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DEPARTMENT OF LAND, AIR AND WATER RESOURCES

HOAGLAND HALL
DAVIS, CALIFORNIA 95616

July 19, 1988

3. F-16

Dr. John Malcolm
Agency for International
Development
SeT/AG
Room 406B SA-18
Washington, D.C. 20523

RE: Grant #DPE-5542-G-SS-4016-00

Dear Dr. Malcolm:

I am referring to our earlier telephone conversation during which I proposed to send you copies of manuscripts related to the above grant when they become available. Enclosed is the first manuscript in draft form. It still needs some more editing which we intend to do in the very near future. The final form of this manuscript will be submitted to the international journal PLANT AND SOIL. Two more manuscripts are in preparation. I will send you copies of them as soon as drafts are completed.

In response to a recent letter by Dr I. M. Asher requesting some pictorial information from our grant, I believe the diagram exhibited in Figure 2 might be useful. If you agree, would you please share this with Dr. Asher. Thank you.

Sincerely yours,

André Läuchli
Professor of Plant Nutrition

AL:dp
Enclosure
cc: I. M. Asher
E. Epstein

Received SEP 29 1988

AN AUTOMATED GREENHOUSE SAND CULTURE SYSTEM SUITABLE FOR STUDIES OF P NUTRITION

KEY WORDS: Phosphorus, alumina, sand culture, Phaseolus, mycorrhizae, yield, leaf nutrients

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ABSTRACT

Maintenance of realistically low solution P concentrations under controlled conditions is a major difficulty in studies of P nutrition. In this report we describe a relatively simple and economical sand culture system capable of sustaining plant growth to maturity under controlled yet realistic P regimes. The system uses Al as a solid-phase P buffer and modern process control technology to control irrigation and addition of other mineral nutrients. Aspects of the design, implementation, and potential applications of automated solid-phase systems are discussed. The system was used to grow *Phaseolus vulgaris* to maturity at 0.4 μM, 1.0 μM, and 27 μM P with and without mycorrhizal inoculation. At flowering, low solution P concentrations were associated with reduced leaf concentrations of P in nonmycorrhizal plants and reduced leaf concentrations of Ca in both mycorrhizal and nonmycorrhizal plants. Mycorrhizal inoculation increased leaf P, K, Mg, and Mn concentrations but reduced leaf N concentration. Low P regimes reduced final seed yield by reducing both the number of pods per plant and the number of seeds per pod. Mycorrhizal inoculation significantly increased seed yield under low P regimes by increasing seed weight, the number of pods per plant, and the number of seeds per pod.

INTRODUCTION

The low concentrations of P in native soil solutions are difficult to reproduce under controlled conditions. Flowing solution culture systems with active nutrient monitoring and regulation are capable of supplying P (and other nutrients) to plants at precisely controlled levels, but such systems are complex and costly. Furthermore, solution culture does not adequately reproduce the temporal and spatial distribution of P available to root systems, which in soil is diffusion-limited and is subject to localized depletion (Barber, 1984).

Solid-phase P buffers provide an excellent alternative to active control of nutrient concentration in plant culture systems. The basic concept of solid-phase P buffers is to use a stationary P ligand to provide a buffered equilibrium P concentration determined by the amount of P on the stationary phase. Cassman *et al.* (1981) used Goethite to provide low, buffered levels of P to solution cultures of *Rhizobia*. Coltman *et al.* (1982) developed a sand-culture system employing P desorption from Al to study the early vegetative growth of tomato under realistic P regimes. Pereira and Bliss (1987) have recently used a system similar to Coltman's to evaluate the vegetative growth and nodulation of *Phaseolus* under a range of P treatments. Elliott *et al.* (1983) have developed an application of this technique to circulating nutrient solutions, and the technique has been extended to include other nutrients through the use of exchange resins (Chekai et al. 1987, 1988).

The method developed by Coltman *et al.* is especially attractive from the viewpoint of mimicking soil conditions, since it

utilizes particles of Al dispersed within a sand substrate, thus duplicating some of the spatial and temporal dimensions of soil P availability. Unfortunately, despite the merits of this procedure it has not as yet been utilized to any significant degree in controlled-environment research, perhaps because of the perceived difficulty in constructing such a system, or its limitation to studies of early vegetative growth.

In this report we describe a relatively simple and economical sand culture system capable of sustaining the growth of annual plants to maturity under controlled yet realistic P regimes. The system uses Al as a solid-phase P buffer like the system developed by Coltman *et al.*, and also employs large containers, *in situ* media preparation, media recycling, mycorrhizae, and modern process-control technology to control irrigation and addition of other mineral nutrients. The primary objective of this report is to present a fairly detailed description of this system, in order to facilitate the design and construction of easily managed solid-phase buffered ('SPB') sand culture systems for routine use in cultivating plants under controlled yet realistic environmental conditions.

