ZEOPONICS

Wheat Response to Differences in Water and Nutritional Status between Zeoponic and Hydroponic Growth Systems

Susan L. Steinberg,* Douglas W. Ming, Keith E. Henderson, Chris Carrier, John E. Gruener, Dan J. Barta, and Don L. Henninger

ABSTRACT

Hydroponic culture has traditionally been used for controlled environment life support systems (CELSS) because the optimal environment for roots supports high growth rates. Recent developments in zeoponic substrate and microporous tube irrigation (ZPT) also offer high control of the root environment. This study compared the effect of differences in water and nutrient status of ZPT or hydroponic culture on growth and yield of wheat (*Triticum aestivum* L. cv. USU-Apogee). In a side-by-side test in a controlled environment, wheat was grown in ZPT and recirculating hydroponics to maturity. Water use by plants grown in both culture systems peaked at 15 to 20 L m^{-2} d^{-1} up to Day 40, after which it declined more rapidly for plants grown in ZPT culture due to earlier senescence of leaves. No consistent differences in water status were noted between plants grown in the two culture systems. Although yield was similar, harvest index was 28% lower for plants grown in ZPT than in hydroponic culture. Sterile green tillers made up 12 and 0% of the biomass of plants grown in ZPT and hydroponic culture, respectively. Differences in biomass partitioning were attributed primarily to NH_4–N nutrition of plants grown in ZPT compared with NO_3–N in hydroponic nutrient solution. It is probable that NH_4–N-induced Ca deficiency produced excess tillering and lower harvest index for plants grown in ZPT culture. These results suggest that further refinements in zeoponic substrate would make ZPT culture a viable alternative for achieving high productivity in a CELSS.

Nutrient solution culture provides a consistent high degree of control of water, nutrient, and aeration status of the plant root zone that is hard to match with solid media (Rawlins, 1979). For this reason, hydroponic culture has often been used in plant studies for controlled-environment life support systems in space-based applications. High plant growth rates can be maintained in relatively small-volume root zones, with a resultant high yield. Crop production systems that have been conceptualized to date for space-based applications have relied on hydroponic water and nutrient delivery systems (Bugbee and Salisbury, 1989b; Kliss and MacElroy, 1990). However, the separation of the liquid and gas phases in the root zone and containment of water becomes a problem in microgravity. In addition, hydroponic culture requires monitoring and control systems to maintain nutrient levels and pH.

Wright et al. (1988) addressed the problem of water containment and liquid and gas phase separation in microgravity by using microporous membranes to control water delivery to plants. In the present configuration of this method, nutrient solution flows under a slight negative pressure through microporous tubes and is delivered by capillary action directly to roots (Dreschel and Sager, 1989) or to solid substrate (Morrow et al., 1994; Tibbitts et al., 1995). A nearly constant matric potential can be maintained in solid substrate by controlling water flow and pressure through microporous tubes. The dynamics of water transport through a microporous tube–solid substrate–plant system was studied by Steinberg and Henninger (1997), who showed that water holding and transport characteristics of solid substrate determine the range of viable operating pressures of the system.

Little is known about the growth and yield of plants grown in solid substrate maintained at a nearly constant matric potential by microporous tube irrigation as compared to hydroponic culture. Cao and Tibbitts (1996) compared biomass production and gas exchange of potato (*Solanum tuberosum* L.) grown in a microporous tube irrigation system containing isolite (a porous ceramic aggregate) with nutrient film technique. They found that the slight water tension of −0.5 kPa in the microporous tube system reduced CO_2 assimilation, transpiration, and biomass production and shifted biomass partitioning towards tuberization, relative to that with nutrient film technique. The stimulation of potato tuberization in microporous tube–solid substrate culture was attributed to the lack of water passing over or near stolons, rather than to water pressures maintained in the system.

A zeoponic substrate has been developed for use in space-based applications. This substrate is largely composed of NH_4-exchanged and K-exchanged zeolites (Ming et al., 1995). Synthetic apatites containing Ca, P, Mg, S, Fe, Mn, Zn, Cu, B, Mo, and Cl (Golden and Ming, 1999) and dolomite [$CaMg(CO_3)_2$] (Henderson et al., 1999) are added to the zeolite. Zeoponic substrate acts like a slow release fertilizer in that nutrients are solubilized through dissolution and ion exchange reactions to become available for plant uptake (Allen et al., 1993, 1995). Zeoponic substrate has been able to support intensive growth and nutrient demands of wheat that

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Abbreviations: CELSS, controlled environment life support system(s); LAI, leaf area index; ZPT, zeoponic substrate and microporous tube irrigation.

are typical of controlled-environment culture (Allen et al., 1995; Ming et al., 1995; Henderson et al., 1999).

The zeoponic substrate provides mechanical support for plants and a large surface area for root exploration. The need for nutrient solutions and pH and nutrient monitoring and control systems associated with hydroponic culture are eliminated. Distilled water can be continuously recirculated through the microporous tubes, reducing the quantity of leachate.

Recent developments of microporous tube irrigation and zeoponic substrate offer an alternative to hydroponic culture that provides high control of the root zone environment and operates in microgravity. Our objective was to determine if differences in water and nutrient status between ZPT and hydroponic culture affect the growth and yield of wheat. Specifically, we examined the ability of microporous tube irrigation to deliver water, and zeoponic substrate to deliver nutrients, to wheat during its growth to maturity. Wheat responds well to continuous light, and this condition shortens the life cycle and increases energy efficiency, advantageous qualities in space-based applications (Bugbee and Salisbury, 1989a). A 24-h day length, high photon flux density, and constant temperature were used to create a high demand for water and nutrients. Any limitation in a culture system's ability to deliver water and nutrients to roots would be accentuated under these conditions with no dark period to recover.

