Using a Porous-tube System to Study Potato Responses to Constant Water Tension in a Rooting Matrix

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Abstract. A system maintaining continuous water tension on a nutrient solution has been developed to control root zone moisture levels for plants in microgravity conditions. This study was conducted in a growth chamber to characterize potato (*Solanum tuberosum* L.) responses to constant water tension compared to plants grown with no tension using a free-water technique. In three separate experiments, plants were grown in trays filled with a 4-cm layer of 1-mm-diameter isolite (porous ceramic) particles. Ten porous stainless-steel tubes, 4 cm apart, were buried in the medium, and nutrient solution was drawn through the porous tubes under a constant water tension of –0.5 kPa maintained with a siphon system. For the free-water treatment, trays were slanted, and solution was supplied along the upper end of trays, passed under the medium, and then collected at the lower end and recirculated. The same nutrient solution was recirculated through both treatments at a flow rate of 150 ml·min^{–1} through each tray and maintained at a pH of 5.6. Uniform micropropagated ‘Norland’ potato plantlets were transplanted into replicate trays and maintained at 18C, 70% relative humidity, and a continuous photosynthetic photon flux (PPF) of 450 μmol·m^{–2}·s^{–1}. Water tension reduced total plant dry weight, leaf area, leaf number, and stolon number by >75%, but specific leaf weight increased compared to free water. However, tubers enlarged more rapidly with water tension, and plants consistently partitioned a greater fraction of biomass into tubers (than into shoots). Tuber weight was greater with water tension than in the free-water culture in Expt. 1 harvested 37 days after transplanting, however it was less in Expt. 2 when plants were grown to a larger size for 52 days before harvest. Leaf CO₂ assimilation rate, stomatal conductance, and transpiration were reduced with water tension, although the relative water content of leaves was not significantly affected. Also, with water tension, concentrations of N, P, Zn, and Cu in leaf tissues decreased, whereas tissue Fe increased compared to plants grown with free water. The results in this study demonstrate that constant water tension significantly affects potato plant growth and shifts biomass partitioning toward tubers.

Growing plants for bioregenerative life-support systems in microgravity requires unique cultural systems for delivering water and nutrients. The nutrient solution must be confined to the rooting zone to encourage the use of water tension to prevent the release of free water and provide adequate aeration. Several techniques have been proposed to meet this need in space facilities, including using acrylic membranes (Wright et al., 1988), hydrophilic microporous ceramic tubes (Dreschel and Sager, 1989; Brown et al., 1992), and stainless-steel porous tubes (Morrow et al., 1992, 1994). These techniques have permitted plant growth at very small water tensions and are modifications of varied types of procedures used in research studies to simulate large water tensions of field soils. (Brewster et al. 1975; Tingey and Stockwell, 1977).

The system used for this study involved using stainless-steel porous tubes through which the nutrient solution was circulated and was provided to the rooting matrix through micropores by capillary movement (Morrow et al., 1992). Experiments have shown that this porous-tube system can effectively deliver water and nutrients to the root zone (Morrow et al., 1994) and produce high yields of lettuce and potatoes (Morrow et al., 1992). Limited studies with potatoes indicate that water tension promotes allocation of assimilates to tubers and reduces shoot growth (Bula et al.,

1995). However, the conclusions from these studies are inconclusive, because the plants grown with water tension were maintained in arcillite, a baked clay medium, and compared to control plants grown in peat vermiculite medium with drip-tube watering.

The primary objective of this study was to characterize potato plant growth and tuber development in response to a constant water tension by determining relative water content, gas exchange, and nutrient composition of leaves. In each of three separate experiments, the water pressure treatment using a porous-tube system was compared to a nonstress treatment maintained with a free-water technique.

Materials and Methods

Growing systems. A recirculating solution culture system was used to grow the potato plants. Culture containers were con-

Fig. 1. Moisture content of 1-mm-diameter porous ceramic medium at varied soil water tensions. Moisture content was determined using a soil moisture retention apparatus where the tension is controlled by changes in water volume (McGuire and Lowery, 1992).

