Optimizing the Calcium Content of a Copolymer Acrylamide Gel Matrix for Dark-grown Seedlings

Patricia Newton Myers¹ and Cary A. Mitchell²

Purdue University, Department of Horticulture, Center for Plant Environmental Stress Physiology, West Lafayette, IN 47907-1165

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ABSTRACT. A copolymer acrylamide acrylate gel was investigated as the sole root matrix for dark-grown seedlings of soybean (*Glycine max* Merr. 'Century 84'). Increasing Ca^{2+} in the hydrating solution of the hydrogel from 1 to 10 mM decreased its water-holding capacity from 97 to 46 $\text{mL}\cdot\text{g}^{-1}$, yet water potential of the medium remained high, sufficient for normal plant growth at all Ca^{2+} concentrations tested. Elongation rate of dark-grown soybean seedlings over a 54-hour period was 0.9, 1.5, and 1.8 $\text{mm}\cdot\text{h}^{-1}$ with 1.0, 2.5, or 5.0 mM Ca^{2+} , respectively, but did not increase with further increases in Ca^{2+} concentration. Further study revealed that Na^+ was released from the hydrogel medium and was taken up by the seedlings as Ca^{2+} increased in the medium. In dry hypocotyl tissue, sodium content correlated negatively with calcium content. Despite the presence of Na^+ in the hydrogel, seedling growth was normal when adequate Ca^{2+} was added in the hydrating solution. Acrylamide hydrogels hold good potential as a sole growth matrix for short-term experiments with dark-grown seedlings without irrigation.

Dark-grown seedlings long have been valued in plant-science research as a source of bioassay (Parker et al., 1949) and extraction material for hormone and metabolite analyses (Furuya et al., 1962). Growth time in photobiological darkrooms typically is on the order of a week or less from start to finish of an experiment (Mitchell, 1977), and a typical goal is to obtain a dense, uniform stand of rapidly growing seedlings. Consequently, it is highly desirable to use artificial plant-growth media that simultaneously provide high water-holding capacity and adequate rhizosphere aeration. Coarse vermiculite commonly is used, but dense seedling stands rapidly deplete vermiculite of moisture, typically requiring rewetting once or even twice during a given experiment. It is experimentally undesirable to allow root-zone water potential to repeatedly ramp down and up during the rapid cell-enlargement phase of seedling growth in darkness, and it is better not to risk physical perturbation of plant tissue during rewatering in darkrooms, especially since growth of etiolated seedlings is extremely sensitive to mechanical stress (Jones and Mitchell, 1989).

Our laboratory has tested various artificial growth media in an effort to find substrates that provide adequate seedling anchorage, that maintain nongrowth-limiting water potentials for at least a week, and which sustain adequate root aeration. Diced agar and cellulosic hydrogels have high hydration capacity, but under nonsterile conditions provide a readily available source of carbon substrate for respiring microorganisms. The resulting competition for rhizosphere oxygen and toxins released severely stunt or kill dark-grown seedlings.

We were aware that hydrophilic polymers have been used successfully as soil amendments in the horticulture industry to improve the water-holding capacity of soil mixes for container-

grown plant material (Johnson, 1984). However, fertilizers rich in the divalent cations Ca^{2+} , Fe^{2+} , and Mg^{2+} have been shown to diminish the hydration capacity of those hydrogels (Bowman et al., 1990; Johnson, 1984; Wang and Gregg, 1990). The efficacy of hydrogels as a soil amendment to improve plant growth has been a controversial issue (Keever et al., 1989; Wallace and Wallace, 1990; Wang, 1987), and modifications of cultural practices have been suggested to enhance their efficacy, especially the acrylamide gels, in nursery crop usage (Bowman and Evans, 1991; Wang and Gregg, 1990).