Our secondary objective is to present a representative study of the effects of root P availability and mycorrhizal colonization on yield and yield parameters in the common bean (*Phaseolus vulgaris* L.). The common bean is an important food crop in many underdeveloped regions, and its production is often limited by low soil P availability. A recent geographic study conducted at the Centro Internacional de Agricultura Tropical (J. Fairbairn and P. Jones, 1987, unpublished data) indicates that of approximately 6

million hectares of beans grown in Latin American, 50% are grown in low P (≤ 8 ppm Bray 2) soils. The extent of P limitation in African bean production is presently unknown but probably comparable (J. Fairbairn and P. Jones, 1988, personal communication).

MATERIALS AND METHODS

Solid Phase P Buffer

Alumina (Alcoa, Grade F1, 28-48 mesh) was mixed with graded silica sand (Ottawa, Flint Shot 3.0, 41-43 mesh, 99.808% SiO_2) to 1.5 % weight/volume and placed in the automated irrigation system described below. Previous studies had verified published reports (Coltman *et al.*, Elliott *et al.* 1983) that the proportion of Al and sand in the mixture did not influence the equilibrium desorption concentration of P. The Al/sand mixture was treated with HCl to obtain a standard equilibrium pH of 5.0 prior to P adsorption, to standardize Al surface charge effects on Al-P binding and subsequent release (Elliott *et al.* 1987). For 1.5 % Al 20 mM HCl replaced every 2 hours for 24 hours produced an equilibrium pH of 5.0 after rinsing with deionized water every 2 hours for 12 hours. Following acid treatment and rinsing with deionized water, P was adsorbed onto the Al by exposing the Al/sand mixture to KH_2PO_4 solutions replaced every 3 hours for 72 hours. Adsorption can attain near-equilibrium levels in much shorter periods with frequent or constant solution replacement (such as would be provided by continuous pumping of solution past the Al; J Bold & G Elliott, personal communication). The kinetics of P adsorption and desorption from Al treated in this manner permit control of desorption solution P concentrations from 0.1 to 50 μM (Fig 1), an ideal range for P fertility studies.

Automated Irrigation System

The layout of the automated irrigation system is shown in Fig 2. Distilled water from the main water supply was passed through a

series of deionizing columns prior to storage. A particle filter downstream from the exchange columns trapped resin debris. The purified water was stored in two 300 gallon Nalgene tanks equipped with a float valve to mechanically shut off water influx when full. Large storage capacity was needed because the pumping requirement exceeded the supply capacity of purified water. The irrigation system was governed by a process controller, a Series One Junior Programmable Controller from General Electric. The Series One Junior is a 120 volt AC device with 15 channels of 24 volt input status recognition, a high-speed counter, and 9 channels of 24 volt relay closure output. Channel monitoring and output control is accomplished through RAM or PROM programs in the electronic control language 'Ladder Logic'. A 5 volt power supply with an operational amplifier conditioned signals from the flow meter, which were then fed directly to the high speed counter of the process controller and banks of Shawnee model 354 preset electronic counters. Relay outputs from the process controller and Shawnee counters were used to pulse drive the metering pumps. All power leads from the control unit were isolated 24 volt for safety.

At preset intervals irrigation cycles were initiated by the process controller. First the controller checked if sufficient water for an irrigation cycle was available in the reservoir by monitoring a float valve. If sufficient water was available, the main water pump (Gorman-Rupp model 14520-001 magnetic drive pump) was activated, pulling water into the greenhouse past an in-line flow meter (Signet Scientific mark 515 Paddlewheel Flosensor). Immediately after activating the main pump the controller opened

the solenoid inlet valve and closed the solenoid drain valve for the manifold. The signal from the flow meter was monitored by preset counters and the high-speed counter in the controller, which at preset volumes activated pulses of nutrient inputs into the water line by chemical metering pumps (Liquid Metronics Incorporated models A751 and A761. These units were designed to handle slurries and suspensions; ordinary diaphragm pumps did not function well with concentrated nutrient solutions because of clogging caused by fine suspended sediments). The concentration of nutrients in the water line was regulated by prior adjustment of pump stroke volume, pulse frequency, and nutrient stock concentration, and could be controlled with a precision of ≤ 5 %. Nutrient mixing in the water line was caused by turbulence from baffles and fittings. Downstream from the nutrient metering pumps all pipes, connections, and fittings were opaque to prevent algal growth. The solenoid inlet valve opened into a pressure-equalized inlet manifold constructed of 1" schedule 40 PVC pipe. It was essential for the proper operation of the system that outlet pressure at each pot be identical, and for this reason various measures were taken to equalize pressure within the inlet manifold. The system was designed to have two 25' benches with an aisle in between to permit access to the pots, numbering 180 in total (3 manifolds, 60 per manifold). Immediately downstream from the solenoid inlet valve the manifold diverged to each of the two benches using inlet pipes of equal length. Inlet pipes fed into the center of a closed '8' pattern, and then diverged to both sides of each bench. Opposite ends of the benches were interconnected to