MATERIALS AND METHODS

Water and Nutrient Delivery System

Our study was conducted in a controlled environment chamber (Model E15, Conviron, Asheville, NC). The chamber was divided in half, and each half contained four replicates (trays) of each of two culture systems.

A recirculating hydroponic system supplied 0.5-strength nutrient solution to four growing trays. The solution contained (in m*M*) 7.5 N (supplied as NO_3–N), 0.5 P, 3.0 K, 2.5 Ca, 1.0 Mg, 0.5 Cl, and 1.0 S; and (in μM) 60 Fe, 0.47 Cu, 0.92 Zn, 19 B, 3.64 Mn, and 0.01 Mo. The trays were covered with white polyvinyl chloride (PVC) tops containing small slits for plants. The tops helped reduce evaporation from the tray and salt build-up in wicks of laminated fiberglass cloth that were used to support the plants. In-line electrodes and pH and conductivity controllers (Omega, Stamford, CT) were used in the nutrient solution containers to maintain solution pH between 5.7 and 5.8, and conductivity between 1.08 and 1.2 dS m^{-1} by addition of 0.5 *M* HNO_3 or nutrient solution, respectively.

The microporous tube irrigation system was assembled in the remaining four trays. Each tray contained five microporous tubes with a 40-μm pore size that were connected in series. Further detail of the system has been described by Steinberg and Henninger (1997). Distilled water was circulated through the porous tube system at −0.4 to −0.5 kPa pressure and 240 to 260 mL min^{-1} flow rate. To minimize evaporation, trays were covered with black-inner-surface–white-outer-surface plastic containing slits for plants. Each tray was filled with 7.5 L of ZPT substrate: a mixture of 30% zeoponic substrate and 70% porous ceramic aggregate (Profile, Aimcor, Deerfield, IL). Physical characteristics of the ZPT substrate were 0.71 g cm^{-3} bulk density, 2.45 g cm^{-3} particle density, 98.7 % of 0.25- to 1.0-mm particles, 71% total pore space, and 6.4×10^{-4} m s^{-1} saturated hydraulic conductivity. A porous tube pressure of −0.5 kPa was the most optimal matric potential that could be maintained without loss of aeration and 100% water saturation of the substrate (Fig. 1; Steinberg and Henninger, 1997).

The zeoponic substrate contained nutrient-enriched zeolite, dolomite, synthetic apatite, and ferrihydrite. The nutrient-enriched zeolite was prepared using methods of Galindo et al. (1993) to make K- and NH_4-exchanged clinoptilolite, a siliceous zeolite. The clinoptilolite was taken from the Fort LeClede deposit in Sweetwater County, Wyoming. Based on cation exchange measurements and X-ray defraction analysis, the material was approximately 90% clinoptilolite (Galindo et al., 1993). The method of Golden and Ming (1999) was used for preparation of synthetic apatites containing the essential plant nutrients Ca, P, Mg, S, Fe, Mn, Zn, Cu, B, Mo, and Cl incorporated into its structure. Dolomitic limestone from Kosota, MN, was supplied by Wards Scientific (Rochester, NY), and 2-line ferrihydrite was precipitated onto the surfaces of NH_4-clinoptilolite as outlined by Schwertmann and Cornell (1991). The final zeoponic substrate consisted of 2:2:1:0.55 by weight of K-clinoptilolite:NH_4-clinoptilolite:synthetic apatite:dolomite + 1 wt. % ferrihydrite coating on NH_4-clinoptilolite. Calcium, P, Mg, S, and the micronutrients were made available to plants by dissolution of synthetic apatite, and N and K were made available from ion exchange of Ca^{2+} for K^+ and NH_4^+ on exchange sites of clinoptilolite. Particle size for the zeoponic substrate was 0.5 to 1.0 mm.

Hydroponic and ZPT trays each had a surface area of 0.106 m^2 and a depth of 0.064 and 0.092 m, respectively. At full development, the planar canopy area of the hydroponic treatment was 0.654 m^2 and the ZPT treatment was 0.684 m^2. The ZPT trays had slightly greater distances between them than hydroponic trays to accommodate pressure transducers associated with the microporous tubes. The nutrient supply reservoir for the hydroponic system and water supply and return reservoirs for the porous tube system were located outside the chamber. The reservoirs were common to the four trays in each system to minimize variability in root zone environment (Bugbee and Salisbury, 1988).

Environmental Conditions

Environmental conditions in the chamber were 23 ± 0.7°C, 70 ± 3% relative humidity, and ambient CO_2. Irradiance in the chamber was provided by four 1000-W high-pressure sodium lamps separated from the plants by Lexan polycarbonate barriers. Photosynthetic photon flux density at canopy height was 1700 ± 60 μmol m^{-2} s^{-1}; the photoperiod was 24 h except as noted. Temperature, light, and humidity sensors were located at the center of the chamber at canopy height to monitor chamber conditions. To minimize edge effects, each culture system (four trays) was surrounded by reflective material (nylon ripstock with 6.35-μm aluminum mylar backing, NASA, Houston, TX) that was adjusted weekly to canopy height. The heights of plant growth trays were adjusted periodically so that the canopy top was at the same height in each treatment. In addition to the vertical air circulation provided in the chamber, two small fans were mounted on each side of the chamber to provide horizontal airflow over the top of the canopy in each culture system.

