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CANOPY PHOTOSYNTHESIS AND TRANSPIRATION IN MICRO-GRAVITY: GAS EXCHANGE MEASUREMENTS ABOARD MIR

O. Monje[1,3], G.E. Bingham[1], J.G. Carman[1], W.F. Campbell[1], F.B. Salisbury[1], B.K. Eames[1], V. Sytchev[2], M.A. Levinskikh[2], and I. Podolsky[2]

[1]*Plants, Soils & Biometeorology Dept., Utah State University, Logan, UT 84322-4820, USA*
[2]*Institute of Biomedical Problems, Moscow, Russia*
[3]*Present Address: Dynamac Corp., DYN-3, Kennedy Space Center, FL 32899*

ABSTRACT

The SVET Greenhouse on-board the Orbital Station Mir was used to measure canopy photosynthesis and transpiration rates for the first time in space. During the Greenhouse IIB experiment on Mir (June – January 1997), carbon and water vapor fluxes from two wheat (cv. Superdwarf) canopies were measured using the US developed Gas Exchange Measurement System (GEMS). Gas analyzers capable of resolving CO_2 concentration differences of 5 μmol mol^{-1} against a background of 0.9% CO_2, are necessary to measure photosynthetic and respiratory rates on Mir. The ability of the GEMS gas analyzers to measure these CO_2 concentration differences was determined during extensive ground calibrations. Similarly, the sensitivity of the analyzers to water vapor was sufficient to accurately measure canopy evapotranspiration. Evapotranspiration, which accounted for over 90% of the water added to the root zone, was estimated using gas exchange and used to estimate substrate moisture content. This paper presents canopy photosynthesis and transpiration data during the peak vegetative phase of development in microgravity.

INTRODUCTION

The SVET Greenhouse, located in the Krystal Module of Mir, is a unique platform for conducting whole-life cycle plant experiments in microgravity, including the measurement of plant photosynthesis and transpiration. Photosynthesis measurements are useful for calculating growth rates nondestructively (Monje and Bugbee, 1998). Measures of transpiration rates in space are needed for determining water potentials in the root zone, which are useful for managing the watering regimes of nutrient delivery systems in microgravity. Simultaneous measurements of transpiration and root zone moisture content are essential for providing enough water for stress free growth in microgravity, but not enough to cause waterlogging of shallow root zones typically used in spaceflight experiments. In this paper, we report the first measurements of canopy photosynthesis and transpiration made in space during the Mir 22/ NASA 3 cooperative mission.

MATERIALS AND METHODS

Gas Exchange Measurement System (GEMS). GEMS is an instrument package used to monitor the environment of the SVET Greenhouse (Bingham *et al.* 1995). GEMS measures and records air temperature, O_2, CO_2 and water vapor concentrations, barometric pressure, air and leaf temperatures, incident photosynthetic photon flux (PPF), and root zone moisture content. These instruments are also

capable of measuring whole canopy gas exchange rates. Gas exchange measurements are made in an open gas exchange system that uses two adjacent, collapsible plant chambers (or leaf bags) that fit inside the SVET chamber over the root module (Bingham *et al.* 1995). The SVET root module is separated into two root zone compartments (cuvettes K1 and K2), and a leaf bag is placed over each cuvette. Mir has large fluctuations in cabin CO_2 and water vapor concentrations, thus a pre-chamber integration bag is used to collect cabin air and average these fluctuations. This buffered cabin air then flows through a flow meter into a pre-chamber infrared gas analyzer (IRGA), which measures the incoming CO_2 and water vapor concentrations. The air then goes through the leaf bag before going into a post-chamber IRGA and is exhausted to the cabin of the Mir station.

