Effects of Low pH of Hydroponic Nutrient Solution on Plant Growth, Nutrient Uptake, and Root Rot Disease Incidence of Basil (*Ocimum basilicum* L.)

Daniel P. Gillespie and Chieri Kubota
Department of Horticulture and Crop Science, The Ohio State University, Columbus, OH 43210

Sally A. Miller
Department of Plant Pathology, The Ohio State University, Wooster, OH 44691

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Abstract. **Rootzone pH affects nutrient availability for plants. Hydroponic leafy greens are grown in nutrient solutions with pH 5.5 to 6.5. Lower pH may inhibit plant growth, whereas pathogenic oomycete growth and reproduction may be mitigated. General understanding of pH effects on nutrient availability suggests likely toxicity and deficiency of specific micronutrients. We hypothesized that if adjustments are made to the micronutrient concentrations in solution, plants will grow in lower-than-conventional pH without nutrient disorders, while oomycete disease incidence and severity may be reduced. To develop a new nutrient solution management strategy, we examined pH of 4.0, 4.5, 5.0, and 5.5 with or without micronutrient adjustments for growing two cultivars of basil plants Dolce Fresca and Nufar in a greenhouse hydroponic deep-water culture (DWC) system. Micronutrient adjustments included reduced concentrations of copper, zinc, manganese, and boron by one-half and doubled molybdenum concentration. Plants harvested 20 to 28 days after transplanting did not show significant effects of pH or the micronutrient adjustment. Phosphorus, calcium, magnesium, sulfur, boron, manganese, and zinc concentrations in leaves significantly declined, while potassium and aluminum concentrations increased with decreasing pH. However, these changes and therefore micronutrient adjustments did not affect basil plant growth significantly. 'Nufar' basil plants were then grown in a growth chamber DWC system at pH 4.0 or a conventional 5.5 with and without inoculation of *Pythium aphanidermatum* zoospores. Fourteen days after inoculation, *P. aphanidermatum* oospore production was confirmed only for the inoculated plants in pH 5.5 solution, where a significant reduction of plant growth was observed. The results of the present study indicate that maintaining nutrient solution pH at 4.0 can effectively suppress the severity of root rot caused by *P. aphanidermatum* initiated by zoospore inoculation without influencing basil growth.**

Culinary fresh herb production in the United States has grown rapidly over the past decade. For example, U.S. Department of Agriculture (USDA) census data show a 96% increase in fresh herb production from 2012 to 2017 (USDA NASS, 2014, 2019) with 74% of fresh herbs produced in California, New Jersey, and Texas in 2017 (USDA NASS, 2019). This rather centralized production in limited areas necessitates long-distance transportation of this highly perishable produce to reach consumers across the country. Hydroponic production in controlled environments allows year-round local production of perishable fresh produce in densely populated areas, closer to the point of consumption. As a result, hydroponic basil quickly became a major product out of local greenhouses throughout the United States. In this report, we refer to ''hydroponics'' as liquid culture (i.e., growing plants without major use of aggregate medium). Leafy greens and herbs are typically grown hydroponically instead of soilless substrate culture. In contrast, fruiting vegetables are grown in soilless substrate culture with large amounts of aggregate media (such as rockwool) to support plants.

Although hydroponic production greatly reduces the incidence of soilborne root diseases, pathogens can still be introduced into production facilities through air, sand, soil, peat, source water, seeds, or insects (Stanghellini, 1996; Stanghellini and Rasmussen, 1994). Once a pathogen, especially a fast-spreading oomycete species, is introduced into a hydroponic system, dispersal can occur quite rapidly due to genetically uniform hosts and consistent environmental conditions (Stanghellini and Rasmussen, 1994; Wohanka, 2002). Prevention of pathogen introduction in hydroponic systems is critical, as effective chemical control agents for root diseases of edible crops are limited and may not be registered for use in greenhouses or indoors (Jensen and Collins, 2011; Stanghellini, 1996). Various disinfection systems (e.g., ultraviolet irradiation) have been introduced to commercial hydroponic systems to mitigate the risk of disease introduction and spread through the recirculation system for the nutrient solution (Wohanka, 2002). However, once a disease outbreak occurs, growers are often forced to suspend production and disinfect growing systems, leading to decreased yields and profit, changes to crop schedules, and increased labor (Stanghellini, 1996).

Among the most common oomycete pathogens experienced in hydroponic crop production are *Pythium* and *Phytophthora* spp. (Stanghellini and Rasmussen, 1994). Although these oomycete pathogens can infest roots of virtually all crop species grown hydroponically, basil and spinach (*Spinacia oleracea*) are particularly susceptible to infection by oomycete pathogens (Mattson, 2018). Several preventive measures, such as reducing the temperature of the hydroponic nutrient solution (e.g., Albright et al., 2007) or adding biofungicides (e.g., Utkhede et al., 2009), have been studied to minimize the risk of disease. This study focuses on a low-cost approach of reducing pH below the conventional range (5.5–6.5), originally suggested as a grower practice for hydroponic spinach in Japan (S. Tsukagoshi, personal communication). However, information on plant responses to specific pH levels is not available.

pH is among the most important parameters affecting sporangium production, germination, and mycelial growth of *Pythium* and *Phytophthora* spp. (El-Sharouny, 1983; Ho and Hickman, 1967; Kong et al., 2009). Ho and Hickman (1967) reported that the average period of motility of *Phytophthora megasperma* var. *sojae* zoospores was more than 20 h at pH 6.25 but was reduced to 1 h at pH 4.85. In addition, in a study conducted with *Rhododendron macrophyllum* grown in a peat/sand substrate inoculated with *Phytophthora cinnamomi*, plants grown in the substrate adjusted to pH 3.4 to 3.7 displayed no symptoms of disease, whereas those grown at pH 5.8 had an average disease symptom rating of 3.6 of 5.0 (Blaker and MacDonald, 1983). However, lower pH (<5.5) is typically avoided for hydroponic nutrient solution, as specific nutrient disorders and growth inhibition are commonly experienced outside the conventional range (Sambo et al., 2019; Savvas and Gruda, 2018; Sonnevelt, 2002). Of interest, numerous studies suggest that hydronium and hydroxide ion toxicity are found only at the extreme ends of acidity and alkalinity (Arnon and Johnson, 1942; Islam et al., 1980; Vlamis, 1953), and growth inhibition can usually be attributed to one or more pH-dependent factors including nutrient availability, ion antagonism, and

precipitation of fertilizer salts (Bugbee, 2004; Fageria, 1983; Hawf and Schmid, 1967; Mengel et al., 2001; Peterson et al., 1984; Sambo et al., 2019).

It has been reported that plants can grow in substrates with a relatively wide range of pH with some necessary nutrient adjustments. For example, tomato (*Solanum lycopersicum*), lettuce (*Lactuca sativa*), and bermudagrass (*Cynodon dactylon*) grew in nutrient solution ranging from pH 4.0 to 8.0, and nutrient solution pH did not affect the pH of the shoot and root sap (Arnon and Johnson, 1942). In addition, this same experiment showed that at pH 4.0, tomato and lettuce shoot and root growth were less than at the more optimum pH of 6.0, but that growth was improved by increasing Ca concentration in the nutrient solution.