Cultural Procedures

The dwarf hard red spring wheat cv. USU-Apogee was used because it had been bred specifically for use in bioregenerative life-support systems in space (Bugbee, 1997). USU Apogee is 45 to 50 cm tall and yields well under conditions favoring rapid development: continuous warm temperature, 24-h pho-

toperiod, and high light. Seeding rates for both treatments were 1000 plants m^{-2} (tray area) or 636 and 608 plants m^{-2} of area occupied by hydroponics and ZPT treatments, respectively. Seeds were subjected to 48 h of moist conditions at 4°C prior to planting. In hydroponic culture, seeds were seeded directly onto wicks and in ZPT culture, the seeds were seeded directly into the substrate. Each ZPT tray was inoculated with 500 mL of a 1:100 dilution of nitrifying bacteria (Nitroseed DBC Plus, Enviroflow, Manassas, VA) on the day of planting and again when the plants were 10 d old. Seeds were germinated in the dark; half the lights were turned on on Day 3, and full lighting commenced on Day 6.

Nutritional Status of Plants

Nutrients were determined in leaves twice during the growing period. Samples of 40 flag leaves from each treatment were taken 22 d after planting, when spikes first appeared. This sampling was limited to 40 leaves per treatment to minimize effects of flag leaf removal on subsequent growth and yield. The second sample of flag leaves was taken from plants at maturity. Nitrogen concentration was determined by the flash combustion method of Sheldrick (1986) using a LECO CHN-600 analyzer (LECO, St. Joseph, MI). Elemental concentrations of P, K, Ca, Mg, S, Zn, B, Mn, Fe, Cu, Al, Na, and Mo were determined using inductively coupled plasma emission spectroscopy. Chloride was analyzed according to the method of Johnson and Ulrich (1959, p. 26–78).

Water Relations of Zeoponic Substrate and Hydroponic Nutrient Solution

The bulk density, particle density, saturated hydraulic conductivity, and percentage pore space of the ZPT substrate were listed earlier; the desorption relation is provided in Fig. 1. Volumetric water capacity and pore size distribution were calculated according to Hillel (1980, p. 165). The matric potential of the substrate in each tray was monitored by a miniature tensiometer (Model 2100F, Soil Moisture Equipment, Santa Barbara, CA) placed at a 4-cm depth midway between two microporous tubes. Osmotic potential of water circulating in the porous tube irrigation system, osmotic potential of hydroponic nutrient solution, and substrate water potential were measured three times during the growing period with an isopiestic thermocouple psychrometer (Isopiestics, Lewes, DE). The hydroponic nutrient solution and water in the porous tube system were sampled from lines returning fluid from trays to their respective supply reservoirs. Small substrate *cores* were obtained by removing the needle attached to 3-mL plastic syringes and inserting the open syringe end into the substrate. Each sample, or core, was placed into a thermally stable chamber covered with melted and resolidified petrolatum. A thermocouple containing a small drop of sucrose solution of known water potential was lowered into each chamber. The measurement was isopiestic and the osmotic potential was obtained when a sucrose solution produced no net vapor exchange with the sample (Boyer, 1995).

Plant Water Status and Water Use

Leaf and root water potentials and leaf osmotic potential were measured three times during the growing period in the light and at the end of a 4-h dark period. A longer dark period was not used because continuous light was one of the experimental conditions. Water potential of flag leaves or secondary leaves was the xylem pressure at balance (Boyer, 1995) obtained with a pressure chamber (Soil Moisture Equipment Model 3000). Osmotic potential of the xylem sap was

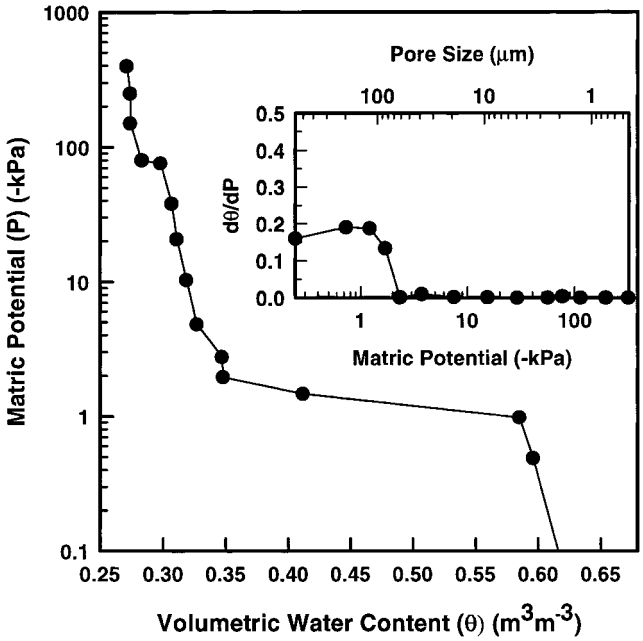

Fig. 1. Matric potential (*P*) as a function of water content (θ) for 30% zeoponic/70% Profile substrate. The saturated hydraulic conductivity was 6.4×10^{-4} m s^{-1}. *Inset:* Volumetric water capacity ($d\theta/dP$) of the substrate as a function of matric potential and calculated pore size.

measured by isopiestic technique to be <0.01 MPa; thus, leaf water potential was assumed to equal balancing pressure. Immediately after water potential measurement, the leaf was placed in a syringe, frozen, and thawed. The osmotic potential of expressed leaf sap was measured by isopiestic technique (Boyer, 1995), and corrected for apoplastic water fraction (Campbell et al., 1979). Leaf turgor was determined as the difference between leaf water and osmotic potential. Root water potential was measured using isopiestic technique corrected for the heat of respiration (Boyer, 1995). In the ZPT treatment, roots were obtained by pulling small samples of roots from the substrate with tweezers, detached, and carefully shaken to remove solid particles. In the hydroponic treatment, the tray lid was elevated slightly to reveal the root mass. Small samples of root were removed and rapidly blotted to remove excess nutrient solution. Detached roots were handled quickly to minimize drying. Leaf and root water potential measurements were repeated three to six times in each treatment during each sampling period.

