HortScience 54(10):1751–1756. 2019. https://doi.org/10.21273/HORTSCI14222-19

Leaf Tissue Nutrient Sufficiency Ranges of Four *Heuchera* Cultivars by Chronological Age

W. Garrett Owen

Department of Horticulture, Michigan State University, 1066 Bogue Street, East Lansing, MI 48824; and Michigan State University Extension, Tollgate Farm and Education Center, 28115 Meadowbrook Road, Novi, MI 48377

Additional index words. coral bells, greenhouse production, macronutrient, micronutrient, nitrogen, perennial, plant nutrition

***Abstract*. Coral bells (*Heuchera* sp.) are popular herbaceous perennials grown for their colorful foliage and venation and their aesthetic appeal in mixed containers and landscapes. Commercial coral bell production requires greenhouse or nursery growers to optimize production inputs such as managing mineral nutrition, thereby maximizing plant growth potential and foliage color. The objective of this study was to determine the optimum fertilizer concentrations, identify leaf tissue nutrient sufficiency ranges by chronological age, and to expand leaf tissue nutrient standards of coral bells grown in soilless substrates during container production. Coral bells (*H. hybrida* 'Black Beauty', 'Cherry Cola', 'Marmalade', and 'Peppermint Spice'), varying in leaf color, were grown under one of six constant liquid fertilizer concentrations [50, 75, 100, 200, 300, or 400 mg·L^{-1} nitrogen (N)] with a constant level of water-soluble micronutrient blend in a greenhouse. Fertilizer concentrations for optimal plant growth and development were determined by analyzing plant height, diameter, growth index, and total dry mass, and were found to be 50 to 75 mg·L^{-1} N after a nine-week crop cycle. Recently mature leaf tissue samples were collected and analyzed for elemental content of 11 nutrients at 3, 6, and 9 weeks after transplant (WAT) from plants fertilized with 50 to 75 mg·L^{-1} N. The black- ('Black Beauty') and red- ('Cherry Cola') colored-leaved cultivars contained higher total N, phosphorus (P), potassium (K), calcium (Ca), sulfur (S), zinc (Zn), and boron (B) than the orange- ('Marmalade') and green- ('Peppermint Spice') colored-leaved cultivars. For instance, in mature growth, total N concentration for 'Black Beauty' and 'Cherry Cola' ranged between 3.45 to 3.63% and 3.92% to 4.18% N, respectively, whereas for 'Marmalade' and 'Peppermint Spice', ranges were between 2.98% to 3.25% and 2.78% to 3.23% N, respectively. Optimal leaf tissue concentration sufficiency ranges determined in this scientifically based study were narrower and often times higher than previously reported survey values for coral bells.**

In the United States, coral bell (*Heuchera hybrida* L.) production increased by 167% ($14.4 million USD) from 1997 to 2014 (USDA, 1998, 2015). The increasing consumer demand for this herbaceous perennial is because of their colorful foliage and venation; mounding growth habit; use in mixed combination containers or landscape plantings; use as pollinator plants and cut flowers; and their drought- and deer-resistance. To continue to meet the increasing consumer demand for coral bells, greenhouse and nursery growers must optimize production inputs (Owen, 2019), such as fertilization. Traditionally, commercial mineral nutrition recommendations for the genera *Heuchera* range from 50 to 250 mg·L^{-1} nitrogen (N) on a continual basis (Biernbaum and Morrison, 2000; Pilon, 2006) or 150 to 200 mg·L^{-1} N as needed (Nau, 2011; Pilon, 2006). These fertility recommendations vary greatly, but the goal of any fertilizer regimen for containerized ornamentals is to provide sufficient but not excessive levels of essential nutrients (Scoggins, 2005). The philosophy of this approach is to monitor the inputs to the crop; and as along as the substrate inputs are within the recommended range, e.g., substrate pH and electrical conductivity (EC), it is assumed the fertility requirements of the crop are being met (Krug et al., 2010). This is consistent with Biernbaum and Morrison (2000), who concluded from a multiple species perennial fertility trial that coral bells (*Heuchera sanguinea* Engelm. 'Firefly') grew best at 62 mg·L^{-1} N provided continuously than 125 or 250 mg·L^{-1} N, thus warning against excessive fertilization. However, the N concentrations trialed and concentrations recently reported in the literature are considered optimal.