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Table 1. Potato growth in response to water-tension treatment after 37 days in Expt. 1 and after 52 days in Expt. 2.

Experiment	Treatment	Plant dry wt (g/plant)	Tuber dry wt (g/plant)	Leaf area (dm ²)	Branches/plant (no.)
1	Water tension	16.5	8.0	6.2	---
	Free water	60.3	5.2	65.1	---
Significance		**		NS	**
2	Water tension	49.9	32.1	17.4	11.0
	Free water	289.4	94.2	247.1	57.0
Significance		**	**	**	**

NS, **Nonsignificant or significant at $P \leq 0.01$, respectively.

structured of opaque polyvinyl chloride, 44 cm long, 32 cm wide, and 8 cm deep (Tibbitts et al. 1994). Ten porous stainless-steel tubes were positioned 1 cm above the bottom of a tray container and spaced 4 cm apart. Porous tubes were covered with a 3-cm layer of isolite, 1-mm-diameter porous ceramic particles (Sumitomo Corp. of America, Denver). This porous ceramic was highly hygroscopic and had a volumetric water content of 74% at saturation and maintained a high water content until tension exceeded 0.5 kPa (Fig. 1). Between 0.5 and 1.0 kPa, the water content dropped significantly to about 54% of saturation and 0.48 volumetric content ($\text{m}^3 \cdot \text{m}^{-3}$). Water content decreased only slightly from 1.0 to 3.0 kPa, (Fig. 1) and insignificantly between 3.0 and 8.8 kPa (data not shown). A black polyethylene plastic sheet was placed on the bottom of the tray and attached to the four sides to prevent leaking and secure the medium inside. The tray was covered with an opaque polyethylene plastic sheeting, white outer surface and black inner surface, to exclude light and maintain high humidity in the rooting surface. Openings were made in the cover sheet of the tray for transplanting plants into the medium.

Separate treatments were set up to compare plants growing with water tension in the rooting zone to plants growing with free water supplied continuously with a nutrient-film technique. The water tension treatment was established using suction of -0.5 kPa (negative pressure) (Tibbitts et al., 1995). Thus, in the 4-cm-deep tray of medium, the water tension at the bottom of the tray was about -0.35 kPa and at the surface about -0.75 kPa. Measurements with porous-cup tensiometers demonstrated that these tension gradients were present and maintained over the period of the studies. Trays were kept level for the water-deficit treatment and slanted at a 4° slope for the free-water treatment. A common nutrient solution was continuously recirculated to both treatments at $150 \pm 10 \text{ ml} \cdot \text{min}^{-1}$. Nutrient solution was recirculated in the level trays through the porous tubes under constant water tension using a siphon system (Tibbitts et al., 1995) and through the medium in the slanted trays by constant supply along the upper end of the tray (Tibbitts and Cao, 1994). Thus, in the free-water treatment, the liquid did not flow through the tubes, although the empty porous

tubes were left in the medium.

Cultural procedures. Three successive experiments were conducted in a walk-in growth chamber at the Biotron of Univ. of Wisconsin-Madison, using 'Norland' potatoes. Transplants used in the experiment were micropropagated stem cuttings grown in sterile agar culture (Tibbitts and Wheeler, 1987). At 21 days, plantlets were transplanted into the culture containers. Transplants were covered for the first 3 days with plastic cups to minimize transplant shock. Single plantlets were transplanted into each tray in Expts. 1 and 2, and two plantlets into each tray in Expt. 3. Treatments were replicated three times and arranged in a randomized complete blocks.

Nutrient solution was a modified half-strength Hoagland solution containing nitrate N (Hammer et al., 1978). Solution pH was maintained at 5.6 with an automatic pH controller using $0.1 \text{ M H}_2\text{SO}_4$. Conductivity of the solution was monitored with a portable Hanna HI8033 meter every 2 to 4 days and adjusted when conductivity varied $>10\%$ from the fresh solution by discarding part of the recirculating solution and adding stock solutions or water as needed.