Water use of plants grown in each culture system was obtained from daily measurements of water level in supply reservoirs for the hydroponic and ZPT systems and has been reported on a treatment-area basis. Water loss from these reservoirs indicated plant transpiration and water stored in plants.

Plant Biomass Characterization

Plants were harvested when the majority of primary tillers were at physiological maturity (Hanft and Wych, 1982), which was 64 d after planting. Tillers were categorized as no spikes, fertile green, fertile mature, sterile green, and sterile mature. Dry weight of roots, leaves, stems, and seeds from the five tiller categories was obtained. Leaves were removed from stems, and leaf areas of five subsamples of green leaves per tray were measured using a leaf area meter (LI 3100, Li-Cor, Lincoln, NE). Subsamples were dried and leaf area and dry weight data were used to calculate leaf area, specific leaf area,

and leaf area index (LAI) of each tray and treatment. Average weights for seeds were determined from weights of three 100-seed samples taken from each tray.

Zeolite Substrate Characterization

Exchangeable K^+ and NH_4^+ were determined on zeolitic exchange sites in the substrate before and after growing plants using atomic absorption spectrophotometry and ion selective electrode methods, respectively (Ming et al., 1993).

Analysis of Data

Data are reported as mean ± 1 SD.

RESULTS AND DISCUSSION

Plant Biomass Partitioning

Percent germination measured 10 d after planting was 96 ± 7% for ZPT as compared to 82 ± 14% in hydroponic culture. In hydroponic culture, wheat seeds were placed on top of wicks, where drying can occur before roots extend down into nutrient solution. By contrast, substrate matric potential was maintained at a nearly uniform level in ZPT (Steinberg and Henninger, 1997), providing optimal moisture conditions for germination. The difference in germination resulted in about 584 plants m^{-2} for ZPT, as compared with 521 plants m^{-2} for hydroponic culture (on a treatment-area basis). This small difference in plant density probably had no significant effect on yield, because tillering readily occurs to fill in areas between plants (Kasperbauer and Karlen, 1986).

The total biomass of the plants was 626 g for ZPT and 576 g for hydroponic culture (Table 1). Total seed weight, number of fertile spikes, weight of individual seeds, and yield (measured on a treatment unit area per day basis) were not significantly higher in hydroponic than in ZPT culture, although there were 26% less seeds per tiller in ZPT culture (Tables 1 and 2). The seed yield per mole of photons (seed dry weight/total moles of photons for growing period) was 0.19 and 0.14 g mol^{-1} in hydroponic and ZPT culture, respectively. This yield efficiency for hydroponic culture corresponds to that of 0.18 g mol^{-1} reported by Monje and Bugbee (1998) for similar controlled environment conditions of 23°C air temperature, long photoperiod, and high light.

The harvest index (percent seed relative to total biomass) was 28% lower, while percent biomass of stems, leaves, and chaff was 30% higher, in plants grown in ZPT than hydroponic culture (Tables 1 and 2). Additionally, total number of tillers was 34% higher for plants grown in ZPT than in hydroponic culture (Table 1). This was largely due to differences in biomass partitioning to different types of tillers (Table 1, Fig. 2). Sterile green tillers made up 12% of the biomass in ZPT vs. 0% in hydroponic culture (Fig. 2). This number of sterile tillers was within the 2 to 12% range reported by Bugbee and Salisbury (1988) for wheat grown in similar controlled environment conditions.

Wheat grown in zeoponic substrate by Goins et al. (1997) also produced excessive sterile tillers compared with wheat supplied with nutrient solution via microporous tubes or drip irrigation. Levine (1998) found that wheat grown in zeoponic substrate not only exhibited increased tillering, but also delayed spike formation when compared with two Russian media, Balkanin and Bion-312, and peat vermiculite. We found that at Day 25, 50% of the spikes had fully emerged from the flag leaf sheath in hydroponic culture, vs. 30% for ZPT culture. Five days later, this developmental difference had disappeared.

Even though differences in harvest index of 36% for ZPT vs. 50% for hydroponics were significant, both were within the range for wheat grown in controlled environments: 30 to 40% (Wheeler et al., 1993) and 36 to 50% (Bugbee and Salisbury, 1988). Bugbee and Salisbury (1988) reported that tillering increased significantly with photosynthetic photon flux density, and was largely due to production of late developing or tertiary tillers. These tillers had a lower harvest index than primary or secondary tillers and reduced overall production efficiency (Bugbee and Salisbury 1988; Camberato and Bock, 1990). However, high light intensity cannot be the direct cause of differences in biomass partitioning

Table 1. Biomass weights, number of tillers, seeds per tiller, and average seed weight of 'USU-Apogee' wheat grown hydroponically and in zeoponic substrate with microporous tube irrigation (ZPT).