We became interested in using a copolymer acrylamide acrylate whose crystals hydrate into irregular, coarse chunks of gel (SuperSorb-C, Aquatrols, Inc., Cherry Hill, N.J.) as a sole growth matrix after preliminary tests indicated that it provided adequate root support for etiolated seedlings and no visible evidence of bacterial or mold growth after roots of soybean seedlings grew in it for a week. However, seedling growth beyond germination was virtually nil unless Ca^{2+} salts were included in the hydrating solution. The objective of the present investigation was to optimize Ca^{2+} level in the hydrating solution for seedling growth.

Materials and Methods

SUPERSORB-C PREPARATION AND CHARACTERIZATION. Dry SuperSorb-C (20 g) was added to 2 L each of 1.0, 2.5, 5.0, 7.5, or 10.0 mM $\text{Ca}(\text{NO}_3)_2$ solution. After 12 h, hydrated gel particles were drained for 30 min, volumes of gel and drained liquid were determined, and the amount of solution absorbed was calculated. The Ca^{2+} concentration in the drained solution was measured using an ion-selective electrode (model 250 ion analyzer; Corning, N.Y.). Ca^{2+} content of hydrated SuperSorb-C was calculated by subtracting the amount in the drained solution from that in the starting solution, and dividing by total gel volume. Plastic vials with bottom drainage holes were filled with hydrated SuperSorb-C, and specific Ca^{2+} content ($\mu\text{mol}\cdot\text{cm}^{-3}$) of the hydrated SuperSorb-C was calculated. Random samples of SuperSorb-C were collected before planting and after 4 d of seedling growth for each Ca^{2+} treatment. Water potential (Ψ_w) was determined for individual gel particles by thermocouple psychrometry (model HR-33T microvoltmeter with a C-52 sample chamber; Wescor, Inc., Logan, Utah). Equivalent-sized particles (≈ 5 mm in diameter) were placed

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¹Postdoctoral research associate.

²Professor; to whom reprint requests should be addressed.

Table 1. SuperSorb-C characteristics following hydration of 20 g dry SuperSorb-C with 2 L of solution.

Ca(NO ₃) ₂ concn (mM)	Solution absorbed (mL·g ⁻¹)	SuperSorb vol (cm ³)	SuperSorb Ca ²⁺		SuperSorb Ψ^w	
			Ca ²⁺ retained (%)	Specific Ca ²⁺ growth (mmol·cm ⁻³)	Before growth (MPa)	After (MPa)
1.0	97.1 a ^c	2399 a	95.7 a	0.74	-0.06 a	-0.10 a
2.5	90.0 b	2195 b	93.6 b	2.20	-0.09 a	-0.10 a
5.0	71.5 c	1769 c	92.8 c	5.29	-0.14 ab	-0.16 a
7.5	58.3 d	1378 d	90.7 c	9.85	-0.21 ab	-0.20 a
10.0	45.5 e	1106 e	84.1 d	14.70	-0.22 b	-0.21 a

^cMean separation in columns at $P \leq 0.01$ by Student-Newman-Keuls test.

in each psychrometer chamber and equilibrated for 4 h at room temperature (24 ± 1 °C) before Ψ_w determinations.

PLANT MATERIAL. Soybean (*Glycine max* 'Century 84') seeds were surface-disinfested by soaking dry seeds in 10% (v/v) chlorine bleach in tap water for 10 min and then rinsed for 20 min under running tap water. Partially imbibed seeds were placed on two layers of Whatman no. 1 filter paper in the center of a large plastic box, covered with an additional layer of filter paper, and moistened with tap water, allowing drainage of excess water to recessed edges of the box. The container was covered to maintain high humidity. After 24 h at 26 ± 1 °C, germinated seeds with straight radicles 5 to 10 mm long were selected and planted 1 cm deep in 68 cm³ vials filled with SuperSorb-C. The seedlings were then cultured in darkness at 26 ± 1 °C under a plastic cover to maintain a humid atmosphere (relative humidity 80%) and to protect against physical disturbances (air currents, etc.). Hypocotyl length was measured against a ruled background under green safelight at 3- to 12-h intervals over a 3-d period. The experiment was repeated 3 times with 12 replicate seedlings for each Ca²⁺ treatment. Data were analyzed by SuperANOVA (Abacus Concepts, Inc., Berkeley, Calif.).