Commonly referenced charts showing nutrient availability at different pH values (e.g., Peterson, 1982) typically indicate that availability of micronutrients such as Cu, Zn, Mn, and B is increased with decreasing pH, while Mo availability decreases. This suggests that the likelihood of Cu, Zn, Mn, and B toxicity and Mo deficiency increases with decreasing pH. Nevertheless, specific responses of leafy greens and herbs to lower-than-conventional pH and possible mitigation of nutrient disorders under low pH by adjusting nutrients are not known.

If leafy greens and herbs can exhibit normal growth in highly acidic conditions (e.g., pH below 5.0), the risk of crop failure due to oomycete pathogens might be reduced. Therefore, the objectives of the present study were primarily to examine the influence of low nutrient solution pH on 'Nufar' and 'Dolce Fresca' basil growth and nutrient concentration in leaf tissue, and secondarily, to determine the efficacy of adjusting micronutrient concentrations in the hydroponic solution, aiming to mitigate possible nutrient disorders at low pH. Our first hypothesis was that adjusting micronutrient concentrations to account for decreased/increased availability of specific nutrients allows basil plants to exhibit normal growth without nutrient disorders in lower-than-conventional pH (Expt. 1). Our second hypothesis was that low pH suppresses pythium root rot initiated by zoospore inoculum (Expt. 2).

Materials and Methods

Plant material, propagation, and water treatment

Rockwool sheets (AO plugs 200 counts, 2.5-cm height; Grodan, Roermond, The Netherlands) were placed in white plastic undertrays and hydrated with reverse osmosis (RO) water containing 0.5 mg·L^{-1} DDAC (didecyl-dimethyl-ammonium chloride; KleenGrow, Pace Chemicals, Delta, BC, Canada) and allowed to drain before seeding. Basil seeds were sown in rockwool sheets on 25 June 2018 and 22 Aug. 2018 for Expt. 1, and 12 Apr. 2019 for Expt. 2. Cultivars Nufar (Johnny's Selected Seeds, Fairfield, ME) and Dolce Fresca (Territorial Seed Company, Cottage Grove, OR) were used for Expt. 1 and only 'Nufar' was used for Expt. 2. After seeding, trays were placed inside a dark growth chamber (Model 2015; VWR International, Radnor, PA) set at 23 °C air temperature. After radical emergence was observed, rockwool sheets were covered with sifted vermiculite and moved to a greenhouse (Expt. 1) or a growth chamber (GR96; Conviron, Winnipeg, MB, Canada) (Expt. 2) for the remainder of the experiment.

For both experiments, municipal water was used and was disinfected with ultraviolet radiation (D4 + Whole Home ultraviolet Water Disinfection System; Viqua, Guelph, ON, Canada). In addition, all water provided to seedlings at the germination and pre-transplanting stage was treated with RO and 0.5 mg·L^{-1} DDAC (KleenGrow). Water used in DWC units was also dechlorinated by the addition of 2.5 mg·L^{-1} sodium thiosulfate. This was done to avoid chlorine phytotoxicity from municipal source water that has been observed in our past experiments. Our water quality analyses typically show low levels of Ca (<30 mg·L^{-1}), Cl (<30 mg·L^{-1}), NO_3-N (<3 mg·L^{-1}), Mg (<8 mg·L^{-1}), S (<20 mg·L^{-1}), K (<5 mg·L^{-1}), P (<0.5 mg·L^{-1}), Zn (<0.5 mg·L^{-1}), Na (<20 mg·L^{-1}), and Al (<0.2 mg·L^{-1}). Alkalinity is typically < 42.0 $CaCO_3$ mg·L^{-1} and approximate electrical conductivity (EC) is 0.2 to 0.3 dS·m^{-1}.

Seedlings grown in the rockwool sheet were sub-irrigated with water as needed until transplanting. pH of water provided to seedlings before transplant was ≈6.4. When cotyledons were fully expanded (10–15 d after seeding), uniform plants with rockwool substrate (15–20 mL) were

Table 1. Elemental concentrations of fresh nutrient solutions (all values in mg·L^{-1}) of standard vs. adjusted nutrient solution (means at pH 5.0 ± SD) examined in Expt. 1 (n = 4). Adjusted nutrient solution had reduced Mn, B, Zn, and Cu concentrations (targeting at 50% of standard) and increased Mo concentration (200% of standard).

	Macronutrients						Micronutrients					
Nutrient solution	NO_3-N	P	K	Ca	Mg	S	B	Cl	Cu	Fe	Mo	Mn	Zn
Standard nutrient solution	88.68 ± 7.41	22.90 ± 0.72	106.60 ± 4.65	139.85 ± 4.42	26.31 ± 0.45	47.12 ± 3.70	0.18 ± 0.02	76.79 ± 4.00	0.03 ± 0.01	0.90 ± 0.25	0.02 ± 0.01	0.28 ± 0.01	0.47 ± 0.06
Adjusted nutrient solution	87.99 ± 7.10	22.93 ± 0.57	105.80 ± 4.52	139.13 ± 3.37	26.18 ± 0.35	49.96 ± 8.37	0.09 ± 0.00	75.70 ± 5.04	0.01 ± 0.01	1.02 ± 0.23	0.04 ± 0.01	0.13 ± 0.01	0.35 ± 0.01

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C.K. is the corresponding author. E-mail: kubota.10@osu.edu.

transplanted into DWC units (7 July and 1 Sept. 2018 for Expt. 1; 27 Apr. 2019 for Expt. 2).

Expt. 1: Effects of nutrient solution pH and micronutrient adjustments on basil plant growth and nutrient uptake. Expt. 1 was conducted in a 93-m^2 glass glazed greenhouse at The Ohio State University (Columbus, OH). Greenhouse day and night air temperatures were targeted at 24/16 °C, respectively. The experiment was conducted twice (July 2018 and Sept. 2018) using a randomized complete block design with a factorial treatment structure with two nutrient solutions (standard and adjusted micronutrients, as described later in this article) for each of four pH levels (4.0, 4.5, 5.0, and 5.5). These treatments were randomized in each of two blocks placed in the greenhouse. Each block had eight hydroponic DWC units each assigned for one of eight treatments. The experiment had a total of four replications consisting of two blocks inside the greenhouse and two trials over time. Due to differences in growth rates between cultivars, 'Nufar' was grown for 20 d (Trial 1) and 21 d (Trial 2), whereas 'Dolce Fresca' was grown for 26 d (Trial 1) and 28 d (Trial 2) after transplanting into DWC units.