correct for pressure gradients between benches. Each bench consisted of 2 x 4" wood beams laid on edge over 4 x 4" wood beams running perpendicular to the 2 x 4's along the length of the bench. The 4 x 4" beams were supported by steel stands spaced 1.5 m apart. This open grid construction allowed ready access of pot inlet and outlet lines to underlying manifolds hung from the sides of the 4 x 4" beams. All wood surfaces were protected with a chemical-resistant vinyl copolymer (Ameron Amercoat 33). Inlet pressure always flowed up to prevent vapor locks. Along the long sides of the benches 1/8" fittings were tapped directly into the manifold from which feeder lines ran to each pot. At the pot the feeder line fed into a loop suspended around the inside rim of the pot with numerous small holes that allowed the solution to evenly fill the pot. Pots were standard food service 5 gallon high-impact plastic cylindrical containers. To render the pots opaque yet reflective they were painted white with a black undercoat using Amercoat 33. To prevent flaking of paint from the pots the outer surfaces were abraded by sandblasting prior to painting. Pot drainage was provided by a 1/2" hole in the bottom of the pot covered by a tightly-woven fiberglass filter to prevent debris from clogging the outlet. An 1/8" fitting threaded into the drainage outlet led the drainage effluent to the drain manifold. Since the solenoid drain valve was closed during an irrigation cycle, the drain manifold was filled as the pots filled, and a stand pipe at the drain outlet had the same water level as the level in the pots. An adjustable float switch (Teel model 1P504) in the stand pipe signalled the controller when the pots were full, prompting the

controller to close the inlet solenoid and terminate the irrigation. After a preset time interval the controller opened the drain solenoid and the pots drained.

The cycle described above and in the accompanying diagram (Fig 2) pertains to one irrigation manifold. In actuality 3 separate manifolds were employed, each consisting of a unique inlet solenoid, outlet solenoid, and intervening plumbing to 60 pots (30 on each bench), allowing 3 separate treatments to be run concurrently without cross-contamination of the solutions. After the first manifold had completed an irrigation cycle the controller shifted to the next one until all pots had been irrigated. The duration of a complete irrigation cycle for all 180 pots was approximately 15 minutes. In addition to automated control through the process controller, the main pump, metering pumps, and each solenoid could be independently operated by manual switches to permit system manipulation without interfering with program execution by the process controller. This was useful, for example, during harvest of roots from the pots, which was facilitated by flooding the pots during harvest.

Following each experiment the sand/Al mixture was treated with HCl, rinsed, and adsorbed with P *in situ* by replacing the nutrient solution stocks with the appropriate chemical stocks. After 2 years of cultivation with beans and careful manual harvesting of all root material from the pots, no significant accumulation of organic debris was evident.

Mycorrhizal Inoculation

Soil and root debris infected with Glomus macrocarpum was provided by Dr. Gabor Bethlenfalvay. This material was mixed with sand/Al substrate and grown to 1 crop of beans in order to generate inoculum in sand/Al substrate. The resulting inoculum, containing approximately 640 viable spores per kg of substrate, was evenly mixed in the top 17 cm of inoculated pots at the rate of 390 g inoculum (250 spores) per pot. Sterilized inoculum was similarly applied to noninoculated pots.

Plant Cultivation

Bean (Phaseolus vulgaris L.) seed cv. EMP-84 (a type III small seeded black variety) was provided by Dr. Michael Thung from material increased in Goiania, Brazil. Seeds were surface sterilized in 1 % NaOCl and 0.25 % Triton X-100 (Sigma) for 10 min, rinsed thoroughly in deionized water for 10 min, and germinated on paper towels moistened with 0.5 mM $CaSO_4$ in sealed glass casserole dishes for 48 hours in the dark at 27 ± 0.5 °C. Germinated seedlings were selected for vigor and uniformity and transplanted into the sand culture system 2 cm below the sand surface with the radical down. Three seedlings were transplanted per pot and thinned to 1 seedling per pot after emergence.