HYPOCOTYL CA²⁺ DETERMINATION. After a total of 122 h of growth, including 98 h at various Ca²⁺ treatment levels, seedlings were removed from the hydrogel and fresh mass was determined for roots, hypocotyls, and cotyledons. Seedling parts were then oven dried at 70 °C for 3 d and dry mass was determined. Each dry hypocotyl was broken into small pieces, placed in a Folin-Wu tube, and incubated with 0.5 mL of 30% (v/v) hydrogen peroxide for 20 min. One milliliter of perchloric acid was then added to each tube and the tissue was digested at 240 °C. After 5 min, and again after 15 min, an additional 1.0 mL of H₂O₂ was added to each tube. Digestion continued until all fumes disappeared, indicating evaporation of the H₂O₂ (Adler and Wilcox, 1985). Samples were diluted appropriately with deionized water, and calcium in the diluted digestion solution was measured by atomic absorption spectroscopy (SpectrAA-10; Varian, Palo Alto, Calif.). Subsequent calcium and sodium contents in dry hypocotyl tissue were determined by inductively coupled plasma (ICP)-atomic emission spectroscopy (Nielsen et al., 1997).

COMPARING SUPERSORB-C AND VERMICULITE. Vermiculite was hydrated overnight in appropriate Ca(NO₃)₂ solutions and then drained in the same manner as SuperSorb-C. Because vermiculite typically dries out during the course of a 5-d growth experiment, whereas SuperSorb-C does not, 1 × 9-cm capillary wicks were inserted 4.5 cm into the 3.6-cm-diameter × 6.0-cm-long cylindrical vials containing vermiculite. The remaining 4.5 cm of wick extended through a slit in the base of the vials supported on plastic grating into Ca(NO₃)₂ solution within petri dishes below the grating. After 5 d of growth in darkness, seedlings were harvested,

hypocotyl length was measured, and hypocotyls were oven dried. Dry hypocotyls were digested as described and analyzed for Ca²⁺ and Na⁺ content by ICP spectroscopy.

Results and Discussion

SUPERSORB-C CHARACTERISTICS. Dry SuperSorb-C crystals readily absorbed Ca(NO₃)₂ solutions, forming coarse chunks of irregular-shaped gel particles with airspace continuity between particles. The volume of aqueous solution absorbed by the gel decreased from 97 to 45 mL·g⁻¹ dry mass of SuperSorb-C crystals as Ca²⁺ was increased in the hydrating solution from 1 to 10 mM (Table 1). Only half of the available 2-L volume of 10 mM Ca(NO₃)₂ solution was absorbed by 20 g of dry SuperSorb-C crystals, yet 84% of the available Ca²⁺ was absorbed or adsorbed by the gel, resulting in a specific Ca²⁺ content of 14.7 mmol·cm⁻³. In contrast, the gel hydrated with 1.0 mM Ca(NO₃)₂ solution had a specific Ca²⁺ content of 0.74 mmol·cm⁻³. None of the differences in Ψ_w among Ca(NO₃)₂ treatments before or after 4 d of seedling growth in darkness were in a range that limit seedling growth (Boyer, 1985). In fact, seedlings grew faster in Ca²⁺ solutions corresponding to the lowest water potential values than to the highest (Table 1, Fig. 1). The hydrogel not only anchored the roots

Fig. 1. Soybean seedling elongation in SuperSorb-C hydrated with 1.0, 2.5, 5.0, 7.5, or 10.0 mM Ca(NO₃)₂. Data points represent the average of three separate experiments with 10 to 12 seedling replications each. Linear regression of elongation over time had a regression coefficient (r) of 0.99 for all Ca²⁺ treatments in the main plot. The inset shows average elongation rates of individual seedlings over a 2.5-d period regressed against Ca²⁺ concentration using a quadratic formula ($y = 0.7706 + 0.3502x - 0.0268x^2 + 0.0056x^3$, $P < 0.0001$). Based on the quadratic model the peak value is estimated at 6.5 mM Ca²⁺.