In each of 16 hydroponic DWC units, 12 plants per cultivar were grown (24 plants per unit, 384 plants in total per trial). The DWC unit consisted of 0.78-m long, 0.51-m wide, and 0.37-m tall black plastic container (Centrex Plastics, LLC Commander 27-Gallon Black Tote; Centrex Plastics, Findlay, OH) and a polystyrene foam raft (Beaver Plastics 72 inches; Beaver Plastics, Acheson, AB, Canada) cut to match the size of container. Each DWC unit contained 90 L of nutrient solution made using dechlorinated and ultraviolet-treated water. The large volume-to-plant ratio (3.75 L per plant) was to act as a buffer in attempts to minimize pH fluctuations. In addition, the nutrient solutions were renewed on the 11th and the 14th day after transplanting in Trials 1 and 2, respectively. Nutrient solution in each unit was continuously aerated by one air stone connected to a small aquarium air pump.

One-half strength of a University of Arizona leafy crop nutrient solution recipe (M.H. Jensen, unpublished data) was used as the baseline formula in this experiment. Elemental concentrations are shown in Table 1. For the adjusted nutrient solution, Mn, B, Zn, and Cu, concentrations were decreased by one-half, and the Mo concentration was doubled. These decisions were made based on the information of nutrient availabilities as affected by pH for soilless culture system (e.g., Peterson, 1982). Before transplant, nutrient solution pH was adjusted to setpoints (4.0, 4.5, 5.0, or 5.5) using sulfuric acid or sodium hydroxide. pH was monitored at least once per day and manually adjusted thereafter as needed by the addition of sulfuric acid or sodium hydroxide to maintain pH within range of ± 0.25 of target pH. As the pH typically increases over time, pH adjustment was made by adding sulfuric acid except two times of sodium hydroxide use in Trial 2.

At the end of each trial (19–28 d), all plants except for border plants along the perimeter of DWC unit (eight plants per unit, 16 plants per treatment per trial for each cultivar) were harvested for quantifying plant growth (fresh and dry leaf, stem, and root mass, plant height, number of axillary shoots per plant, and number of leaves per plant) and assessing visible symptoms of nutrient disorders. Once dry weights were recorded, leaf tissue of eight plants from each unit was combined into one sample (four samples per treatment per cultivar out of two trials) and sent to a commercial analytical laboratory (JR Peters, Allentown, PA) to determine leaf tissue nutrient concentrations of each treatment and cultivar.

Expt. 2: Effect of low pH nutrient solution and infection by P. aphanidermatum on basil plant growth and root rot disease symptoms. Expt. 2 was conducted in a 9-m^2 Conviron walk-in growth chamber (GR96; Conviron). The experiment used a randomized complete block design with four treatments consisting of pH (4.0 or 5.5) combined with the presence/absence of *P. aphanidermatum* inoculation of the nutrient solution. The treatments were replicated in eight blocks inside the growth chamber. 'Nufar' seedlings were grown for 19 d after transplanting into DWC units. There were 32 small DWC units each consisting of a plastic bucket (36.2 cm tall and 31.8 cm diameter; United Solutions 5-gallon Residential Bucket; Lowes,

Table 2. Mean environmental parameters in the greenhouse (Expt. 1, two trials) and the growth chamber (Expt. 2).

Expt.	Air temp (°C)	Nutrient solution temp (°C)	VPD[z] (kPa)	DLI[y] ($mol \cdot m^{-2} \cdot d^{-1}$)
Expt.1 (Trial 1)	Day: 24.5 ± 1.8	Day: 26.2 ± 2.1	Day: 0.8 ± 0.3	14.1 ± 6.4
	Night: 22.6 ± 1.8	Night: 26.0 ± 2.3	Night: 0.4 ± 0.2	
Expt. 1 (Trial 2)	Day: 24.2 ± 3.0	Day: 26.3 ± 3.0	Day: 0.9 ± 0.4	14.2 ± 7.0
	Night: 22.5 ± 2.9	Night: 26.4 ± 2.9	Night: 0.4 ± 0.2	
Expt. 2	Day: 28.3 ± 0.7	Day: 26.5 ± 1.4	Day: 0.7 ± 0.1	14.0 ± 0.7
	Night: 23.7 ± 0.7	Night: 25.4 ± 1.4	Night: 0.2 ± 0.2	

[z]Vapor pressure saturation deficit of the air.
[y]Daily light integral (400–700 nm).

Table 3. Mean pH, electrical conductivity (EC) ($dS \cdot m^{-1}$), and dissolved oxygen (ppm) of nutrient solutions. Means ± SD of daily measurements for nutrient solutions with or without micronutrient adjustments (A, adjusted; S, standard concentrations) and *Pythium aphanidermatum* inoculation (Yes; No).

Expt.	Target pH	pH	EC	Dissolved oxygen
Expt. 1 (Trial 1)	4.0-A	4.1 ± 0.2	1.4 ± 0.04	7.6 ± 0.5
	4.0-S	4.1 ± 0.2	1.4 ± 0.03	7.8 ± 0.4
	4.5-A	4.6 ± 0.2	1.4 ± 0.03	7.8 ± 0.4
	4.5-S	4.5 ± 0.2	1.4 ± 0.03	7.6 ± 0.3
	5.0-A	5.0 ± 0.2	1.4 ± 0.04	7.5 ± 0.4
	5.0-S	5.0 ± 0.2	1.4 ± 0.03	7.3 ± 0.7
	5.5-A	5.5 ± 0.2	1.4 ± 0.05	7.5 ± 0.4
	5.5-S	5.5 ± 0.1	1.4 ± 0.04	7.3 ± 0.7
Expt. 1 (Trial 2)	4.0-A	4.0 ± 0.1	1.5 ± 0.05	7.9 ± 0.5
	4.0-S	4.0 ± 0.1	1.4 ± 0.06	7.9 ± 0.5
	4.5-A	4.5 ± 0.1	1.4 ± 0.04	7.9 ± 0.5
	4.5-S	4.5 ± 0.1	1.4 ± 0.07	7.9 ± 0.4
	5.0-A	4.9 ± 0.2	1.4 ± 0.04	7.9 ± 0.5
	5.0-S	4.9 ± 0.1	1.4 ± 0.05	7.9 ± 0.5
	5.5-A	5.4 ± 0.2	1.4 ± 0.05	7.9 ± 0.5
	5.5-S	5.5 ± 0.1	1.4 ± 0.04	7.8 ± 0.4
Expt. 2	4.0-Yes	4.0 ± 0.1	1.5 ± 0.00	3.8 ± 2.8
	4.0-No	4.0 ± 0.1	1.5 ± 0.00	4.3 ± 2.8
	5.5-Yes	5.6 ± 0.2	1.5 ± 0.00	4.3 ± 2.9
	5.5-No	5.5 ± 0.2	1.5 ± 0.00	4.6 ± 2.9

Mooresville, NC) each with a polystyrene foam raft (1.9 cm × 1.2 m × 2.4 m R-4 Unface Polystyrene Foam Board Insulation; Kingspan Insulation, Winchester, VA) cut to match the size of bucket. Three holes in the size of rockwool cubes (diameter: 2.5 cm) were cut into each raft (three plants per raft). Each unit contained 15 L of nutrient solution made using dechlorinated and ultraviolet-treated water.