Plants were grown in Davis California between May and July of 1987. The greenhouse was well ventilated with evaporative coolers and had steam heating. A light coat of whitewash was necessary in mid-June. Maximum temperature (day) was 32 °C, minimum temperature (night) was 20 °C. Minimum RH (day) was 60 %, maximum RH (night) was 87 %. Maximum photosynthetically active radiation on clear days ranged from 850 to 1400 $\mu E \cdot m^{-2} \cdot s^{-1}$.

Nutrient solution was provided twice daily (06:00 and 12:00) with the irrigations. Three distinct nutrient solution stocks were required: Ca and SO_4 had to be separated to prevent precipitation at high concentration, and a third solution provided PO_4 at different levels for the three different manifolds. The first two nutrient solution stocks were diluted by a factor of 1000 when input into the irrigation system. The composition of the first stock was (in mM): 1,500 KNO_3, 1,200 $Ca(NO_3)_2$, 400 NH_4NO_3, 25 $MgCL_2$, 5 FeEDTA. The composition of the second stock was (in mM): 500 $MgSO_4$, 300 K_2SO_4, 300 NH_4SO_4, 1.5 $MnSO_4$, 1.5 $ZnSO_4$, 0.5 $CuSO_4$, 0.143 $NH_4Mo_7O_{24}$, 0.5 $Na_2B_4O_7$. The solid-phase buffer supplied either 0.4, 1.0, or 27 µM P to the plants, and these concentrations were also supplied with each irrigation as KH_2PO_4 from the third stock of 15 mM KH_2PO_4.

Plant Analysis

At anthesis (33 days after planting) the youngest fully-expanded leaf from appropriate plants was excised, rinsed briefly in 1.0 M HCl, rinsed briefly in deionized water, and dried at 70 °C for 48 hours. After weighing the samples were pulverized in plastic containers on a 'Wig-L-Bug' shaker, digested in peroxymonosulfuric acid (Hach *et al.* 1985), and analyzed for elemental content by inductively-coupled plasma spectrometry. Nitrogen was analyzed conductimetrically (Carlson ref). Harvest parameters were collected from fully senescent plants after drying at 70 °C for 24 hours. Solution P levels were analyzed by the method of Murphy and Riley (1962).

Statistical Analysis

Data were analyzed using unbalanced multiple analysis of variance,from which the $LSD_{(0.05)}$ was calculated for comparison of individual means (Sokal and Rohlf, 1981).

RESULTS

Leaf Nutrient Content

Leaf nutrient content at anthesis is shown in Table 1. In nonmycorrhizal plants low P levels were associated with reduced leaf P concentration, although leaf P concentration was unresponsive to P supply in mycorrhizal plants. Phosphorus was the only nutrient for which mycorrhizal inoculation showed a significant interaction with P supply. Low P supply was also associated with reduced leaf Ca concentration, perhaps by reducing Ca phosphate precipitation in the vacuole.

Mycorrhizal inoculation increased leaf P concentrations at low P supply, but not at adequate P levels. Mycorrhizal inoculation elevated leaf concentrations of K, Mg, and Mn, but reduced leaf N concentration under low P regimes. Reduced leaf N concentration in mycorrhizal plants could be accounted for by growth dilution resulting from alleviation of P deficiency.

Compared to published values for field-grown plants, the levels of leaf nutrients in P-sufficient plants is in the normal range for beans, although K is somewhat higher and Ca and Mg somewhat lower (Howeler 1980). Al concentrations are somewhat higher than expected but below the toxic range. Neither P supply nor mycorrhizal inoculation had interactions with leaf Al accumulation (Table 1).

Yield Parameters

Yield parameters as affected by P supply and mycorrhizal inoculation are shown in Table 2. Low P supply without mycorrhizal inoculation dramatically reduced seed yield, largely by reducing the

number of pods per plant and the number of seeds per pod, and also by reducing seed weight at the lowest P level. Mycorrhizal inoculation substantially increased seed yield at low and medium P levels but not at adequate P levels, predominantly by increasing the number of pods per plant, and secondarily by increasing the number of seeds per pod and seed weight. The interaction of P supply and mycorrhizal inoculation was statistically significant for all yield parameters.

DISCUSSION

The merits of the sand culture system described above resolve to 2 basic factors: the use of Al as a solid-phase buffer (SPB) for P, and the use of contemporary process control equipment to automate system operation. Technical dimensions of P exchange with Al are beyond the scope of this report and have been discussed elsewhere in this context (Coltman *et al.* 1982, Elliott *et al.* 1983, Elliott *et al.* 1987): this discussion will focus on practical dimensions of designing and implementing SPB systems.