	Culture system	
Growth parameter	Hydroponic	ZPT
Total biomass, g dry wt.		
(% of total biomass)	576 ± 105†	626 ± 54
Roots	43 ± 12 (7.4 ± 0.7)	57 ± 15 (9.0 ± 1.7)
Stems	100 ± 18 (17.4 ± 0.7)	141 ± 24 (22.4 ± 2.8)
Leaves	35 ± 2 (6.2 ± 0.8)	49 ± 1.6 (8.0 ± 0.8)
Chaff	107 ± 18 (18.6 ± 0.3)	151 ± 15 (24.2 ± 2.2)
Seed, total	290 ± 57 (50.4 ± 1.2)	228 ± 34 (36.4 ± 5.3)
Mature	266 ± 47	212 ± 36
Green	24 ± 11	16 ± 5
Tillers, total, no.	441 ± 37	593 ± 42
Fertile mature, no.	360 ± 14	332 ± 38
Fertile green, no.	69 ± 23	64 ± 30
Sterile mature, no.	0.5 ± 1	13 ± 5
Sterile green, no.	5 ± 3	176 ± 48
Seeds $tiller^{-1}$, no.	25 ± 2.8	18.5 ± 0.9
Weight $seed^{-1}$, g	0.027 ± 0.0021	0.031 ± 0.0025

† Data represent means ± 1 SD (n = 4).

Table 2. Yield per tray and treatment area, and harvest index for 'USU-Apogee' wheat grown hydroponically and in zeoponic substrate with microporous tube irrigation (ZPT).

	Culture system	
Measure of yield	ZPT	Hydroponic
Yield per tray†		
kg m^{-2}	2.2 ± 0.33‡	2.7 ± 0.5
g m^{-2} d^{-1}§	33.7 ± 5.1	43.0 ± 8.5
Yield per treatment area¶		
kg m^{-2}	1.3 ± 0.2	1.8 ± 0.35
g m^{-2} d^{-1}§	20.8 ± 3.1	27.8 ± 5.5
Harvest index#	0.36 ± 0.05	0.50 ± 0.01

† Growing area per tray = 0.106 m^2.
‡ Data are means ± 1 SD (n = 4).
§ Yield per day was calculated for a 64-d growing period.
¶ Growing area for hydroponic culture was 0.654 m^2; growing area for ZPT culture was 0.684 m^2.
# Harvest index (seed mass/total biomass) was determined for the entire biomass, including roots.

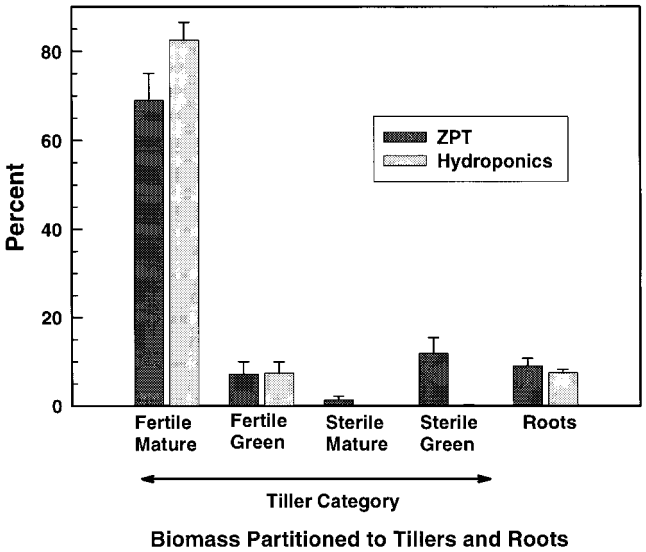

Fig. 2. Percentage of wheat biomass partitioned to roots and tillers (including stems, leaves, grain, and chaff) of different types for zeoponic substrate with microporous tube irrigation (ZPT) or hydroponic culture. Bars represent means; error bars indicate standard deviation (n = 4).

between ZPT and hydroponically grown plants, because light was the same for both culture systems.

Specific leaf area and canopy height were similar for both culture systems (Table 3). Leaf area and LAI per treatment area at harvest were 30 and 24% higher in ZPT vs. hydroponic culture, respectively (Table 3). This was probably due to the increased tillering found in ZPT culture. On a treatment-area basis, the LAI was 4.1 and 5.1 for hydroponic and ZPT culture and on a tray-area basis, the values were 6.3 and 8.2, respectively (Table 3). Bugbee and Salisbury (1988) note that LAI values nearing 10 at harvest may be superoptimal for high-density wheat plantings. After canopy closure, lower leaves are below the photosynthetic photon flux compensation point and senesce before harvest.

In our study, root biomass was 7 to 9% of total biomass for plants grown in both culture systems (Table 1). This was higher than the 3 to 4% reported for optimal hydroponic growth, but within the 5 to 20% range reported for field-grown wheat (Bugbee and Salisbury, 1988). Increased partitioning of biomass to roots can be indicative of plant stress. Both culture systems were exposed to high light (1700 μmol m^{-2} s^{-1}) and a 24-h photoperiod that could have created transient nutrient and water stresses during the exponential growth phase. During this time, nutrients may not have been absorbed and transported quickly enough to meet growth demands (B.G. Bugbee, personal communication, 1997).