An average (± SD) photosynthetic photon flux density (PPFD) over the plant growing area (32 locations) was 324 ± 16.3 µmol·m^{-2}·s^{-1} with a photoperiod of 12 h·d^{-1}, provided by white fluorescent lamps (Master TL5 54W/840; Philips, Amsterdam, Netherlands). Air temperature was set at 28/23 °C for photo/dark period. The same nutrient solutions and pH adjustment as described earlier were used, but without renewal throughout Expt. 2. Initially, nutrient solution was not aerated to create less than optimal conditions to increase the likelihood of disease establishment; however, as dissolved oxygen levels began to deviate between treatments and became very low (i.e., < 3.0 mg·L^{-1}), nutrient solution aeration was configured 3 d after inoculation (8 d after transplant). In this practice, each treatment received 2 d of aeration followed by 2 d of no aeration, as a sufficient number of air pumps was not available to continuously aerate all treatments.

P. aphanidermatum isolate SM1804-18 recovered from spinach roots from a commercial hydroponic facility growing basil and spinach using DWC systems (Wilmington, OH) was used in Expt. 2. Before the experiment, it was confirmed that the isolate was pathogenic to 'Nufar' basil by inoculating nutrient solution being supplied to the plants. Cultures were maintained on potato carrot agar (PCA; Van Der Plaats-Niterink, 1981) at room temperature. Motile zoospores were used as inoculum and produced aseptically following the protocol described by Waterhouse (1967) with some modifications as described in Gillespie (2019). Briefly, *P. aphanidermatum* cultures were plated on fresh PCA plates and allowed to grow for 60 to 72 h at room temperature (≈23 °C). Agar squares (≈3 mm) covered with mycelium were transferred to a petri dish containing four to eight sterile grass leaf blades (≈9 cm in length) and a mix (15–30 mL) of sterilized deionized water and sterilized river water (2:1 volume ratio). After ≈36 h of incubation at 24 to 25 °C under fluorescent lights, the previously mentioned river water mix was renewed and the plates were moved to a dark incubator at 17 to 18 °C, to induce sporangia development and release of zoospores. After 24 h, once zoospores were observed, water from plates was filtered through double-layered cheese cloth and zoospore concentration was quantified from the bulk inoculum solution in a large beaker continuously stirred at a very low speed to avoid encysting the zoospores. A total of 20 counts were taken on five grids of a hemocytometer under a microscope. Counts were then averaged to determine a representative concentration of 9.0 × 10^3 zoospores per liter in the bulk inoculum solution.

Once bulk inoculum solution concentration was determined, this solution was placed in the experimental growth chamber (controlled at 28 °C) for 1 h for inoculum solution to reach a similar temperature of hydroponic nutrient solution. After 1 h in the chamber, the inoculum solution was again continuously stirred. Fifty-two milliliters of inoculum solution were then added directly to the 15-L nutrient solution for inoculated treatments, resulting in a final concentration of 3.1 zoospores per liter per inoculated treatment. Through preliminary testing, this zoospore concentration proved to be an appropriate concentration to cause root rot disease symptoms. Inoculation was performed 5 d following transplanting (15 d after seeding).

Root damage was rated for all plants (24 plants per treatment) on a visual scale of 0 to 10 where a score of 0 = no symptoms of root rot disease, white healthy roots, turgid root tissue, and no visible damage, whereas 10 = severe infection, 91% to 100% of root tissue area was brown, damaged, losing turgor, or completely decaying. Each 1.0 increment represented an additional 10% increase in root area being brown, discolored, or damaged. Small root samples were taken from one plant per treatment for each replication to examine microscopically for oospores (eight plants per treatment in total). Following plant growth measurements (3 plants × 8 blocks per treatment), plant material was dried in a drying oven at 55 °C for a minimum of 1 week.

Environmental measurements

T-type thermocouples were placed in the center of each block at plant canopy level for monitoring air temperature (gauge 36; Omega Inc., Stamford, CT) and submerged in nutrient solution (gauge 24; Omega Inc.) of the middle DWC unit of each block for monitoring nutrient solution temperature. Relative humidity was measured with an aspirated and shielded temperature and humidity probe (HMP60 Humidity and Temperature Probe; Vaisala Corporation,