Environmental conditions. Light was provided with cool-white fluorescent lamps at a PPF of $420 \pm 10 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ at the top of the canopy. Light period was continuous, except for the first 14 days in Expt. 1, when light period was 12 h. Temperature was $18 \pm 0.2^\circ\text{C}$ and relative humidity at $70\% \pm 3\%$. The CO_2 levels were about $350 \mu\text{l} \cdot \text{liter}^{-1}$.

Relative water content and gas exchange. Fully expanded terminal leaflets were used to determine gas exchange variables and relative water content on day 21 and 28 after transplanting in Expt. 3. Stomatal conductance, photosynthesis, and intercellular CO_2 concentration were measured in situ with a photosynthesis system (LI-6000; LI-COR, Lincoln, Neb.). These were taken during the middle of the light period at ambient CO_2 levels. Measurements were taken using fourth and fifth terminal leaflets from the tip (first leaflet >2 cm) on the main stems of three replicate plants in each treatment. These terminal leaflets were fully exposed and assumed to be most sensitive to environmental conditions.

Table 2. Partitioning of total plant biomass into different parts of potatoes in response to water-tension treatment.

Experiment	Treatment	Total biomass (%)			
		Leaf	Stem	Tuber	Root
1	Water tension	23.8	23.9	48.2	4.1
	Free water	52.1	31.5	8.6	7.8
Significance		**	NS	**	**
2	Water tension	22.3	10.8	64.2	2.7
	Free water	37.3	25.9	32.6	4.2
Significance		**	**	**	NS

NS, **Nonsignificant or significant at $P \leq 0.01$, respectively.

Fig. 2. Time-course changes in growth and development of potato plants grown with free-water technique (open triangles) and constant water tension (solid triangles). SLW = specific leaf weight.

Plant harvest. Plants were harvested at 37 days in Expt. 1, 52 days in Expt. 2, and at 7, 14, 21 and 28 days in Expt. 3. For the harvests in Expts. 1 and 2, measurements were made of leaf area; stem length; number of branches >10 cm long; number of tubers; and dry weights of leaves, stems, tubers, and roots plus stolons. To determine leaf area, green leaflets were separated from petioles and area was measured with an area meter (LI-3100; LI-COR). At each harvest in Expt. 3, to establish time course responses of plant growth and tuberization, three replicate plants for each treatment were randomly taken from three separate trays and sampled so that only a single plant was left in each tray after the second harvest. Additional measurements were taken of number of leaves on main stems, and number of primary stolons. Leaves and stolons were counted when they were >1 cm long. Tuber dry weight was not taken because there were only a few small tubers present even at the last harvest 28 days after transplanting.

Mineral analysis. Dried green leaves from Expt. 1 were ground to pass through a 40-mesh sieve. Concentrations of P, K, Ca, Mg, S, Fe, Mn, B, Zn, and Cu in the leaf tissues were determined with

inductively-coupled argon plasma spectroscopy after nitric-perchloric acid digestion (Jones et al., 1991). Total N concentration in the leaf tissues was determined by a micro-Kjeldahl method (Jones et al., 1991).

Statistical analysis. The data was analyzed using analysis of variance (ANOVA) procedures in SAS (SAS Institute Inc., Cary, N.C.).

Results and Discussion

Growth and partitioning. The porous-tube system under water tension substantially affected biomass production and plant morphology of potatoes compared to the free-water culture. When plants were harvested at 37 days or 52 days after transplanting in Expts. 1 and 2, total plant dry weight, leaf area, and branch number were all significantly lower with the porous-tube system than with the free-water treatment. (Table 1). With the porous-tube system, total dry weight, leaf area and branch number were only 20% of those with the free-water treatment. These data support previous observations that potato plant growth is reduced with constant water tension (Morrow et al., 1992; Bula et al., 1995).