Water Status of Plants and Growth Substrates

Water use by wheat for the first 20 d averaged 9.6 and 8.3 L m^{-2} d^{-1}, and was 17.9 and 17.7 L m^{-2} d^{-1} from Day 21 to Day 35 for plants grown in hydroponic and ZPT culture, respectively (Fig. 3). After Day 35, the water use of wheat grown in ZPT culture began to decline to less than 10 L m^{-2} d^{-1}. A similar decline was not observed for plants grown in the hydroponic culture until Day 50. Leaves of plants grown in ZPT culture senesced more rapidly than those of plants grown in hydroponic culture during this time. Total water use during the 64-d growing period was 567 L for ZPT and 626 L for hydroponic culture.

Table 3. Mean values of leaf area, leaf area index, specific leaf area, and canopy height at harvest (64 d) for wheat grown hydroponically and in zeoponic substrate with microporous tube irrigation (ZPT).

	Culture system	
Growth parameter	Hydroponic	ZPT
Leaf area (m^2)	0.67 ± 0.06†	0.87 ± 0.04
Leaf area index		
per tray‡	6.3 ± 0.6	8.2 ± 0.4
per treatment area§	4.1 ± 0.4	5.1 ± 0.2
Specific leaf area (m^2 kg^{-1})	19.5 ± 2.2	17.3 ± 1.4
Canopy height (cm)	46 ± 0.82	47.5 ± 1.3

† Data are means ± 1 SD (n = 4).
‡ Growing area per tray = 0.106 m^2.
§ Growing area for hydroponic culture = 0.654 m^2; growing area for ZPT culture = 0.684 m^2.

Water movement through a microporous tube–solid substrate–plant system is along a gradient in water potential, the driving force for water movement (Kramer and Boyer, 1995). We measured water potentials of the nutrient solution or solid substrate, roots and leaves to evaluate water movement through each culture system.

The water potential of solid substrate reflects both matric and osmotic forces, while the water potential of nutrient solution equals its osmotic potential. As the experiment progressed, the water potential of the ZPT substrate declined from −0.03 to −0.1 MPa, while the osmotic potential of the nutrient solution remained −0.05 MPa (Fig. 4, left). Matric potentials of ZPT substrate midway between microporous tubes were consis-

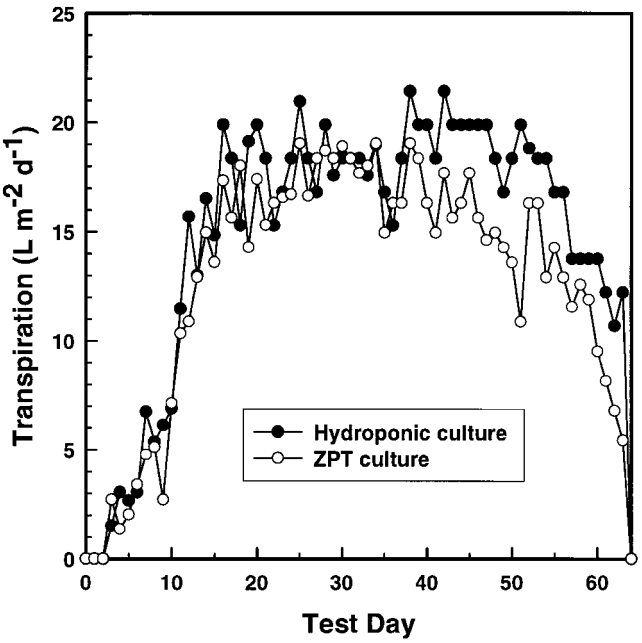

Fig. 3. Water use of 'USU-Apogee' wheat grown in zeoponic substrate with microporous tube irrigation (ZPT) vs. hydroponic culture for 64 d. Data were normalized on a treatment-area basis.

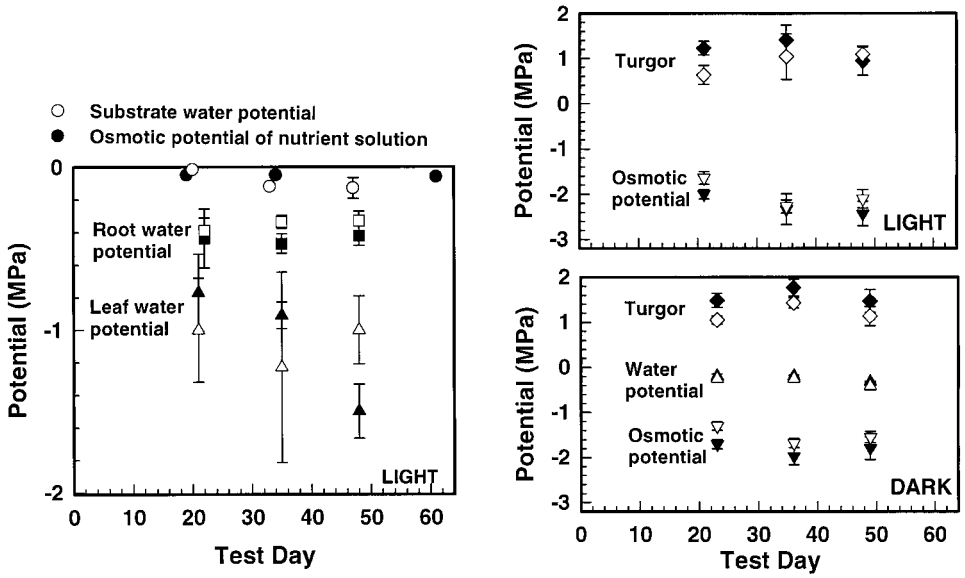

Fig. 4. Water potential gradients from substrate or hydroponic nutrient solution to roots and then leaves measured in the light (*left*) and water status of flag leaves in the light and dark (*right*). Dark measurements were made 4 h after lights had been turned off. Closed symbols represent hydroponic culture; open symbols represent zeoponic substrate with microporous tube irrigation culture (ZPT). Symbols represent means; error bars indicate SD, where larger than symbol size. Substrate and root water potentials, and nutrient solution osmotic potential, $n = 3$; leaf water potential, $n = 6$.

tently −1.5 to −2.0 kPa (data not shown). Figure 1 shows that water is available to plants from 0 to −2.0 kPa, but that the majority is released from 0 to −1.0 kPa (Fig. 1, inset). Throughout the experiment, root water potentials remained at −0.3 to −0.5 MPa, or 0.2 to 0.4 MPa lower than the osmotic potential of the nutrient solution or the water potential of the ZPT substrate.