GEMS Analyzers. The GEMS has two CO_2/H_2O nondispersive IRGAs (Space Dynamics Lab, Logan UT) for each leaf bag that were designed to resolve small differences in CO_2 concentration against a large background CO_2 concentration. Their operating range is 0-3% CO_2; accuracy: 0.1% (water vapor); optical pathlength: 15 cm; and a signal-to-noise ratio of 4000:1. Ground calibration tests determined that they could measure differences in CO_2 of 5 μmol mol^{-1} against a background of 0.9% CO_2, thus permitting the measurement of photosynthesis and respiration rates. The IRGAs had been in space for over two years when the gas exchange measurements were made, and the soda lime and dessicant for removing CO_2 and water vapor from the sealed detector housings was exhausted. Thus, it was necessary to perform an inflight zero-calibration of the IRGAs. Each day the cosmonauts configured the SVET air ducts so that the pre- and post-chamber IRGAs measured the same air stream. This provided a daily correction factor between the IRGAs. Water vapor and barometric pressure were used to correct the CO_2 concentration for dilution due to water vapor in the air stream.

Gas Exchange Measurements. The gas exchange measurements were made during the second planting of the Greenhouse 2 experiment when leaf bags were used. Seeds (wheat cv. Superdwarf) were planted in each cuvette of the root module used during the first planting of the experiment. The root module still contained the roots from the previous crop. The planting media was a nutrient-rich solid substrate (a zeolite) called Balkanine and water was provided by the automated watering system of the SVET Greenhouse. The water contained 0.2 mg/L of Ag^+ to reduce fungal and algal growth. Each cuvette of the root module had a planted area of 0.05 m^2. The PPF was 450 μmol m^{-2} s^{-1}, pre-chamber CO_2 concentration fluctuated between 7500-9100 μmol mol^{-1}, and the ethylene concentration ranged between 1-2 μmol mol^{-1} (James *et al.* 1997). The leaf bags were placed over the canopies inside the SVET on the13th day after planting (DAP), and were removed on the 25th DAP. After 30 days, the plants were harvested, frozen and packed in the shuttle GN_2 freezer and returned to earth for analysis. Canopy photosynthesis and transpiration rates were calculated from the product of mass flow rate times the difference in pre- and post-chamber CO_2 and water vapor concentrations (Monje and Bugbee, 1996).

Water Management. The volume of water added into the root module was recorded daily using flow meters placed in the supply lines. The water content of the root module was monitored every 20 minutes at eight locations in each cuvette by sixteen moisture probes positioned at three different depths, which operate using the heat pulse method (Bingham *et al.* 1996). These measurements facilitated water management of the root module to avoid root zone flooding or drought by manually changing the setpoints of the SVET watering program each day.

Canopy Water Balance. A water balance for the canopy was calculated during the 12 days that gas exchange was measured. The water loss was determined from the volume of water added to the root module minus the water transpired minus the water remaining in the root module. The cumulative amount of transpired water was obtained by integrating the evapotranspiration rates during the 12-day period. The amount of water remaining in the root module was determined from the inflight moisture measurements made with the GEMS moisture probes. This water balance was used to verify the root zone moisture measurements and to estimate water loss through the porous sidewalls of the root module.

RESULTS AND DISCUSSION

Cabin Environment. The Mir cabin environment was not constant during the gas exchange measurements (Figure 1A-E). The lights warmed air temperature in the leaf bags by two degrees during the day. These changes in temperature are also reflected in the partial pressures of O_2 and CO_2. Leaf temperature was only 0.5°C warmer than air temperature in the day and equally cooler at night (data not shown). Moisture probe measurements of root zone water content (Figure 1F) show a large irrigation event the 15th DAP, followed by a decrease in water content due to evapotranspiration.

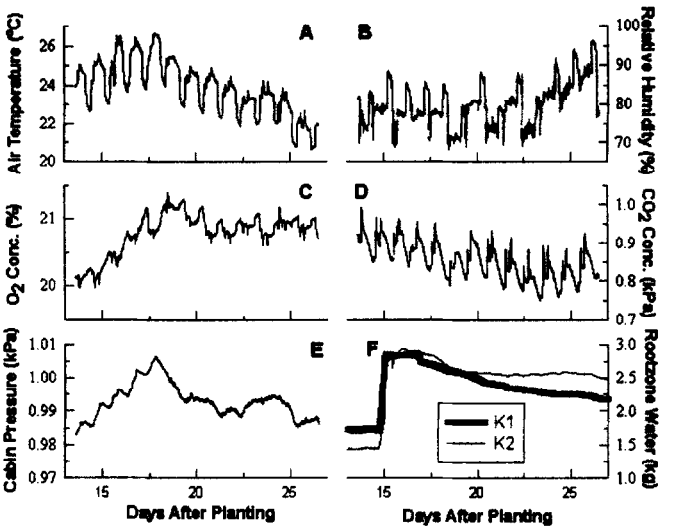

Fig. 1 Daily fluctuations in cabin environment (A-E) and in the root module water content (F) during the gas exchange measurements.