Tuber dry weight for 37-day plants in Expt. 1 was essentially the same with the water tension treatments as with free-water culture, whereas tuber dry weight for the harvest of 52-day plants in Expt. 2 was about 30% less with the water tension treatment than with free-water culture (Table 1). In each experiment, however, dry weight partitioning into tubers (i.e., harvest index) was greater with water tension than with free-water culture (Table 2). With water tension, partitioning into tubers was 48% in Expt. 1 and 64% in Expt. 2, whereas, with free-water culture, partitioning percentage was 9% in Expt. 1 and 33% in Expt. 2.

If plants had grown to maturity in this study, it is anticipated that the percentage of the biomass partitioned into tubers with free-water culture would have increased with time, as shown by the high proportion of dry weight in tubers in 112-day growth studies by Wheeler et al. (1990). However with free-water culture, plants at maturity would presumably have had a large amount of shoot growth with long extended stems, a problem with limited growing space under microgravity. Thus, reduced size of shoots and increased partitioning between tubers and shoots with the porous-tube system is of particular importance for controlling plant morphology in life-support systems or other controlled facilities where space and lighting are limited for growing plants. It is likely that increasing the density of the smaller plants under water tension would have enhanced tuber yield per unit growing area, or per unit space volume, even though the tuber production from a single plant was reduced (Tibbitts et al., 1995).

Time course response. Data for time-course response of plants in Expt. 3 indicate that the effect of water tension on plant growth was not obvious at 14 days after transplanting, but plant dry weight

Table 3. Relative water content (RWC), net CO₂ assimilation rate (A), stomatal conductance (g_s), and internal CO₂ concentration (C_i) of potato leaves in response to water-tension treatment.

Plant age (days)	Treatment	RWC (%)	A (μmol·m ⁻² ·s ⁻¹)	g _s (mmol·m ⁻² ·s ⁻¹)	C _i (μl·liter ⁻¹)
21	Water tension	74.3	8.51	382.3	314.1
	Free water	72.1	10.55	432.1	308.9
	Significance	NS	**	*	NS
28	Water tension	61.0	6.66	122.9	281.4
	Free water	64.1	9.66	391.1	306.1
	Significance	NS	**	**	*

NS, **, * Nonsignificant or significant at $P \leq 0.05$ or 0.01, respectively.

Table 4. Concentrations of major nutrients in the leaves of potatoes in response to water-tension treatment.

Element	Concn (mg·g ⁻¹)		Significance ^z
	Water tension	Free water	
N	53.8	69.2	**
P	4.0	7.9	**
K	40.5	47.8	NS
Ca	21.8	17.6	NS
Mg	6.2	7.2	NS
S	4.5	4.7	NS
Fe	0.316	0.194	*
Mn	0.118	0.116	NS
B	0.035	0.036	NS
Zn	0.034	0.062	**
Cu	0.012	0.019	**

NS,*,** Nonsignificant or significant at $P \leq 0.05$ or 0.01 , respectively.

and leaf area were substantially reduced at the 21- and 28-day harvests compared with free-water culture (Fig. 2). Similar patterns were seen with stem length and branch number (data not shown). Specific leaf weight was higher with the porous-tube system than with the free-water system at these two later harvests.

Number of leaves on main stems was similar at the first harvest and then steadily decreased with time in response to water tension (Fig. 2). However, the difference at the 28-day harvest was only three leaves, 14 vs. 17 leaves, on plants with water tension vs free water, respectively. It seems that the main effect of water tension was on leaf expansion, not on leaf emergence. The sensitivity of leaf expansion to water stress has been also reported with different potato genotypes grown under dry field environments (Jefferies, 1993).

A few stolons had developed in both treatments at the first harvest, 7 days after transplanting (Fig. 2). In the following harvests, stolon number was significantly lower with porous-tube system than with free-water culture. From days 21 to day 28, stolon number increased steadily in the free-water culture but did not change with the porous-tube system. Also, the stolons were longer in the free-water than in the porous-tube system. Similar differences in stolon development were found at the 37- and 52-day harvests in Expts. 1 and 2.