We used a relatively low Al concentration (1.5 % weight/volume) to increase the probability of obtaining localized P depletion in the rhizosphere, as occurs in the soil. Low Al concentration also means low total buffering capacity, and for this reason we continually replenished the system by including the equilibrium concentration of P with each irrigation, rather than allowing the original adsorbed P fraction to supply all the P taken up by the plant. In addition to plant P uptake, repeated flushing during irrigation would have depleted the supply of adsorbed P in the pots. Had we been interested only in early vegetative growth, replenishment may not have been necessary, but in this case gradually falling equilibrium P levels would have complicated the reproducibility and interpretation of the experiment. Addition of dissolved P with the nutrient solution irrigations would seem to negate the advantages of dispersed solid phase P sources noted above. However, the kinetics of P adsorption onto the Al and P uptake by roots are such that the low concentrations of P added with the nutrient solution would be depleted within a very short period after

irrigation, in those zones already depleted by root activity. In zones not already depleted by root activity the added P would serve merely to replace the leached solution at the same equilibrium concentration.

The validity of our method is shown by the similarity in bean responses to P supply in our system as compared with published data for beans grown in low-P soils (CIAT ref 1977). In the system of Coltman *et al.* tomato grown on an Al/sand substrate without P replenishment shows an order of magnitude greater demand for P. Our high P level of 27 µM P was selected as abundantly adequate, since earlier experiments showed that bean growth response saturated at 3 µM P. Our present data show that seed yield was 25 % of maximal for nonmycorrhizal plants at 1 µM P, whereas the system of Coltman *et al.* can barely sustain growth at 1 µM P (Coltman *et al.* 1982· Fig 3). Some of this difference could of course be due to differences between tomato and bean, although bean is not normally considered to be particularly adapted to low P conditions. Coltman *et al.* present data that increasing Al concentration at a given equilibrium P concentration significantly increased plant growth and altered shoot nutrient concentrations, indicating that the buffering capacity of the system limited root P acquisition. Use of lower Al concentrations with periodic replenishment such as described here may minimize this complication while maintaining key features of soil P availability. Coltman *et al.* also observed very high levels of Al in their tomato tissue (up to 920 ppm, well within the toxic range), which we did not observe in bean leaves (Table 1). At high substrate Al concentrations localized rhizosphere acidification may

solubilize Al, leading to excessive Al accumulation and increased P requirements (Marschner 1986). This may be another reason to employ low Al concentrations with replenishment rather than relying entirely on P desorption from higher Al concentrations. An additional advantage of low Al concentrations is that the system is more flexible during system operation, since P regimes can be changed during ontogeny by changing the P content of the nutrient solution, whereas this is more difficult with high Al concentrations having larger buffer capacity. In view of these factors, as well as the excellent and quite reasonable response obtained to mycorrhizal inoculation, we propose that a low buffer capacity, replenished SPB system such as that described here is entirely suitable for studies of P nutrition.

Optimal components for construction of an automated irrigation system will change with the rapid development of microprocessor-based electronic hardware. The process controller described above, a GE Series One Junior, was well suited to our application, and at a 1985 cost of US$ 400 was an economical alternative to assembling our own relay control circuitry. Two shortcomings to this particular model were its low-level control language and its lack of an internal real-time clock. However, industrial process controllers in general have several important features that make them ideal for experimental greenhouse use. Most experimental applications require more flexibility, complexity, and logical capacity than commercial irrigation timers supply. Microcomputers, while powerful and flexible, are not designed to withstand the harsh environmental conditions of a greenhouse,

which include exposure to water, corrosive fumes and solutions, extremes of temperature and humidity, pesticides, bright sunlight, and uneven power supply. Furthermore, interfacing a microcomputer with diverse hardware requiring exogenous DC power can be complex. The modern process controller is essentially a microcomputer specifically designed to withstand harsh conditions and to monitor and control an array of hardware devices. Sophisticated process controllers are expensive and can be difficult to program, but simpler models now widely available are ideal for the control of small greenhouse systems such as that described above. It is increasingly common to find simpler models with high-speed electronic counters able to monitor an in-line flow meter. Units not having this feature can be used in conjunction with stand-alone counters as described above.

Certainly realistic P concentrations and mycorrhizal inoculation must be included in any serious simulation of natural soil conditions, particularly low P soils such as the Oxisols and Ultisols of the humid tropics. Furthermore, growing evidence of the importance of P in many fundamental plant processes such as photosynthesis (Sivak and Walker 1986) suggests that SPB systems would find useful applications in many physiological investigations beyond the realm of P fertility *per se*. A striking example of the importance of using realistic P regimes is provided by the work of Gratton and Maas (1984), who found that millimolar concentrations of P in conventional nutrient solutions substantially enhanced the sensitivity of soybeans to salinity stress.