Fig. 2. Dry mass of soybean seedling hypocotyls and roots after 4-d of growth in SuperSorb-C hydrated with 1.0, 2.5, 5.0, 7.5, or 10.0 mM $\text{Ca}(\text{NO}_3)_2$. Different letters denote mean separation among treatments (within a given plant part) by Student-Newman-Keuls test at $P < 0.05$.

of developing seedlings physically, but maintained nonlimiting root-zone Ψ_w without the mechanical or Ψ_w perturbations that occur when a medium is irrigated periodically. Nongrowth-limiting Ψ_w values were maintained across a 10-fold range of $\text{Ca}(\text{NO}_3)_2$ levels from 1 to 10 mM. Additionally, no signs of microbial growth were observed in the growth matrix formed by the acrylamide hydrogel, unlike our previous observations with agar and cellulose-based hydrogels tested for plant growth.

EFFECTS OF Ca^{2+} ON ROOT DEVELOPMENT AND HYPOCOTYL ELONGATION. The addition of Ca^{2+} to SuperSorb-C proved to be essential for normal seedling development. SuperSorb-C hydrated with distilled water did not support root or hypocotyl development, hence no measurements could be made on what normally would be a zero-calcium control. Preliminary studies conducted with various anions in combination with Ca^{2+} indicated no substantial differences in early seedling growth characteristics as long as Ca^{2+} was present. Hypocotyls were 86% as long in 5 mM CaCl_2 as in 5 mM $\text{Ca}(\text{NO}_3)_2$ after 5 d of growth, while roots were 124% as long. Root branching was identical for the two Ca^{2+} salts but was nonexistent if K^+ was substituted for Ca^{2+} in the hydrating solution. Seedling fresh mass using CaCl_2 was 87% of that using $\text{Ca}(\text{NO}_3)_2$, but in KNO_3 it was 21%, and in distilled water there was no growth beyond germination to measure. Soybean hypocotyl elongation responded positively to increases in external Ca^{2+} from 1 to 5 mM (Fig. 1). Calcium at 5 mM in the hydrating solution supported hypocotyl elongation at $1.8 \text{ mm} \cdot \text{h}^{-1}$ (Fig. 1 inset), but further increasing Ca^{2+} to 10 mM began to suppress elongation rate. Effects of supraoptimal Ca^{2+} on cell enlargement are more likely due to effects on cell wall and/or membrane properties than to ionic strength or water potential in this case. Apoplastic free Ca^{2+} may interfere with acid-induced cell-wall loosening (Tepfer and Cleland, 1979), possibly by down-regulating the rate of proton extrusion through the plasma membrane into the cell wall space (Rubenstein et al., 1977), or by reacting with carboxyl groups attached to pectin

within the wall space to form calcium bridges that resist the viscoelastic extensibility needed for cell enlargement (Virk and Cleland, 1988). As Ca^{2+} replaces H^+ within the Donnan free space of cell walls, ambient pH rises, walls tighten, and cell enlargement is effectively retarded (Hepler and Wayne, 1985).

Hypocotyl and root dry mass were enhanced by hydrating the gel growth matrix with Ca^{2+} at 5 mM relative to those at 1 mM (Fig. 2). Increasing Ca^{2+} concentration to 7.5 or 10 mM did not further enhance dry mass. Since these experiments were conducted with dark-grown seedlings, the increases in dry mass occurring with increasing $\text{Ca}(\text{NO}_3)_2$ concentration clearly were a result of salt accumulation being greater than seedling respiratory losses. Vigorous root elongation and branching were observed for seedlings grown at $\text{Ca}(\text{NO}_3)_2$ concentrations > 2.5 mM, but root development was limited at ≤ 1 mM Ca^{2+} . Root cell divisions require minimal Ca^{2+} (e.g., 10^{-7} M) for normal mitoses (Burström, 1968). Root cell enlargement, however, requires higher levels of Ca^{2+} (10^{-5} to 10^{-2} M) in the root zone, depending on species and the ionic environment of the growth matrix (Burström, 1968). With SuperSorb-C, the best root development of soybean seedlings occurred using 5×10^{-3} M (i.e., 5 mM) Ca^{2+} .