Canopy Gas exchange. Figure 2 depicts the daily average canopy photosynthesis and transpiration rates from cuvette K1. The photosynthesis and evapotranspiration data from cuvette K2 are not shown. The carbon flux data from cuvette K2 was too noisy to resolve into actual rates of photosynthesis. Photosynthesis was fairly constant from day to day since the canopy was at full cover, in spite of large fluctuations in cabin air environment. Daily net photosynthesis rates were similar to dark respiration rates because of C efflux from root decay from the previous planting. The measured respiration rates include shoot and root respiration and respiration from decaying roots. Therefore, the daily C efflux gas exchange data could not be used to calculate daily growth rates because the exact contribution from root decay was largely unknown. Root decay respiration was measured only once prior to seed imbibition and was probably not constant during the duration of the gas exchange measurements. Respiration from root decay essentially shifts the net photosynthesis curve downward leading to increased carbon loss and therefore a smaller daily carbon gain than predicted by the crop growth curve derived from harvest mass.

Evapotranspiration was not constant during the 12-day measurement window, probably due to stomatal response to the large fluctuations in cabin relative humidity and CO_2 concentration (Figure 1). Evapotranspiration in the dark was nearly as high as in the light suggesting that stomata of the plants in the SVET did not close at night, mimicking the behavior of well-watered, hydroponically grown plants (Monje and Bugbee, 1996). About 40% of the water loss due to evapotranspiration occurred at night. Such behavior suggests that the roots experienced adequate moisture for transpiration during the experiment.

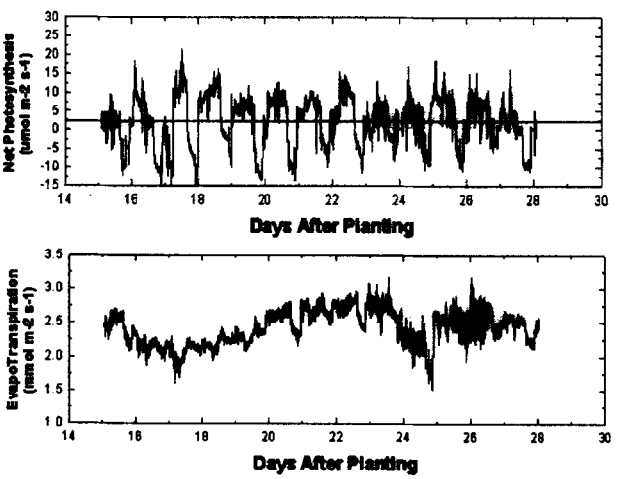

Fig. 2 Canopy photosynthesis and evapotranspiration rates measured during the 2nd planting of the Greenhouse II experiment.

Canopy Water Balance. The canopy water balance for each cuvette of the root module was determined from measurements of irrigated water, canopy evapotranspiration,

and root zone moisture content. The relative change in cuvette root zone moisture during the 12 days that gas exchange was measured equals the volume of irrigated water minus transpired water lost via evapotranspiration (solid lines; Figure 3). For example, during the 12-day measurement period 2.83 L of irrigated water were added to cuvette K1 and 2.36 L of transpired that water were lost via evapotranspiration (Figure 3A). This represents a change of 0.47 L of water in the substrate. The moisture sensors measured a 35% (0.30 L) smaller change in root zone moisture (open triangles) because of water loss through the porous walls of the root module that was not included in the rates of evapotranspiration measured in the leaf bags. The transpiration rate in cuvette K2 was smaller (1.6 L) than in cuvette K1, 2.5 L of irrigation water were added, and there was a greater change in root zone moisture (0.89 L) during the 12-day period. The difference in transpiration between the two cuvettes occurred because more plants germinated in cuvette K1.