SPB techniques could be extended to a number of simulations of temporal and spatial variations in root environments. For example, pH can be controlled by stationary buffers (Checkai *et al.* 1987), cation and anion exchange capacity can be controlled with commercial resins, Fe can be supplied as a solid substrate (Juaregui and Reisenaur 1982), zeolites such as clinoptolilite could supply K, and so on. Solid-phase nutrient sources could be distributed in space to simulate highly stratified soils such as Spodosols or could be kinetically manipulated to reproduce temporal fertility dynamics.

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REFERENCES

Barber S A 1984. Soil Nutrient Bioavailability. A Mechanistic Approach. John Wiley, New York.

Carlson reference RE N conductimetric method

Cassman K G, Munns D N, and Beck D P 1981. Phosphorus nutrition of Rhizobium japonicum: strain differences in phosphate storage and utilization. Soil Sci. Soc. Amer. J. 45:517-520.

Checkai R T, Norvell W A, Welch R M and Brown P H 1987. Using exchange resins to impose nutrient treatments on hydroponically grown seedlings from germination to transplanting. J. Plant Nutr. 10, 1447-1455.

Checkai R T, Hendrickson L L, Corey R B, and Helmke P A 1988. A method for controlling the activities of free metal, hydrogen, and phosphate ions in hydroponic solutions using ion exchange and chelating resins. Plant and Soil 99, 321-334.

Coltman R R, Gerloff G C, and Gabelman W H 1982. A sand culture system for simulating plant responses to phosphorus in soil. J. Am. Soc. Hort. Sci. 107:938-942.

Elliott G C , Carlson R M , Läuchli A , and Rosen C J 1983. A solid-phase buffer technique to maintain low concentrations of phosphate in nutrient solutions. J. Plant Nutr. 6:1043-1058.

Elliott, G C , Lynch, J , Läuchli A , and Anderson E L 1987. Solid-phase buffering of phosphate in sand cultures. J. Plant Nutr. 10, 1499.

Gratton S R and Maas E V 1984. Interactive effects of salinity and substrate phosphate on soybean. Agron. J. 76, 668-676.

Hach C C, Brayton S V, and Kopelove A B 1985. A powerful Kjeldahl nitrogen method using peroxymonosulfuric acid. J. Ag. Food Chem. 33, 1117-1120.

Howeler R H 1980. Nutritional disorders. In: Bean Production Problems. Disease, Insect, Soil and Climate Constraints of *Phaseolus vulgaris*. Schwartz H F and Galvez G E, editors. pp 341-357. CIAT, Cali.

Juaregui M A, Reisenaur H M 1982. Calcium carbonate and manganese dioxide as regulators of available manganese and iron. Soil Sci. 134, 105-110.

Marschner H, 1986. Mineral Nutrition of Higher Plants. Academic Press, London, Orlando, San Diego, New York, Austin, Boston, Sydney, Tokyo, Toronto.

Murphy J and Riley J P, 1962. A modified single solution reagent for the determination of phosphate in natural waters. Anal. Chim. Acta 27,31-36.

Pereira P A A and Bliss F A 1987. Nitrogen fixation and plant growth of common bean (Phaseolus vulgaris L. at different levels of phosphorus availability. Plant and Soil 104,79-84.

Sivak M N, and Walker D A 1986. Photosynthesis in vivo can be limited by phosphorus supply. New Phytol. 102,499-512.

Sokal, R.R. and Rohlf, F.J., 1981. Biometry. 2nd edition. W.H. Freeman and Company, New York.

FIGURE CAPTIONS

Figure 1. Sorption curves for P with Al. The Al was pretreated with HCl to give an equilibrium pH of 5.0, then exposed to the indicated concentration of KH_2PO_4 replaced every 3 hours for 72 hours. Desorption concentrations were measured after repeated rinsing of the Al in deionized water for 72 hours.

Figure 2. Diagram of automated greenhouse irrigation system. Solid lines; flow of water. Dotted lines; electrical connections. For explanation see text.

TABLE 1

Effect of P supply and mycorrhizal inoculation on nutrient concentrations (dry weight basis) in young fully-expanded leaves of bean variety EMP 84 at anthesis. 3 replicates per treatment.