Water potentials of leaves on Day 21 were −0.8 to −1.0 MPa, which is 0.3 to 0.6 MPa lower than in roots for plants in both ZPT and hydroponic culture (Fig. 4, left). At this time, plants had not yet attained full leaf area and canopy closure was not completed. Leaf water potentials, although not significantly different between culture systems, ranged from −0.7 to −1.2 MPa in hydroponic plants and −0.7 to −1.7 MPa in ZPT plants on Day 35. At this time, leaf area as well as demand for water should have been maximal. The higher variation in water potentials of leaves from plants in ZPT culture suggests that water flow through the ZPT system might have been beginning to lag demand. The fact that differences in water potential between nutrient solution or solid substrate and roots remained nearly constant, while differences between root and leaf water potential ranged from 0.3 to 0.7 or 1.4 MPa in hydroponic and ZPT plants, respectively, points to greater resistance to water flow in the plant than ZPT substrate. Steinberg and Henninger (1997) showed that unless the substrate water potential was considerably more negative than −0.1 MPa (matric potential: −1.5 to −2.0 kPa), resistance within the plant limited water flow in the microporous tube–solid substrate–plant system.

On Day 49, leaf water potential of hydroponic plants was −1.5 MPa, and significantly lower than the −1.0 MPa measured for ZPT-grown plants. This difference was probably due to more rapid senescence of lower leaves of plants grown in ZPT culture, which allowed remaining upper leaves to maintain a more favorable water status.

Measurements made in the light on Day 21 indicated that leaf osmotic potential was about 0.4 MPa lower, and the resulting turgor was 0.6 MPa higher, in hydroponic than in ZPT-grown plants (Fig. 4, right). Measurements made after a 4-h dark period on Day 23 also showed that for similar leaf water potentials, the osmotic potential was significantly lower and the turgor significantly higher in hydroponic vs. ZPT-grown plants. On later test days, no differences in osmotic potential or turgor in leaves of plants grown in ZPT or hydroponic culture were observed.

It is not clear why a difference in leaf osmotic potential and turgor occurred between plants grown in the two culture systems around Day 22, and whether these differences affected growth and yield. Calcium, K, and Mg were higher in plants grown in hydroponic culture at Day 22 (Table 4), and accumulation of these nutrients could have contributed to lower leaf osmotic potential. Water deficits most probably limit reproduction during floral development, pollination, and fertilization (Gifford et al., 1984; Kramer and Boyer, 1995). Wheat was exposed to a 24-h photoperiod, which meant that water transport for both growth and reproduction occurred in the light. Lower osmotic potential and higher turgor in leaves of plants grown in hydroponic culture may have been an indicator of more favorable water status within the plant when seed set was occurring in primary tillers.

Nutritional Status of Substrate and Plants

Substrate

Post characterization of the zeoponic substrate indicated that N was nearly exhausted during intensive

Table 4. Nutrient concentrations for flag leaves of wheat grown hydroponically (H) or in zeoponic substrate with microporous tube irrigation (ZPT).

	Concentration				
		22 d‡		64 d§	
Element	Optimal†	H	ZPT	H	ZPT
N, g kg^{-1}	40	51	50.7	24.3 ± 4	24.4 ± 5
P, g kg^{-1}	6	6.2	6.3	2.9 ± 0.7	12.6 ± 1.4
K, g kg^{-1}	31	27.8	24.1	35.8 ± 8	34.1 ± 5
Ca, g kg^{-1}	10	11.5	4.3	16.6 ± 6.4	5.8 ± 2
Mg, g kg^{-1}	3	4.5	3.8	9.7 ± 3	4.4 ± 1
S, g kg^{-1}	3	6.3	5.5	6.7 ± 1	7.0 ± 1
Fe, mg kg^{-1}	112	176	123	456.0 ± 107	33.9 ± 26
B, mg kg^{-1}	44	80	82	144.0 ± 43	80.4 ± 29
Mn, mg kg^{-1}	55	123	85	50.3 ± 28	69.0 ± 34
Zn, mg kg^{-1}	32	37	31	14.5 ± 8	7.9 ± 1.6
Cu, mg kg^{-1}	10	19	10	3.5 ± 1	2.2 ± 0.4
Mo, mg kg^{-1}	0.5	18	5.8	19.3 ± 8	11.3 ± 3.5

† Desired concentration in fully expanded flag leaves (Bugbee and Salisbury, 1988).
‡ 1 sample per treatment.
§ Data are means ± 1 SD (n = 4).

growth of wheat under high light and 24-h photoperiod. About 4.6 ± 2.2% of the original NH_4–N remained in the substrate after the 64-d plant growth period. Originally, the ZPT substrate was fabricated with 28 $cmol_c$ (+)NH_4^+ kg^{-1} and at the end of the experiment, only 1.28 ± 0.63 $cmol_c$(+) NH_4^+ kg^{-1} remained on the exchange sites.