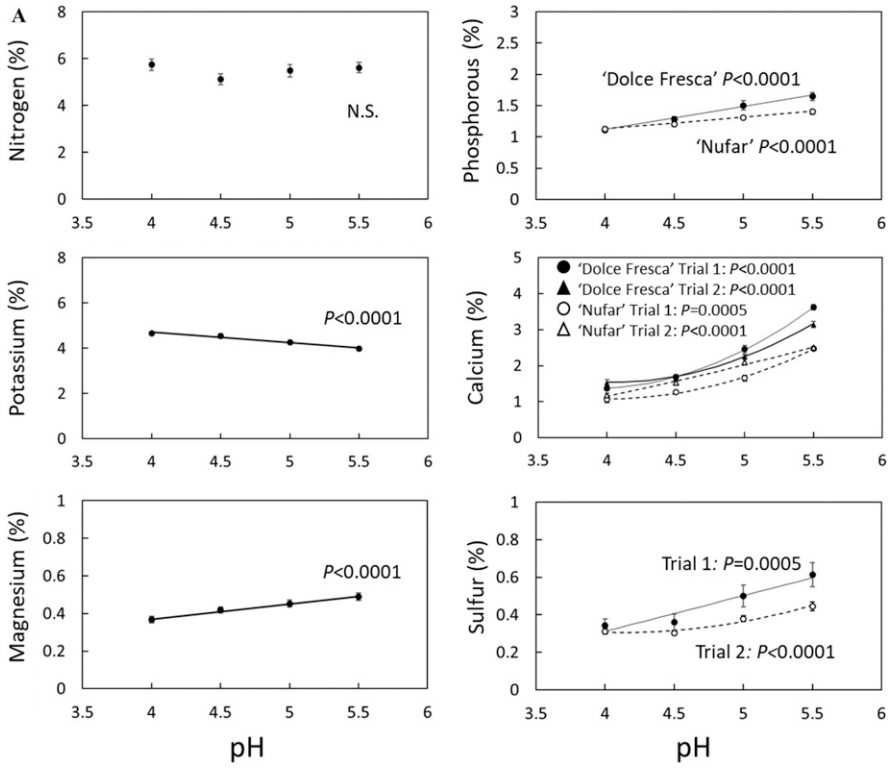

Fig. 1. (**A**) Macronutrient concentrations (% in dry mass) in basil leaves as affected by nutrient solution pH, cultivar, and trial. Means and SE are shown (n = 16 for N, K, and Mg; n = 8 for P and S; n = 4 for Ca). Significant linear responses were observed for P, K, Mg, and S (Trial 1), and significant quadratic response was observed for Ca and S (Trial 2). Interactions were observed between pH and cultivar for P, between pH and trial for S and between pH, cultivar, and trial for Ca. Regression equations are as follows: $P = -0.36 + 0.37 \cdot pH$ ($R^2 = 0.61$, Dolce Fresca); $P = 0.37 + 0.19 \cdot pH$ ($R^2 = 0.55$, Nufar); $K = 6.56 - 0.46 \cdot pH$ ($R^2 = 0.77$); $Ca = -5.11 + 1.50 \cdot pH + 0.85 (pH - 4.75)^2$ ($R^2 = 0.97$, Dolce Fresca Trial 1); $Ca = -3.25 + 1.09 \cdot pH + 0.76 (pH - 4.75)^2$ ($R^2 = 0.96$, Dolce Fresca Trial 2); $Ca = -2.95 + 0.92 \cdot pH + 0.62 (pH - 4.75)^2$ ($R^2 = 0.96$, Nufar Trial 1); $Ca = -2.53 + 0.91 \cdot pH + 0.07 (pH - 4.75)^2$ ($R^2 = 0.95$, Nufar Trial 2); $Mg = 0.05 + 0.08 \cdot pH$ ($R^2 = 0.54$); $S = -0.45 + 0.19 \cdot pH$ ($R^2 = 0.34$, Trial 1); $S = -0.116 + 0.095 \cdot pH + 0.076 (pH - 4.75)^2$ ($R^2 = 0.59$, Trial 2). (**B**) Micronutrient concentrations (mg/kg in dry mass) in basil leaves as affected by nutrient solution pH. Means and SE are shown (n = 16). Significant linear responses were observed for Al, B, Mn, and Zn. Regression equations are as follows: $Al = 77.29 - 11.34 \cdot pH$ ($R^2 = 0.13$); $B = 15.19 + 2.57 \cdot pH$ ($R^2 = 0.21$); $Mn = -55.00 + 29.17 \cdot pH$ ($R^2 = 0.42$); $Zn = -96.53 + 41.46 \cdot pH$ ($R^2 = 0.82$).

Helsinki, Finland) located at plant canopy level in the middle of the experimental plant-growing area of greenhouse or growth chamber. A quantum sensor (LI-800; LI-COR Biosciences, Lincoln, NE) was placed at the center of each block to measure PPFD and daily light integral (DLI) in the greenhouse. All sensors were connected to dataloggers (CR10X and CR1000 dataloggers; Campbell Scientific, Logan, UT) and sensor readings were scanned every 10 s to record averages each 15 min. pH was measured daily and EC and dissolved oxygen of each DWC unit were measured at least three times a week, using handheld meters (pH/EC Combo Meter; Bluelab, Tauranga, New Zealand; and 407510 DO meter; Extech, Nashua, NH). EC and pH meters were calibrated weekly. Nutrient solutions were sent to the same commercial laboratory for micro and macronutrients (Table 1).

Statistical analyses

Plant growth data (fresh/dry mass, plant height, number of axillary shoots per plant, and leaves per plant) were subjected to two-way analysis of variance (ANOVA) with means separated using Tukey's honestly significant difference (HSD) test when appropriate ($P < 0.05$). Plant growth responses in Expt. 1 did not display a significant interaction with trial, thus two trial data (repeated over time) were combined. Growth data of two cultivars were separately analyzed.

To investigate the effect of pH on nutrient concentration of the leaf tissue (Expt. 1), data were subjected to regression analysis. However, before regression analysis, data were subjected to two-way ANOVA when appropriate ($P < 0.05$) to determine if pH displayed an interaction between nutrient solution, trial, and/or cultivar. If a specific element displayed an interaction between any factor(s), multiple regressions were fit to data. Specifically, P concentration displayed a significant interaction between pH and cultivar, thus 'Dolce Fresca' and 'Nufar' P concentration data were fit separately. Calcium concentration displayed a significant interaction between trial and pH as well as cultivar and pH, therefore data for 'Dolce Fresca' Trial 1, 'Dolce Fresca' Trial 2, 'Nufar' Trial 1, and 'Nufar' Trial 2 were fit separately. Sulfur concentration displayed a significant interaction between trial and pH; thus, data in Trial 1 and Trial 2 were fit separately. The remaining elements did not display an interaction between factors. Therefore, trial, cultivar, and nutrient solution data were combined for the remaining elemental concentrations. In Expt. 2, data were analyzed using a two-way ANOVA followed by Tukey's HSD mean separation ($P < 0.05$). All statistical analyses were performed using JMP software (SAS Institute, Cary, NC).