P level (µM)	Myco. inoc.	P	N	K	Ca	Mg	Fe	Mn	Zn	Al
		<----------(%)----------					<----------(ppm)---------->			
0.4	no	0.12	5.46	2.37	0.57	0.22	80.5	25.4	44.0	56.6
1.0	no	0.16	5.44	2.70	0.82	0.25	63.4	32.0	51.1	44.4
27.0	no	0.19	4.24	2.72	0.89	0.27	74.8	33.1	62.4	56.5
0.4	yes	0.21	4.32	2.77	0.65	0.26	89.8	37.6	52.1	48.6
1.0	yes	0.18	3.21	2.70	0.72	0.29	77.3	38.2	62.7	53.8
27.0	yes	0.21	4.45	2.99	0.95	0.28	76.8	38.6	60.9	58.4
$LSD_{(0.05)}$		0.04	1.78	0.38	0.23	0.07	19.0	6.8	22.7	29.2
Significance of F Test†										
P Level		*	ns	ns	**	ns	ns	ns	ns	ns
Myco. Inoc.		**	*	*	ns	*	ns	**	ns	ns
interaction		*	ns	ns	ns	ns	ns	ns	ns	ns

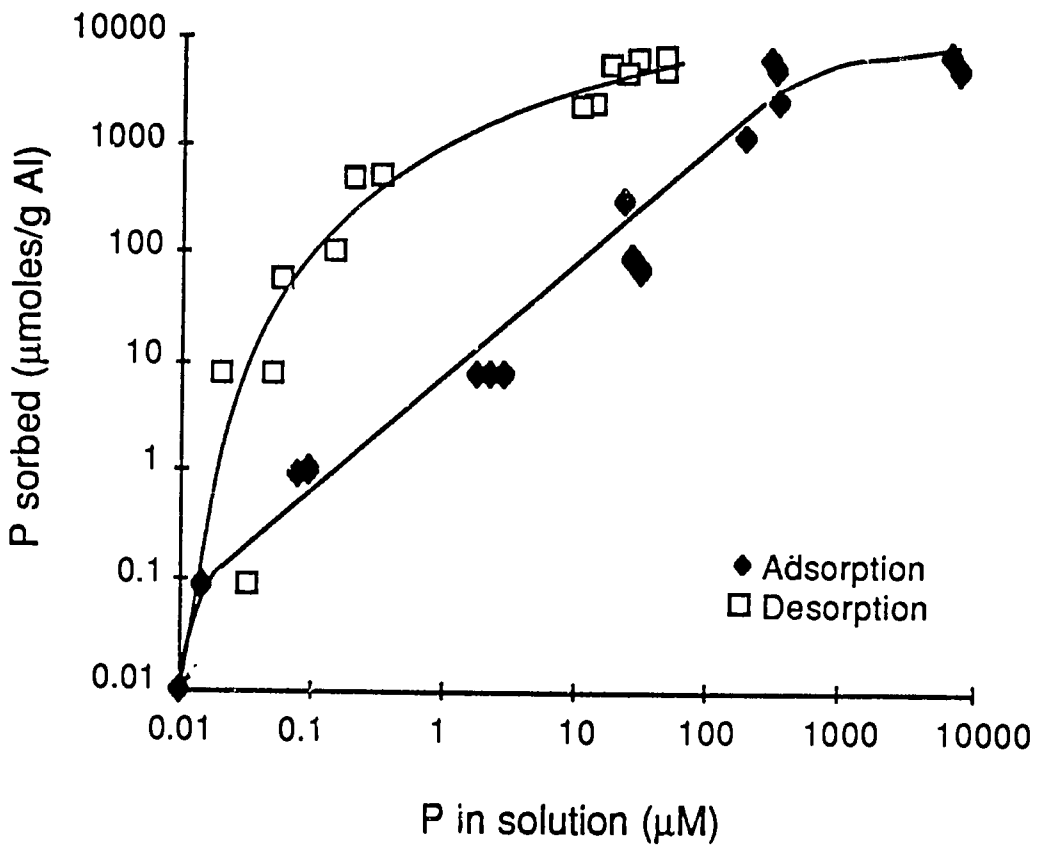
† '*' : $0.05 \geq p > 0.01$. '**' : $0.01 \geq p > 0.001$. '***' : $p \leq 0.001$.

TABLE 2

Effect of P supply and mycorrhizal inoculation on yield parameters for individual plants of bean variety EMP 84. 15 replicates per treatment.

