauk Azerbaidzhanskoi SSR Seriya Biologicheskikh Nauk* (6) 18-23 (1985).

2 Adiku, S. G. K. Uptake by plant roots. *Encyclopedia of Water Science, 2nd edition, Ed. S. W. Trimble CRC Press*, 1261-1263 (2008).

3 Barta, D. J. & Tibbits, T. W. Calcium localization and tipburn development in lettuce leaves during early enlargement. *Journal of the American Society for Horticultural Science* **125**, 294-298 (2000)

4 Bayonove, J. F., Mir, A. & Burg, M. Effects of long duration space flight on rice seed (or embryo) radiation sensitivity and element microlocalizations. *Advances in Space Research* **14**, 109-113 (1994).

5 Belyavskaya, N. A. Free and membrane-bound calcium in microgravity and microgravity effects at the membrane level. *Advances in Space Research* **17**, 169-177 (1996).

6 Belyavskaya, N. A. Ultrastructure and calcium balance in meristem cells of pea roots exposed to extremely low magnetic fields. *Advances in Space Research* **28**, 645-650 (2001).

7 Casson, S. & Gray J.E. Influence of environmental factors on stomatal development. *New Phytologist* **178** 9-23 (2008).

8 Clemens, S., Palmgren, M. G. & Kramer, U. A long way ahead: understanding and engineering plant metal accumulation. *TRENDS in Plant Science* **7**, 309-315 (2002).

9 Heyenga, A. G., Forsmar, A., Stodieck, L. S., Hoehn, A. & Kliss, M. Approaches in the determination of plant nutrient uptake and distribution in space flight conditions. *Advances in Space Research* **26**, 299-302 (2000).

10 Hopmans, J. W. & Bristow, K. L. Current capabilities and future needs of root water and nutrient uptake modelling. *Advances in Agronomy, Academic Press* **77**, 104-185 (2002).

11 Kirkham, M. B. Horizontal root growth: water uptake and stomatal resistance under microgravity. *Vadoze Zone Journal* **7**, 1125-1131 (2008).

12 Kitaya, Y. Importance of air movement for promoting gas and heat exchanges between plants and atmosphere under controlled environments. *Plant Responses to Air Pollution and Global Change*, *Ed. K. Omasa, I. Nouchi and L. J. KokSpringer-Verlag, Tokio,* 185-193 (2005).

13 Kitaya, Y., Kawai, M., Tsuruyama, J., Takahashi, H., Tani A., Goto, E., Saito T. & Kiyota, M. The effect of gravity on surface temperatures of plant leaves. *Plant, Cell and Environment* **26**, 497-503 (2003).

14 Kittang, A.-I., Wolff, S., Coelho, L. H., Karoliussen, I., Fossum, K. R. & Iversen, T.-H. "Literature Study of Higher Plants in Space for MELiSSA (LiRHiPliSME) - Input to the MELiSSA Phase II project". *CEAS Space Journal* (Submitted 2009).

15 Levine, H. G. & Krikorian, A. D. Changes in plant medium composition after a spaceflight experiment: Potassium levels are of special interest. *Advances in Space Research* **42**, 1060-1065 (2008).

16 Liao, J., Liu, G., Monje, O., Stutte, G. W. & Porterfield, D. M. Induction of hypoxic root metabolism results from physical limitations in O_2 bioavailability in microgravity. *Advances in Space Research* **34**, 1579-1584 (2004).

17 Marschner, H. Mineral nutrition of higher plants, *2nd edition*, *Academic Press, London*. (1995).

18 Monje, O., Bingham, G. E., Carman, J. G., Campbell, W. F., Salisbury, F. B., Eames, B. K., Sytchev, V., Levinskikh, M. A. & Podolsky, I. Canopy photosynthesis and transpiration in microgravity: gas exchange measurements aboard Mir. *Advances in Space Research* **26**, 303-306 (2000).

19 Monje, O., Stutte, G., Chapman, D. Microgravity does not alter plant stand gas exchange of wheat at moderate light levels and saturating CO_2 concentration. *Planta* **222**, 336-345 (2005).

20 Monje, O., Stutte, G. W., Goins, G. D., Porterfield, D. M. & Bingham, G. E. Farming in Space: environmental and biophysical concerns. *Advances in Space Research* **31**, 151-167 (2003).

21 Nechitailo, G. & Gordeev, A. Effect of artificial electric field on plants grown under microgravity conditions. *Advances in Space Research* **28**, 629-631 (2001).

22 Novak, V. & Vidovic, J. Transpiration and nutrient uptake dynamics in maize (*Zea mays* L.). *Ecological Modelling* **166**, 99-107 (2003).

23 Paul, A.-L., Daugherty, C. J., Bihn, E. A., Chapman, D. K., Norwood K. L. L. & Ferl, R. J. Transgene expression patterns indicate that spaceflight affects stress signal perception and transduction in Arabidopsis *Plant Physiology* **126**, 613-621 (2001)

24 Porterfield, D. M. The biophysical limitations in physiological transport and exchange in plants grown in microgravity. *Journal of Plant Growth Regulation* **21**, 177-190 (2002).

25 Porterfield, D. M., Crispi, M. L. & Musgrave, M. E. Changes in soluble sugar, starch, and alcohol dehydrogenase in *Arabidopsis thaliana* exposed to N_2 diluted atmospheres. *Plant Cell Physiology* **38**, 1354-1358 (1997a).

26 Porterfield, D. M., Matthews, S. W., Daugherty, C. J. & Musgrave, M. E. Spaceflight exposure effects on transcription, activity, and localization of alcohol dehvdrogenase in the roots of *Arabidopsis thaliana. Plant Physiology* **113**, 685-693 (1997b).

27 Porterfield, D. M., Barta, D. J., Ming, D. W., Morrow, R. C. & Musgrave, M. E. Astroculture^{TM} root metabolism and cytochemical analysis. *Advances in Space Research* **26**, 315-318 (2000).

28 Roelfsema, M. R. G. & Hedrich, R. In the light of stomatal opening: new insights into ‘the Watergate’. *New Phytologist* **167**, 665-691 (2005).

29 Rygalov, V. Y., Fowler P. A., Metz, J. M., Wheelwr R. M. & Bucklin R. A. Water cycles in closed ecological systems: effects of atmospheric pressure. *Life Support and Biosphere Sciences* **8** 125-135 (2002).

30 Salisbury, F. B. & Ross, C. W. Plant Physiology, *4th edition*, *Wasworth Inc*., *Belmont, California* (1991).

31 Stout, S. C., Porterfield, D. M., Briarty, L. G., Kuang, A. & Musgrave, M. E. Evidence of root zone hypoxia in *Brassica rapa* L. grown in microgravity. *International Journal of Plant Sciences* **162**, 249-255 (2001).

32 Stutte, G. & Monje, O. Microgravity effects on plant boundary layers. *KC-135 and Other Microgravity Simulations, NASA Technical Report* 27-32 (2004).

33 Taiz, L. & Zeiger, E. Plant Physiology, *3rd edition, Sinauer Associates Inc.,Sunderland, Massachusetts* (2002).

34 Webb, A. A. R. The physiology of circadian rhythms in plants. *New Phytologist* **160**, 281-303 (2003).

35 Wheeler, R. M., Mackowiak, C. L., Yorio, N.C. & Sager, J. C. Effects of CO_2 on stomatal conductance: do stomata open at very high CO_2 concentrations? *Annals of Botany* **83**, 243-251 (1999).