Nearly all of the original K^+ remained on zeolitic exchange sites at the end of the plant growth. Originally, the substrate contained 28 $cmol_c$(+)K^+ kg^{-1}; it contained 22.0 ± 2.3 $cmol_c$(+)K^+ kg^{-1} after plant growth. Hence, the substrate retained 78.5 ± 8.1% of its original K^+.

Plants

Flag leaf samples taken from plants grown in both hydroponic and ZPT culture on Day 22 and at harvest were analyzed for nutrients (Table 4). Nitrogen depletion of the zeoponic substrate probably did not contribute to the early senescence of leaves for plants grown in ZPT culture. At 22 d and at harvest, leaf tissue N was similar in leaves of plants from both ZPT and hydroponic culture (Table 4). Approximately 1.42 mol N was removed from exchange sites. Assuming that plants contained 3% N (Smart et al., 1996), 626 g biomass in ZPT culture meant that 1.34 mol N was in plant tissue, or a N mass balance recovery of 94%. This was significantly greater than the N mass balance of recovery reported for hydroponic systems, which is typically 70 to 85% due to denitrification (Smart et al., 1996).

Nitrate N was used in the hydroponic nutrient solution; NH_4–N was the initial source of N in the ZPT substrate, although the addition of nitrifying bacteria at planting should have ensured that some nitrification occurred. Ammonium N at levels used may be toxic to plants if pH is allowed to fall below ≈4.5 (Henry and Raper, 1989; Rideout and Raper, 1994). Although we did not measure the pH in the rhizosphere, pH in zeoponic substrate generally ranges between 6 and 7 (D.W. Ming, unpublished data, 1997). Further, wheat growth in our experiment did not exhibit symptoms of NH_4 toxicity, which include decreased N uptake and inhibition of leaf emergence and expansion (Henry and Raper, 1989). Therefore, we conclude that NH_4 toxicity was not responsible for the differences in biomass partitioning between plants grown in ZPT and hydroponic culture.

Several other problems are associated with NH_4 nutrition. Ammonium may inhibit uptake of cations such as K^+, Mg^{2+}, and Ca^{2+} (Hoff et al., 1974; Rideout and Raper, 1994). In the present study, Ca appeared to be the only major nutrient to be consistently lower in leaves of ZPT-grown than in hydroponic plants over the whole growing period, although K and Mg were lower in leaves of ZPT-grown plants at 22 d. At 22 d, Ca concentration in leaves from ZPT-grown plants was 4.3 g kg^{-1}; leaves from plants grown in hydroponic culture had Ca concentrations of 11.5 g kg^{-1}. Bugbee and Salisbury (1988) suggest that the optimal Ca concentration for mature leaves from wheat grown in solution culture in a high-light, controlled environment is 10.0 g kg^{-1}. The concentration of Ca in leaves from plants grown in ZPT culture was within the range of 2.0 to 5.5 g kg^{-1} suggested by Karlen and Whitney (1980) for wheat grown in the field at this stage of growth. While NH_4^+-induced Ca^{2+} deficiency may be one possible cause of low flag leaf Ca concentrations, other researchers have suggested that the low Ca content in wheat leaves grown in zeoponics is due to Ca^{2+} being tied up on the exchange sites of clinoptilolite and not available for plant uptake (Allen et al., 1995; Ming et al., 1995; Henderson et al., 1999).

The greater number of tillers produced by plants grown in ZPT culture may have been a direct result of N and/or Ca nutrition of plants. Camberato and Bock (1990) report that tillering of spring wheat increased with the proportion of NH_4^+ in fertilizer. While NH_4^+ generally increased total dry matter production, no direct correlation was noted between number of spikes and enhanced NH_4^+ supply due to detrimental effects of competition for water, light, and nutrients on late-developing tillers. Fenn et al. (1995) observed increased tillering in wheat when Ca^{2+} was added with NH_4^+, as well as increased N absorption and grain yield. The authors concluded that Ca in small grains was important to nutrient absorption and deposition of carbohydrates in seeds. By contrast, Ca deficiency in sorghum has been documented to be associated with excessive tillering due to death of the apical meristem and delayed flowering and maturity (Clark, 1993).

SUMMARY

Wheat biomass production and yield were not significantly different in ZPT or hydroponic culture, although seed number per tiller and harvest index were 26 and 28% lower, respectively, in plants grown in ZPT. It is probable that the major cause of excess tillering in plants grown in ZPT culture was the nutritional imbalance of NH_4^+-induced Ca deficiency. While we have no proof that the 60% lower Ca concentration in leaves of ZPT-grown plants at anthesis was the direct cause of differences in biomass partitioning, excess tillering did not enhance harvest index. Lack of seed set in green tillers of

ZPT-grown plants indicate that they could not compete with primary tillers for water, nutrients, and photoassimilate. The average weight per seed was similar for plants grown in either treatment, which indicates that seed filling was unaffected by differences between ZPT and hydroponic culture.

No consistent differences were noted in water status of plants grown in the two culture systems. This result led to the conclusion that the porous tube water delivery system is able to meet the water demands of wheat as well as hydroponics does under the highly rigorous growing conditions of high light and 24-h photoperiod.

Zeoponic–microporous tube culture has the potential to maintain the optimal root zone environment associated with hydroponic culture. Additional study of the chemistry of zeoponic substrate and the dynamics of water flow through the microporous tube–solid substrate–plant system would further improve ZPT culture.

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