Hypocotyl calcium content increased between 1 and 5 mM Ca^{2+} (Fig. 3). However, further increasing Ca^{2+} to 10 mM in the hydrating solution did not further enhance calcium specific content. As the concentration of Ca^{2+} in the gel medium increased above 1 mM, root dry mass was enhanced (Fig. 2), which in turn enhanced the capacity of the root system to support additional shoot growth.

Although the levels of Ca^{2+} required for adequate seedling growth in SuperSorb-C were more than what usually is required in nutrient solutions, the electroconductivity of a 5 mM $\text{Ca}(\text{NO}_3)_2$ solution (1175 S/cm) is less than half that of single-strength Hoagland's nutrient solution. Even with adequate Ca^{2+} available for growth, the calcium contents of hypocotyl tissue were within a low-to-normal range (Epstein 1972). Since Ca^{2+} typically is absorbed nonmetabolically by roots (Moore et al., 1961), one might expect higher tissue contents of calcium than were measured using amended SuperSorb-C as a growth medium. Root and shoot elongation typically are enhanced by additional Ca^{2+} when seedlings are cultured under Ca^{2+} -limiting conditions. In fact, root weight of etiolated peas more than doubled by increasing Ca^{2+}

Fig. 3. Hypocotyl calcium content ($\mu\text{g} \cdot \text{mg}^{-1}$) on a dry weight basis after 4-d growth in SuperSorb-C hydrated with 1.0, 5.0, or 10.0 mM $\text{Ca}(\text{NO}_3)_2$. SEMs of 10 to 12 replications are shown by the bars.

Fig. 4. (top) Hypocotyl calcium and sodium contents (on a dry weight basis) of seedlings grown either in vermiculite or in SuperSorb-C hydrated with 0.1, 1.0, or 5.0 mM $\text{Ca}(\text{NO}_3)_2$. (bottom) Hypocotyl lengths of the seedlings analyzed for calcium and sodium. SEMs of three to four replications are shown by bars where they exceed the dimensions of symbols.

concentration from 10^{-4} to 10^{-3} M (Burström, 1964). In the present study, doubling of root fresh mass occurred by increasing Ca^{2+} in the gel-hydrating solution 10-fold, (i.e., from 10^{-3} to 10^{-2} M). Dark-grown soybean seedlings growing in SuperSorb-C with what should have been adequate Ca^{2+} responded as if the external Ca^{2+} environment was lower than it actually was.

A likely explanation for the enhancement of root and shoot growth by increasing Ca in the hydrating solution is the presence of Na^+ in the structure of the gel medium. Information supplied by the manufacturer indicated that Na^+ within the gel structure was not released to the roots of plants grown in SuperSorb-amended soils. However, we were puzzled why more than the usual amount of Ca^{2+} was needed for adequate growth when SuperSorb-C was used as a sole root matrix. Analysis of hypocotyl tissue by inductively coupled plasma emission spectroscopy indicated an almost 20-fold higher specific sodium content in the hypocotyls of seedlings cultured in SuperSorb-C hydrated with 0.1 mM Ca^{2+} than in seedlings grown in vermiculite at the same Ca^{2+} level (Fig. 4). The endogenous sodium content of seedlings grown in vermiculite was very low, whereas their calcium content was not. Increasing Ca^{2+} in vermiculite from 0.1 to 5 mM substantially increased the calcium content of hypocotyl tissue but had virtually no effect on hypocotyl length. However, hypocotyl length of seedlings grown in SuperSorb-C correlated positively with hypocotyl calcium content ($r = 0.743$) but negatively with sodium content ($r = 0.749$).