Tuberization started about 21 days after transplanting for both treatments. No differences were seen in the number of tubers for the two treatments. This contrasts to the increasing stolon development with free-water treatment and suggests that tuber formation is not necessarily linked with stolon development, as reported by Struik et al. (1989).

Water content and CO₂ assimilation. Net CO₂ assimilation rates and stomatal conductance in leaves were reduced with the porous-tube system, and intercellular CO₂ concentrations were reduced on day 28 but not on day 21 (Table 3). It appears that the reduced carbon-exchange rate of plants in the water tension treatments resulted primarily from the reduced stomatal opening and that reductions in mesophyll activities were of minor significance. No significant differences between treatments were detected in relative water content of the leaves, although it was markedly lower at day 28 than at day 21 as plants and leaves matured. This indicates that photosynthetic responses are not closely dependent on tissue water content, as shown by Munns (1992).

Mineral composition. Concentrations of certain nutrients in leaves were significantly affected by constant water tension, although plants did not exhibit any particular symptoms of nutrient deficiency or toxicity. In the water-stress treatment, tissue concentrations of N, P, Zn, and Cu were reduced, whereas tissue Fe was

increased, compared to the free-water technique (Table 4). Changes in P, Zn, and Cu are of particular significance because tissue concentrations under water tension were only about 50% of those with free water. In contrast, concentrations of K, Ca, Mg, S, Mn, and B in leaf tissues did not significantly vary with treatments.

Studies with wheat by Berry et al. (1992) have documented that a small water tension of 0.8 kPa reduced growth significantly over a water tension of 0.4 kPa. This system used no medium and required that the root system develop within a circular enclosure around a porous tube containing nutrient with an applied water tension. However, no growth comparisons were made with a system that eliminated the water tension on the liquid. The dramatic effects of water tension as small as 0.5 kPa is surprising in light of the evidence that the water content of the medium was about 90% of saturation levels at 0.5 kPa tension (Fig. 1). Also, even though there was a gradient in water content from the surface to the base of the medium in the trays, there was no significant concentration of the roots around the tubes or at the bottom of the trays. Response to such small water deficits has not been reported in field studies with potatoes, although it is recognized that potatoes are drought sensitive and growth and yields are decreased with increasing soil moisture tension (Gregory and Simmonds 1992, Harris, 1978). Gregory and Simmonds (1992) stated that differences in partitioning with water deficits are, in general, small, although Shock et al. (1992) demonstrated improved tuber quality with water deficits during the early growth period.

One might suspect that using isolyte medium in this study may have contributed to the water tension response that was found. However, negative pressure studies undertaken with arcillite (baked montmorillinitic clay) medium by Bula et al. (1995), and other nonreplicated studies with arcillite by ourselves, have demonstrated similar growth partitioning to tubers.

An additional concern is that the stainless-steel tubes in the system may have released heavy metals to induce the water tension response. However, preliminary studies undertaken with two separate recirculating free-water treatments, one supplying nutrient to trays with plastic drip tubes and the second supplying nutrient through stainless-steel tubes (under slight positive tension), demonstrated no growth differences and no evidence of shifting partitioning to tubers as seen with water-tension systems.

Results in this study demonstrate that small constant water tension significantly affects plant growth and shifts biomass partitioning toward tubers. Additional studies are needed to elucidate the unique controlling mechanisms in the plants that are sensitive to these very low levels of water tension.

Author's Note

The stimulation of tuberization with tension systems may have resulted from the lack of water or solution passing over or near the stolons, rather than the water tension. This lack of water may have permitted the accumulation of a tuber-promoting substance at the stolon tips. This possibility is supported by the fact that, when stolons have been permitted to develop with constant washing in solution culture or with misting systems, tuberization has been greatly delayed (Tibbitts et al., 1994).

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