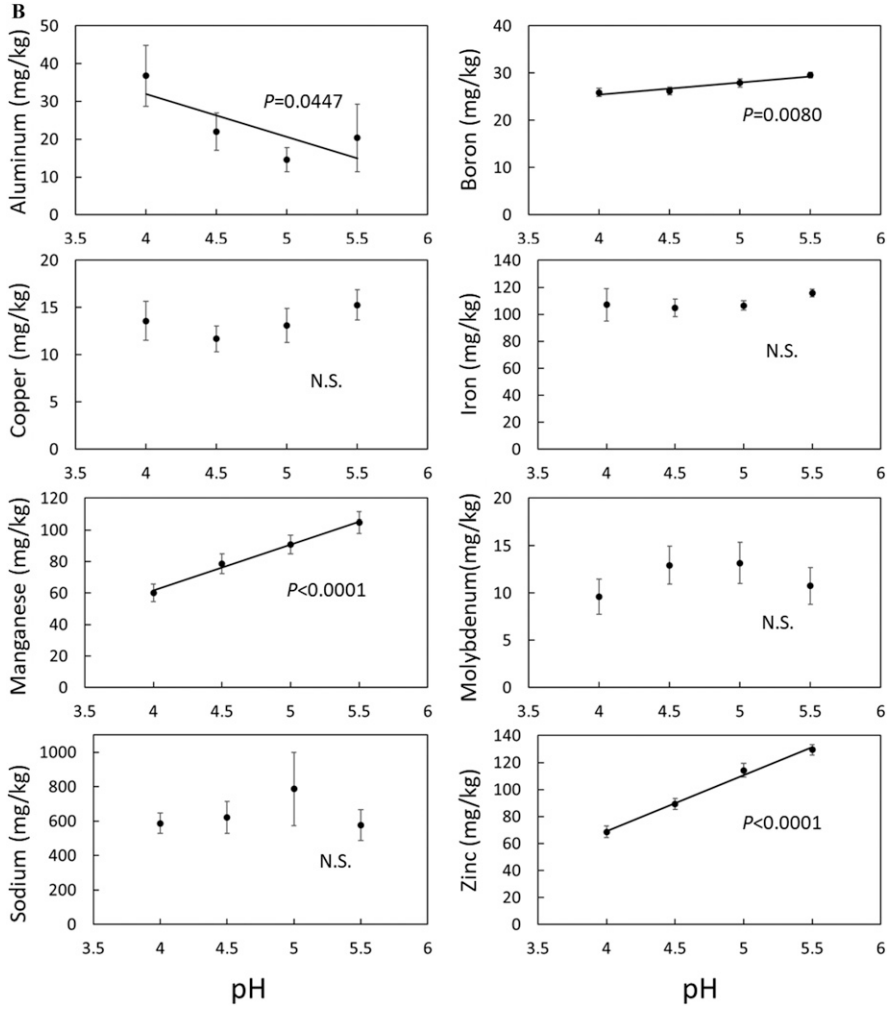

Fig. 1. *Continued*

Results

Greenhouse environment and nutrient solution pH

Average day and night air temperature, nutrient solution temperature, vapor pressure deficient (VPD), and DLI are summarized in Table 2. Average pH, EC, and dissolved oxygen (DO) of experimental nutrient solutions from daily measurements are reported in Table 3. All environmental and nutrient solution setpoints were maintained at targets (except DO in Expt. 2). In Expt. 2, although average DO was lower than optimum (>5 ppm), differences between inoculated and noninoculated treatments were small (<0.5 ppm) regardless of pH. Pythium root rot incidence is known to increase at low DO of hydroponic solutions (Mattson, 2018).

Plant growth as affected by nutrient solution EC and micronutrient adjustments (Expt. 1)

Neither pH nor the nutrient solution adjustments significantly affected fresh/dry mass, number of leaves per plant, plant height, or number of axillary shoots per plant for both cultivars. Specifically, plant mass, plant height, number of axillary shoots per plant, and number of leaves per plant at the end of the experiment were in the range of 13.6 to 23.7 g fresh mass/plant, 0.94 to 1.69 g dry mass/plant, 11.8 to 18.6 cm/plant, 7 to 13 shoots per plant, and 16 to 36 leaves per plant for 'Nufar' and 19.8 to 33.4 g fresh mass/plant, 1.18 to 2.25 g dry mass/plant, 13.3 to 19.8 cm/plant, 11 to 14 shoots per plant, and 35 to 51 leaves per plant for 'Dolce Fresca' (data not shown). Throughout the duration of both trials, no symptoms of nutrient disorders were found. These results

Table 4. Mean leaf nutrient concentration ± SE (all values in mg·kg^{-1} dry tissue sample). Data were combined for cultivars, pH, and replications as there were no significant effects.

Nutrient solution	Mn	B	Cu	Zn	Mo
Standard nutrient solution	96.1 ± 5.5 a	26.6 ± 0.6 b	14.7 ± 1.4 a	99.6 ± 5.2 a	11.8 ± 1.6 a
Adjusted nutrient solution	71.2 ± 4.0 b	28.2 ± 0.6 a	12.2 ± 1.1 b	101.6 ± 5.3 a	11.4 ± 1.3 a

Means in a column followed by same letter are not significantly different ($P \leq 0.05$), using analysis of variance (n = 16).

indicate 'Nufar' and 'Dolce Fresca' basil plants can be grown in nutrient solution pH as low as 4.0 without significantly reducing plant growth or causing physiological disorders.

Nutrient concentration of plant leaf tissue as affected by solution pH and micronutrient adjustments (Expt. 1)

Dry leaf tissue concentrations of P, Ca, Mg, S, B, Mn, and Zn displayed a linear or quadratic decrease as pH decreased (Fig. 1). Significant but small degree of interactions between pH, cultivar, and/or trial were observed in P, Ca, and S, in which an overall decreasing trend with decreasing pH was consistent. Leaf concentration of K and Al displayed the opposite trend, in which concentration exhibited a linear increase as pH decreased. Nitrogen, Fe, Cu, Mo, and Na leaf tissue concentrations were unaffected by pH, regardless of cultivar or trial.

Micronutrient adjustments made to the nutrient solution proved to be effective in significantly decreasing leaf concentration of Mn and Cu but was not effective in decreasing leaf concentration of B and Zn or increasing leaf concentration of Mo (Table 4). In fact, B leaf concentration was significantly higher for plants grown with the nutrient solution adjusted to have a lower B concentration, whereas Zn and Mo concentrations were not significantly affected by nutrient solution adjustments. However, as stated previously, no symptoms of nutrient disorders were observed across treatments. This observation indicates that adjustments to nutrient solution are not necessary for growing 'Nufar' and 'Dolce Fresca' basil at pH 4.0 to 5.5.

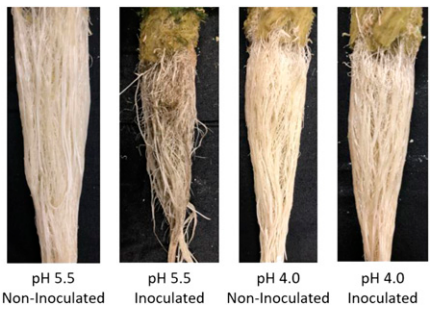

Fig. 2. 'Nufar' basil roots 19 d after transplanting and 14 d after inoculation with *Pythium aphanidermatum* zoospores (Expt. 2). From left to right: sample plant roots from pH 5.5–noninoculated, pH 5.5–inoculated, pH 4.0–noninoculated, and pH 4.0–inoculated treatments rated as 0, 4, 0, and 0, respectively. The roots were rated using the disease rating described in Table 5.

Root symptoms of plants inoculated with *P. aphanidermatum* at low vs. conventional pH (Expt. 2)

Root damage was almost exclusively limited to the roots of plants grown in pH 5.5–inoculated treatment (Fig. 2, Table 5). This symptom was first observed in roots when lifted up from the nutrient solution 5 d following inoculation. The degree of root browning progressed over time and reached an average root damage rating of 2.5 (on a scale of 1–10 as described before) at the end of the experiment (Table 5). Symptoms observed at the end of the experiment included root browning, discoloration, and small lesions (Fig. 2). Little root damage (<0.1) was observed in noninoculated plants grown at pH 5.5 and inoculated plants grown at pH 4.0 (Table 5). The root damage observed in noninoculated plants grown at pH 5.5 was likely due to mechanical stress when plants were briefly lifted from the nutrient solution for inspection every day. No disease symptoms were observed in roots of noninoculated plants grown at pH 4.0. At the end of the experiment, oospores were observed in roots of all plants (n = 8) sampled from those grown in the pH 5.5–inoculated solutions (Fig. 3) but were not observed in roots of the other treatments (Table 5).

Plants infected with *P. aphanidermatum* exhibited significantly lower fresh leaf, stem, and root mass when compared with pH 5.5–noninoculated treatment plants (Fig. 4). Dry leaf and root mass were not significantly affected by inoculation with the pathogen regardless of pH, but dry stem mass was reduced by inoculation at pH 5.5. None of the growth variables were reduced by *P. aphanidermatum* at pH 4.0. When noninoculated, plant growth was unaffected by pH, which was consistent with the results in Expt. 1. The number of leaves (47–50) and axillary shoots (11–12) per plant was unaffected by pH or inoculation (data not shown).