P level (µM)	myco. inoc.	yield (g)	#seeds	#pods	seed wt. (g)	seeds per pod
0.4	no	0.3	1	2.3	0.32	0.43
1.0	no	17.0	40	13.6	0.43	2.93
27.0	no	67.6	188	45.2	0.36	4.17
0.4	yes	6.2	16	9.4	0.39	1.71
1.0	yes	38.0	86	27.5	0.44	3.13
27.0	yes	71.4	171	41.9	0.42	4.09
$LSD_{(0.05)}$		5.3	15	4.8	0.10	0.52
Significance of F Test†						
P Level		***	***	***	*	***
Myco. Inoc.		***	***	***	**	***
interaction		***	***	***	*	***

† '*' : $0.05 \geq p > 0.01$. '**' : $0.01 \geq p > 0.001$. '***' : $p \leq 0.001$.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Desorption

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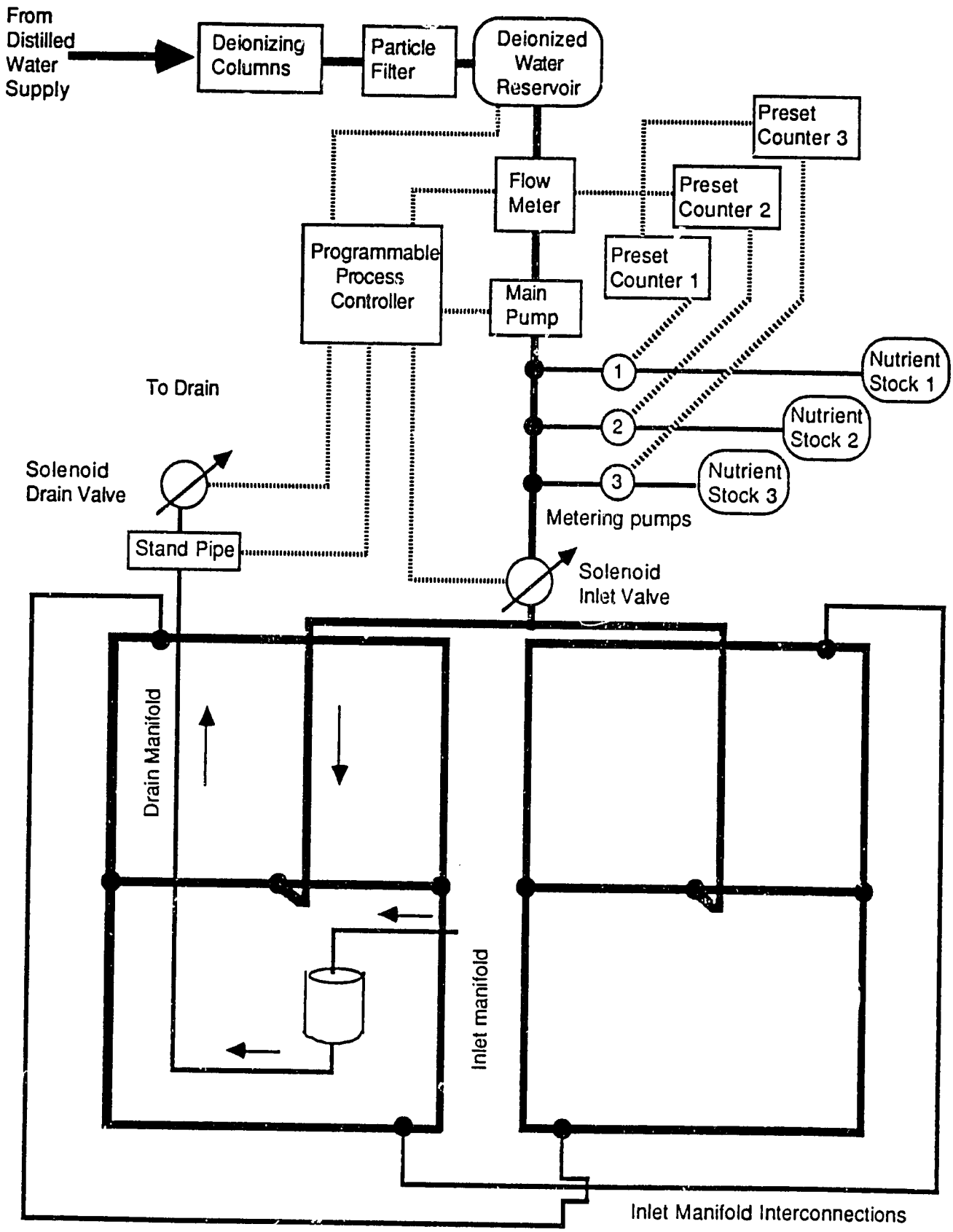
From Distilled Water Supply
Deionizing Columns
Particle Filter
Deionized Water Reservoir
Preset Counter 3
Flow Meter
Preset Counter 2
Programmable Process Controller
Preset Counter 1
Main Pump
1
Nutrient Stock 1
To Drain
2
Nutrient Stock 2
Solenoid Drain Valve
3
Nutrient Stock 3
Metering pumps
Stand Pipe
Solenoid Inlet Valve
Drain Manifold
Inlet manifold
Inlet Manifold Interconnections