A Na^+ and Ca^{2+} antagonism clearly explains the need for higher-than-normal Ca^{2+} in this study. Whether that effect occurs within the elongation zone of the soybean hypocotyl, within the root

system, or at both locations presently is unclear. The Na^+ content of hypocotyl tissue was much higher when seedlings were grown in SuperSorb-C than in vermiculite, at all Ca^{2+} levels tested. If high Na^+ content in cell walls antagonized the normal regulatory actions of Ca^{2+} on cell wall extensibility, on membrane permeability, and/or on membrane hydraulic conductivity in the elongation zone, then hypocotyl elongation would have been directly inhibited at the site of growth by Na^+ . If, on the other hand, hydraulic conductivity of roots was reduced by Na^+ , as shown for soybean by Joly (1989) and for bean (*Phaseolus vulgaris*) by Ortiz et al. (1994), then delivery of water to the cell elongation zone of the hypocotyl would be a more indirect growth-limiting factor. Boyer and Wu (1978) found tissue water potential of dark-grown soybean hypocotyls to be as much as 0.31 MPa below that of the root environment. In actively growing tissues, cell enlargement is accompanied by substantial osmotic gradients, caused by resistance to inward movement of water. Since Ca^{2+} plays important regulatory roles in membrane permeability and conductivity, antagonism of normal Ca^{2+} action by Na^+ at either the root or shoot level could disrupt water transport rate and inhibit cell enlargement. Regardless of the specific site or mechanism of Na^+ and Ca^{2+} antagonism involved in the SuperSorb-C growth system, the antagonism was overcome by raising the external level of Ca^{2+} . Since Na^+ was not supplied exogenously, it had to be displaced from SuperSorb-C, ironically by the action of added Ca^{2+} , and was taken up by the roots. Sodium inhibited normal seedling growth unless additional exogenous Ca^{2+} was provided to ameliorate those effects.

SuperSorb-C hydrated with adequate Ca^{2+} -containing solutions allowed us to grow uniform seedlings in darkness for physiological experiments. The simplicity of medium preparation, lack of microbial growth in the gel, and ease of root system removal suggest that acrylamide-based hydrogels are a promising culture medium for physiological, nutritional, and root development studies; however, the potential for complications arising from the sodium content of the hydrogel need to be considered.

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Corrigenda

Volume 123(3):438–444, “Potential Maturity Indices and Developmental Aspects of Melting-flesh and Nonmelting-flesh Peach Genotypes for the Fresh Market,” by Ernesto A. Brovelli, Jeffrey K. Brecht, Wayne B. Sherman, and Charles A. Sims. On p. 439, in the Materials and Methods section, under Methodological approach, on lines 19–22 in the second column, after the sentence that ends, “...in 0.16-cm increments,” the next sentence should read: “Since FL 90-20, FL 86-28C, and ‘TropicBeauty’ have fruit innately larger than those of ‘Oro A’, the initial size class was 5.24 through 5.40 cm for the first three genotypes and 4.60 through 4.76 cm for ‘Oro A’.” Note: the change from the original is in the diameter measurements for the size classes.

Volume 123(3):426–432, “Volatile Compounds Emitted by ‘Gala’ Apples following Dynamic Atmosphere Storage,” by J.P. Mattheis, D.A. Buchanan, and J.K. Fellman. The figure legends in this paper were omitted from the figure captions.

This is the legend for Figs. 1–3:

■ RA; static O₂, kPa: ▨ 1; ▧ 1.9; ▩ 2.8; □ 3.7; 8 h ambient O₂, d per week:
▨ 1 d; ▤ 2 d; ▥ 3 d

This is the legend for Figs. 4–6:

■ RA; static O₂, kPa: ▨ 1; ▧ 1.9; ▩ 2.8; □ 3.7; 8 h ambient O₂, d per week:
▨ 1 d; ▤ 2 d; ▥ 3 d