Discussion

The result of Expt. 1 indicates 'Nufar' and 'Dolce Fresca' basil plants can be grown in nutrient solution pH as low as 4.0 without growth inhibition. Although basil-specific pH responses could not be found in the available literature, some plants, such as *Calluna vulgaris, Vaccinium myrtill,* and *Erica cinereal* (Grime, 1977), are known to be naturally adapted to grow in acidic soils, whereas most plant species are not. Acidic soils are typically deficient in most major elements (N, P, K, Ca, and Mg) (Rorison, 1980). Therefore, species-specific sensitivity to acidic soils may be due to low nutrient requirements and/or efficient uptake and utilization of nutrients (Rorison, 1980). This fact may help understand the reason why basil plant growth was unaffected by nutrient solution pH 4.0 to 5.5, despite that some elemental concentrations were sharply declined with lowering pH. With the exception of N, K, Cu, Fe, Mo, Na, and Al measured in this experiment, concentrations of all other elements in leaf tissue displayed a linear or quadratic decrease as pH decreased. However, as described earlier, decreased nutrient concentration did not cause reductions in plant growth and no visible nutrient disorders were observed. The apparent low nutrient requirement of basil is also in agreement with the work reported by Walters and Currey (2018), which showed that growth of basil plants grown hydroponically (nutrient film technique) was unaffected by EC in a range of 0.5 to 4.0 $dS \cdot m^{-1}$, varied at 0.5 increments by increasing overall strength of the nutrient solution. These data may explain the plant tolerance to low pH and suggest that nutrient solution pH and EC do not play a significant role in influencing basil plant growth in a wider range than those considered conventional. Nevertheless, various types of hydroponic systems and nutrient solutions are used commercially, as reviewed by Maloupa (2002), and therefore response to low pH needs to be examined especially when the hydroponic system does not allow full contact of nutrient solution with roots. In addition, possible interactions with nutrient formulation affecting root-zone pH, such as the ratio of NH_4 and NO_3 (e.g., Dickson and Fisher, 2019) need to be considered. Especially when nutrient solution volume is limited, the impact of plant anion and cation uptake on nutrient solution pH may become more pronounced than in a system like DWC in which a relatively large volume of nutrient solution is used.

It was unexpected to observe a consistent decrease of B, Mn, and Zn concentrations and no significant change in Cu concentration in leaves with decreasing pH, as reported toxicities of these nutrients suggest that availability and uptake of these nutrients should

Table 5. Average visual root damage rating and oospore production (% of plants sampled) with SE (n = 8) for roots of basil 'Nufar' plants grown in nutrient solution at pH 4.0 or 5.5 and inoculated or not inoculated with *Pythium aphanidermatum* (Expt. 2). Roots were rated on a scale of 0 to 10 where a score of 0 = no disease symptoms, white healthy roots, turgid root tissue, no brown tissue, no visible disease damage, long taproot, and many lateral roots, whereas 10 = severe infection, 91% to 100% of root tissue area was brown, damaged, losing turgor, or completely decaying. Each 1.0 increment represented an additional 10% increase in root area being brown, discolored, or damaged. Values in a column followed by same letter are not significantly different ($P \leq 0.05$), using analysis of variance and Tukey's honestly significant difference mean separation.

Treatment	Root damage rating	Oospore production (%)
pH 4.0–Inoculated	0.04 ± 0.04 b	0 ± 0.00
pH 4.0–Noninoculated	0.0 ± 0.00 b	0 ± 0.00
pH 5.5–Inoculated	2.5 ± 0.22 a	100 ± 0.00
pH 5.5–Noninoculated	0.08 ± 0.06 b	0 ± 0.00

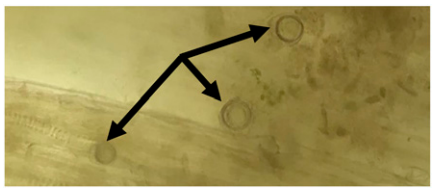

Fig. 3. Oospores of *Pythium aphanidermatum* (arrows) in basil 'Nufar' roots inoculated with zoospores of the pathogen. Basil plants were grown in nutrient solution at pH 5.5 (Expt. 2). No oospores were observed in roots of other treatments.

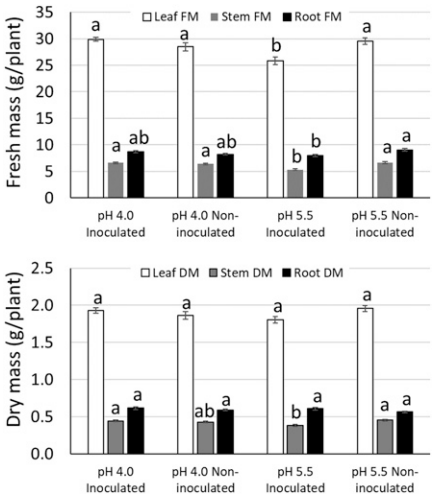

Fig. 4. Fresh and dry mass of 'Nufar' basil grown in nutrient solution at pH 4.0 or 5.5 with or without inoculation with zoospores of *Pythium aphanidermatum* (Expt. 2). Means and SE are shown (n = 8). Means within each variable indicated with the same letter are not significantly different by Tukey's honestly significant difference test ($P < 0.05$).

increase as pH decreases (Peterson, 1982). However, the discrepancy was likely because these previous results were based on plants grown in peat-based soilless substrates. In such systems, for example, toxicities of positively charged metal ions occur at low pH (e.g., Peterson, 1982; Smith et al., 2004). As pH decreases, cationic nutrients adsorbed to negatively charged substrate particles are increasingly exchanged with hydronium ions. Thus, the concentrations of cationic metal nutrients available to the plant are increased. However, in our experiment, negatively charged particles are absent in liquid culture (hydroponics). This fact and the present results indicate that the pH-dependent factors affecting nutrient availability and nutrient uptake in hydroponics are different compared with those of soil and soilless substrate culture.

It seems that a primary factor affecting nutrient availability, nutrient uptake, and therefore nutrient concentration of the leaf tissue in the present study was the concentration of cations in hydroponic nutrient solution. As pH decreases, the concentration of positively charged hydronium ions in solution is thereby increased. The result is increased competition between hydronium ions and cationic nutrients for cellular binding and uptake through negatively charged root surfaces. That is, hydronium ions increasingly depress cationic nutrient uptake as pH decreases, similar to what Peterson et al. (1984) observed with algae nutrient uptake. The phenomenon typically referred to as cation antagonism or cation competition, is likely responsible for the linear or quadratic decrease in concentration of cationic nutrient Ca, Mg, Mn, and Zn. Potassium was the only cationic nutrient where leaf concentration significantly increased with decreasing pH in our experiment. One possible explanation regarding potassium may lie in the fact that high-affinity K transporters require an H^+ ion to be transported with the K ion (Mengel et al., 2001), which may have been stimulated by the increased supply of hydronium ions at lower pH.