Optimum fertilization requirements (Biernbaum and Morrison, 2000; Scoggins, 2005) and nutritional leaf tissue sufficiency ranges and standards (Biernbaum and Morrison, 2000; Bryson and Mills, 2014) for the genera *Heuchera* are limited. Bryson and Mills (2014) reported nutritional leaf tissue sufficiency ranges for *H. micrantha* Douglas ex Lindl. 'Palace Purple' and *H. sanguinea*; but values represent samples collected mostly from specimens planted in mineral soils at botanical gardens and arboretums, thus providing a wide variability of recommended nutrient levels (Owen, 2019). Therefore, these nutritional standards do not accurately represent the nutritional status nor sufficiency ranges of the genera *Heuchera* grown by commercial greenhouses and nurseries in soilless substrates. Furthermore, little attention has been given to identifying nutrient requirements and nutritional status of container-grown coral bells by chronological age or as plants developed.

For herbaceous perennials, leaf tissue nutrient sufficiency ranges by chronological age have only been reported for perennial hibiscus (*Hibiscus hybrid* L. 'Mocha Moon' and 'Starry Starry Night'; Owen, 2019). For annual bedding plants, leaf tissue nutrient sufficiency ranges by chronological age have been reported for pot gerbera (*Gerbera jamesonii* Bolus ex Hook. f. 'Festival Light Eye Yellow'; Jeong et al., 2009), osteospermum (*Osteospermum hybrida* L. 'Lemon Symphony', 'Serenity Lavender Dark', 'Summertime Red Velvet', and 'Tradewinds Purple Bicolor'; Papineau and Krug, 2014), and zonal geranium (*Pelargonium* ×*hortorum* L.H. Bailey 'Tango Dark Red' and 'Rocky Mountain Dark Red'; Krug et al., 2010). Determining sufficiency ranges and leaf nutritional standards by chronological age for the genera *Heuchera* will establish nutrient recommendations that may aid in identifying nutritional deficiencies and/or toxicities (Owen, 2019) and further define fertilizer recommendations. Therefore, the objectives of this study were to determine the optimum fertilizer concentrations, identify leaf tissue nutrient sufficiency ranges by chronological age, and to expand leaf tissue nutrient standards of coral bells grown in soilless substrates during container production.

Materials and Methods

Plant material and culture. On 27 Sept. 2017, 72-cell plug trays of coral bells (*Heuchera hybrida* L. 'Black Beauty', 'Cherry Cola', 'Marmalade', and 'Peppermint Spice') were received from a commercial supplier (Ball Horticultural Co., West Chicago, IL). Young plants of each cultivar with similar heights,

Received for publication 5 May 2019. Accepted for publication 21 June 2019.

I gratefully acknowledge Darby Anderson, Melanie Connors, and Kyle Martin for greenhouse assistance; Dr. James Altland and Erin Lowe for substrate analysis; and the Americana Foundation and Michigan State University College of Agriculture and Natural Resources for greenhouse space and maintenance. I thank Ball Horticultural, Inc. for plant material; Barson's Greenhouse for substrate; and Bordine's Farm for fertilizer. For funding support, I thank the Fred C. Gloeckner Foundation, Inc. and Michigan State University Extension Agriculture and Agribusiness Institute (AABI) Generating Research and Extension to meet Economic and Environmental Needs (GREEEN).

The use of trade names in this publication does not imply endorsement by Michigan State University or Michigan State University Extension of products named or criticism of similar ones not mentioned.

W.G.O. is the corresponding author. E-mail: wgowen@msu.edu.

stem caliper, and node numbers were selected and transplanted, one plant per 16.5-cm (1.9-L) diameter container (Landmark Plastic Corp., Akron, OH). Containers were filled with premoistened, commercial soilless peat-based substrate comprised of (by volume) 65% peat, 20% perlite, and 15% vermiculite, amended with dolomitic limestone, wetting agent, and a starter nutrient charge with gypsum (Fafard 2; Sun Gro Horticulture, Agawam, MA). Substrate physical properties were determined using three representative samples that were analyzed using the North Carolina State University Porometer Procedure (Fonteno et al., 1995). Physical properties of the substrate were (by volume) 8.3% ± 0.8% air space, 77.9% ± 0.8% total porosity, 69.5% ± 0.5% container capacity, and 0.10 $g \cdot cm^{-3}$ bulk density. Plants were irrigated to container capacity with water supplemented with 35% sulfuric acid (AutoCraft Battery Acid, Johnson Controls Battery Group, Milwaukee, WI) at 0.16 $mg \cdot L^{-1}$ to neutralize alkalinity from 4.0 to 1.6 $meq \cdot L^{-1}$ calcium carbonate ($CaCO_3$) and reduce pH from 7.3 to a range of 5.8 to 6.0.