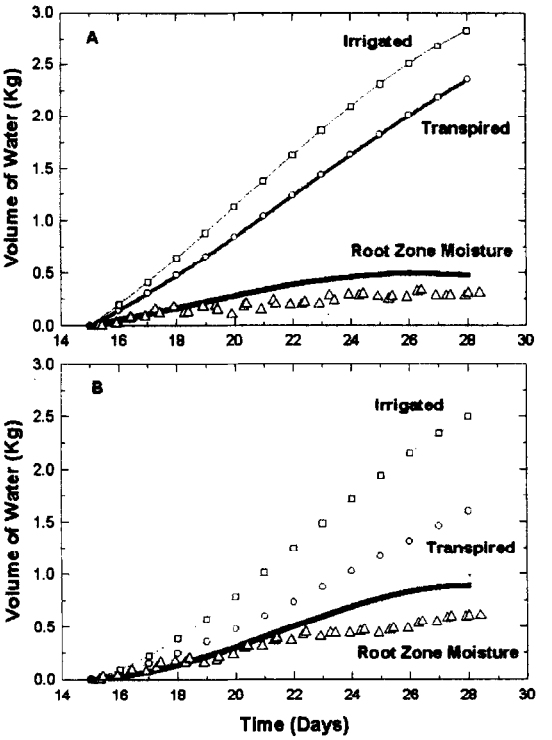

Fig. 3 Changes in cuvette K1 (A) and cuvette K2 (B) root zone moisture relative to moisture on the 15th DAP.

Summary. GEMS demonstrated that open gas exchange measurements are possible in space, and that physiological C fluxes are discernible in a background of 0.9% CO_2. Measurements of evapotranspiration rates on Mir indicated that transpiration from well-watered plants grown in microgravity behaves like transpiration from hydroponic plants. Measurements of irrigated water, canopy evapotranspiration, and root zone moisture content were used to calculate a detailed water balance for each cuvette of the root module. Changes in root zone moisture estimated from measured evapotranspiration were greater than changes measured with moisture probes due to water loss through the porous walls of the root module.

REFERENCES

Bingham, G. E., S. Jones, D. Or, I. Podolsky, M. Levinskikh, V. Sytchev, T. Ivanova, P. Kostov, S. Sapunova, I. Dandolov, D. Bubenheim, and G. Jahns, Microgravity effects on water supply and substrate properties in porous matrix root support systems, *IAF/IAA-97-G.3.03*, 48th Intl. Astronautical Congress, October (1997).

Bingham, G. E., S. B. Brown, F. B. Salisbury, W. F. Campbell, J. G. Carman, G. Jahns, D. Pletcher, D.B. Bubenheim, B. Yendler, V. N. Sytchev, M. A. Levinskikh, I. G. Podolsky, Plant growth and plant environmental monitoring equipment on the Mir space station: Experience and data from the Greenhouse II Experiment. *SAE Technical Series Paper No. 961364*, July, (1996).

Bingham, G. E., F. B. Salisbury, W. F. Campbell, J. G. Carman, D.L. Bubenheim, B. Yendler, V. N. Sytchev, Yu. A. Berkovitch, M. A. Levinskikh, and I. G. Podolsky, The Spacelab-Mir-1 "Greenhouse 2" Experiment, *Adv. Space Res.*, **18**, 225-229 (1995).

Monje, O., and B. Bugbee, Characterizing photosynthesis and transpiration of plant communities in controlled environments, *Acta Horticulturae*, ISHS, **440**, 123-128 (1996).

Monje, O., and B. Bugbee, Adaptation of plant communities to elevated CO2: radiation capture, canopy quantum yield, and carbon use efficiency, *Plant, Cell, and Environment*, **20**, 315-324 (1998).

James, J. T., T. F. Limero, S. W. Beck, L. Yang, M.P. Martin, M. L. Matney, J. F. Boyd, P.A. Covington, D.A. Lind, Toxicological assessment of air contaminants during the NASA 4 expedition. *NASA/JSC SD2-97-543*(1997).