Phosphorus, S, and B are elements that are absorbed by the plant as an anion and displayed linear or quadratic decreases in concentration as pH decreased in our experiment. It is not exactly clear why the concentration of these specific nutrients decreased with pH, as these nutrients should not be affected by the increased concentration of hydronium ions as pH decreases. It can, therefore, be assumed that some other pH-dependent factor must have been responsible for these results. There is no obvious explanation as to what caused B uptake to display a linear decrease with decreasing pH. One explanation as to why S and P concentrations decreased with pH, may be the result of the reduced nutrient concentration of the leaf tissue at low pH leading to decreased ATP production, which is required for active S and P uptake (Mengel et al., 2001).

Initially, partly due to limited information specific to hydroponics (without substrates), we considered that pH-dependent factors known to affect nutrient availability and uptake would be similar in soilless substrate culture and hydroponic systems. Our results show that this was not the case. Based on the nutrient concentration of the plant leaf tissue under different pH, we proposed a new pH response chart specific to hydroponic conditions for basil plants (Gillespie, 2019), as a comparison with charts commonly referenced for soil- or substrate-based conditions. Further studies are necessary using additional crops to develop better understanding of hydroponic nutrient availability at varied pH.

The results of Expt. 2 indicate that growing basil in nutrient solution pH 4.0 can effectively reduce *P. aphanidermatum* disease incidence and severity after zoospore inoculation without influencing basil fresh/dry leaf, stem, or root mass. The results agree with those of Blaker and MacDonald (1983), who reported that *P. cinnamomi* disease symptoms were eliminated when rhododendron was grown in inoculated peat/sand substrate with a pH 3.4 to 3.7. However, although Blaker and MacDonald (1983) attributed reductions of *P. cinnamomi* incidence to low pH suppressing sporangia development and release, the reduction in *P. aphanidermatum* disease severity shown in the present study was likely due to reduced infection at low pH (4.0). This may have been the result of negative effects on zoospore chemotaxis (Allen and Harvey, 1974) and/or duration of zoospore motility (Ho and Hickman, 1967). Low pH may reduce zoospore motility due to higher concentrations of cations associated with decreasing electrostatic force, which causes zoospore flagella to relax from their extended state (Allen and Harvey, 1974). Further plant pathological studies are needed to elucidate the mechanism of reducing the disease incidence at low pH of hydroponic nutrient solution.

If this disease management strategy is shown viable for a wide range of hydroponic systems, the low cost of acid to reach lower-than-conventional pH is an advantage compared with other means. In the present study, using a typical market price of 93% sulfuric acid ($390 for a 208-L container) and assuming a hazardous freight cost (e.g., $100), the price of sulfuric acid is roughly $2.50 per liter. Using this acid price point and the total usage of acid recorded in our experiments, the additional cost to lower and maintain pH 5.5 to 4.0 over 4 weeks of basil production was $0.000046 per liter (based on our acid usage in the present volume of DWC nutrient solution). This is considerably less expensive than fungicides and biocontrol agents applicable in hydroponics ($0.016–1.62 per liter, estimated for typical usage cases). The amount of acid needed to reach 4.0 will vary depending on an operation's specific location or water quality; however, at such a low cost, it is unlikely that this cost would become significant, even when water with high levels of alkalinity is used. Furthermore, in our experiment, pH became relatively more stable when pH was maintained at 4.0 than 5.5, thus decreasing the frequency of pH adjustment. This is likely due to the high hydronium concentrations (i.e., low pH) mitigating the typical increase of pH as a result of hydroxide ions exchanged along with anion uptake by the plants (especially when nitrate is the sole N source).

When considering lowering pH as a commercial practice, the effects of lowering pH on plant nutritional value, postharvest quality and flavor need to be considered. Lowering pH did reduce the overall mineral nutrient contents and we noticed that basil flavor was slightly milder when pH was 4.0 compared with that at pH 5.5; however, this difference was not distinct and should not be problematic for marketing, although further analyses of organoleptic quality as affected by pH may be of interest.

Applicability of low nutrient solution pH for root rot disease control will depend on crop species-specific responses to low pH. For example, spinach plant productivity was significantly reduced at pH lower than 5.0 (Gillespie, 2019) and it was determined that appropriate overall nutrient adjustment based on their nutrient uptake was necessary at low pH (D.P. Gillespie et al., unpublished data).

Responses of other important horticultural crops to low pH are yet to be quantified. Arnon and Johnson (1942) demonstrated that tomato, lettuce, and bermudagrass can grow in nutrient solution pH 4.0 to 8.0, although the growth rate is largely reduced outside of optimum pH of 5.0 to 6.0. They also showed that at pH 4.0, tomato and lettuce shoot and root growth increased as calcium concentration in the nutrient solution increased (Arnon and Johnson, 1942). Voogt (1995) showed that carnation (*Dianthus caryophyllus*) flower yield increased with decreasing root zone pH varied between 4.5 and 7.1 by different NH_4 and NO_3 ratios.

Although many species may not be as tolerant to pH as low as 4.0, they may tolerate low pH when applied briefly (Arnon and Johnson, 1942; Bugbee, 2004; Islam et al., 1980; Mengel et al., 2001; Savvas and Gruda, 2018; Vlamis, 1953). Thus, one potential management strategy may include intermittently reducing pH to 4.0 for short periods (i.e., ≈1 week) when disease pressure is high, such as during hot and humid conditions or after transplant. Oomycete disease may still be established via oospores or mycelia; however, dispersal via zoospores may be limited by such short-term low-pH disturbance treatment. Impact of low pH to plant nutrition and thereby plant growth may not be significant if only applied intermittently. However, the effective duration of zoospore exposure to low pH will need to be determined. For example, Albright et al. (2007) reported that electrochemically reducing pH to 2.0 for 30 min did not have a large impact on zoospores.

Although this study suggests that the incidence of root rot is greatly reduced at pH 4.0 compared with pH 5.5 when zoospores were used as inoculum, it does not indicate that infection or dispersal through oospores or mycelia is not possible at pH 4.0. In fact, oospores and mycelia may be minimally affected by low pH, as these structures are surrounded by cell walls that motile zoospores lack (Blaker and MacDonald, 1983; Kong et al., 2009). It would also be of interest to determine the efficacy of low pH in the suppression of other *Pythium* species or other pathogenic oomycete species and at higher inoculum concentrations.

Conclusion

We discovered that basil plants exhibited normal growth in pH as low as 4.0, although nutrient concentrations of many elements of the leaf tissue decreased. As most commercial operations for leafy greens grow more than one species in the same hydroponic system, species-specific responses to pH and nutrient requirements must be better understood before applying this strategy in commercial practice. Nevertheless, our study demonstrated the utility of low pH as a management tactic against *P. aphanidermatum.* Further research is needed to determine its potential for suppression of other oomycete pathogens.

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