Plant fertility. Thirty-six plants per cultivar were placed on one of four greenhouse benches. Each bench was equipped with three independently controlled benchtop 1.9-cm black irrigation lines fitted with twenty-four 12-cm diameter drip rings (Dramm USA, Manitowoc, WI) that were placed on top of the substrate of each container, corresponding to one of six fertilizer concentrations. Each of the six fertilizer concentrations was replicated twice, for a total of 12 irrigation lines. These lines were randomized in two blocks, each consisting of two benches. Irrigation lines were connected to sump-pumps (model 1A, Little Giant Pump Co., Oklahoma City, OK), which delivered one of six constant liquid fertilizer concentrations [50, 75, 100, 200, 300, or 400 $mg \cdot L^{-1}$ nitrogen (N)], based on balanced ratios of N, phosphorous (P), and potassium (K) supplied by 15N–1.7P–12.5K (GreenCare Bordine's Special; Blackmore Co., Belleville, MI) containing 1.9% ammoniacal (NH_4^+)-N and 13.1% nitrate (NO_3^-)-N. Fertilizer concentrations were selected based on grower practice and to determine minimum and maximum sufficiency ranges.

Regardless of fertilizer treatment, plants received a constant level of water-soluble micronutrient blend (GreenCare Bordine's Special; Blackmore Co.) supplying (in $mg \cdot L^{-1}$) 2.0 iron (Fe), 0.5 manganese (Mn) and zinc (Zn), 0.25 boron (B) and copper (Cu), and 0.1 molybdenum (Mo). The water-soluble fertilizer and micronutrient blend were weighed and dissolved together in separate 100 L fertilizer barrels. Plants were irrigated as needed to the point of leaching and were never allowed to dry out. Each month, plants received a 150-mL drench containing 50 $mg \cdot L^{-1}$ magnesium sulfate ($MgSO_4 \cdot 7H_2O$). No solution was leached or drained from the containers after application.

Greenhouse environment. Plants were grown in a double polyethylene-covered greenhouse with roll-up side curtains [MSU Tollgate Farm and Education Center, Novi, MI (lat. 42° N)] at 20 °C under ambient daylight, supplemented with a photosynthetic photon flux density (*PPFD*) of ≈34.8 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at plant height [as measured with a quantum sensor (LI-COR Biosciences)], delivered from 150 W high-pressure sodium (HPS) lamps (Sun System® HPS 150 Grow Light Fixture; Sunlight Supply, Inc., Vancouver, WA) from 0600 to 2200 HR (a 16-h photoperiod). On each bench, an enclosed thermocouple recorded air temperature every 30 s, and averages were logged every 15 min by a data logger (WatchDog Model 2475 Plant Growth Station; Spectrum Technologies, Inc., Aurora, IL). Line quantum sensors (SQ-316-SS; Apogee Instruments, Inc., Logan, UT), mounted 60 cm above the benchtop, measured *PPFD* every 30 s. The average of each sensor was logged every 15 min by a data logger (WatchDog 2800 Weather Station; Spectrum Technologies, Inc.). Average daily light integral, air temperature, and relative humidity throughout the nine-week duration of the experiment were 10.2 ± 4.1 $mol \cdot m^{-2} \cdot d^{-1}$, 20.8 ± 5.6 °C, and 63.6% ± 5.7%, respectively.

Growth and nutritional data and calculations. Data were collected on three randomly selected experimental units (individual plants) of each cultivar. Data were collected at 3, 6, and 9 WAT. At each collection date, substrate solution was extracted 1 h after irrigation using the pour-through method (Wright, 1986) and analyzed for pH and electrical conductivity (EC) using a HI 9813-6 portable meter (Hanna Instruments, Woonsocket, RI). Plant height was determined by measuring from the substrate surface to the apical meristem with a digital caliper (digiMax; Wiha, Schönach, Germany). Plant diameter was determined by measuring the widest dimension and the axis perpendicular to the widest dimension and averaging. Growth index [GI = (plant height + plant diameter) ÷ 2] was calculated for each plant.

At 3, 6, and 9 WAT, the recently mature leaves (meaning the youngest, fully expanded leaves) were removed from the selected three experimental units from each cultivar. Leaves were washed in a solution of 0.5 N hydrochloric acid (HCl) for 1 min and rinsed in deionized water before being individually bagged and then dried in an oven at 70 °C for 1 week. After 7 d, dried tissue was weighed to determine young leaf dry mass (YDM) and then ground with a mortar and pestle to pass a ≤0.5-mm sieve, placed in 15-mL polypropylene conical centrifuge tubes (Falcon 17 × 120 mm; Corning, Corning, NY), and analyzed for nutrient concentrations by AgSource Laboratories (Lincoln, NE). Total N was processed by Kjeldahl digestion, and determined by flow injection analysis (FIA). Extractable K was processed by 2% acetic acid digestion and determined by inductively coupled plasma mass spectrometry (ICP-MS). Total P and all other plant minerals [Ca, Mg, Fe, Mn, Zn, B, and Cu] were processed by nitric acid/hydrogen peroxide digestion, and determined by ICP-MS.

The remaining plant tissues were destructively harvested by severing the stem at the substrate surface, individually bagging them, and drying them in an oven at 70 °C. After 1 week, plant dry mass (PDM) was determined. The total plant dry mass (TDM = YDM + PDM) was calculated for each plant.

Experimental design and statistical analyses. The experiment was laid out in a randomized complete block design with 2 blocks and 6 fertilizer concentrations arranged in a split-plot, with 2 replications within each split-plot. Cultivars were randomized within each replication. There were 3 experimental units per cultivar, per fertilizer concentrations, per replication. Within each block, no significant differences occurred among replications per cultivar; therefore, data were pooled. Effects of fertilizer concentrations per cultivar were analyzed using the Statistical Analysis System (SAS; version 9.2; SAS Institute, Cary, NC) general linear model procedure (PROC GLM) for ANOVA. For each cultivar, regression analyses of plant height, diameter, GI, and TDM at 9 WAT were performed using SAS regression procedure (PROC REG). For all analyses, a $P \leq 0.05$ was used to determine significant effects.

Results and Discussion

Sufficiency range. Plant growth was analyzed to determine lower and upper optimal nutritional limits. At 9 WAT, the height, diameter, GI, and TDM were statistically similar for most all *Heuchera* cultivars fertilized with 50 to 400 $mg \cdot L^{-1}$ N (Table 1; Figs. 1–4). However, increasing fertilizer concentrations significantly influenced the diameter and TDM of 'Cherry Cola' and the TDM of 'Peppermint Spice' plants. For instance, plant diameter and TDM of 'Cherry Cola' decreased by 30.8% (9.9 cm) and 46.9% (3 g), respectively, as fertilizer concentration increased from 50 to 400 $mg \cdot L^{-1}$ N. Because *Heuchera* growth was generally similar or larger at 50 $mg \cdot L^{-1}$ N than at 75 to 400 $mg \cdot L^{-1}$ N, thus 50 $mg \cdot L^{-1}$ N was determined as the lower nutritional limit.

Except for 'Peppermint Spice', plant growth of all other *Heuchera* cultivars was statistically similar among ascending fertilizer concentration from 75 to 400 $mg \cdot L^{-1}$ N (Table 1). Total dry mass of 'Peppermint Spice' was smallest at 50 $mg \cdot L^{-1}$ N, but it increased by 63.6% (4.2 g) as fertilizer concentrations increased from 50 to 75 $mg \cdot L^{-1}$ N. Smaller dry mass is likely attributed to fewer (to no) inflorescences present on plants fertilized at 50 $mg \cdot L^{-1}$ N than at 75 to 400 $mg \cdot L^{-1}$ N. Though TDM was not significantly influenced by increasing fertilizer concentrations for most all *Heuchera* cultivars, plants did, however, exhibit lower leaf necrosis at concentrations between ≥100 $mg \cdot L^{-1}$ N (personal observation). Lower leaf necrosis and smaller TDM for 'Peppermint Spice' is most likely attributed to sensitivity of an elevated substrate EC (Scoggins, 2005). For instance, average substrate EC extracted from all *Heuchera* cultivars grown at 100 to 400 $mg \cdot L^{-1}$ N were 2.98 to 4.22 $mS \cdot cm^{-1}$, respectively. They were 189% to 309% (1.95 to 3.19 $mS \cdot cm^{-1}$) and 135% to

Table 1. Average plant height, diameter, growth indices (GI), and total plant dry mass (TDM) for coral bells (*Heuchera hybrida* L.) with black- (‘Black Beauty’), red- (‘Cherry Cola’), orange- (‘Marmalade’), and green-colored leaves (‘Peppermint Spice’). Plants were grown under one of six constant liquid fertilizer concentrations [50, 75, 100, 200, 300, or 400 $mg \cdot L^{-1}$ nitrogen (N)], based on balanced ratios of N–phosphorous (P)–potassium (K) supplied by 15N–1.7P–12.5K containing 1.9% ammoniacal-N and 13.1% nitrate-N with a constant level of water-soluble micronutrient blend in a greenhouse. Plants (n = 6) were harvested at 9 weeks after transplant (WAT).

Cultivar and nitrogen (N) concn ($mg \cdot L^{-1}$ N)	Ht[z] (cm)	Diam[y] (cm)	GI[x] (cm)	TDM[w] (g)
Black Beauty				
50	3.33	58.7	37.0	6.5
75	3.40	57.4	36.8	5.5
100	3.03	54.1	34.0	5.2
200	3.00	56.9	35.5	5.3
300	2.67	48.4	30.2	4.0
400	3.03	44.9	29.5	3.5
Significance[v]	NS	L*	L**	L**
Cherry Cola				
50	3.27	32.1	32.3	6.4
75	3.50	28.3	30.5	5.4
100	3.57	27.9	30.5	4.2
200	3.50	25.7	28.8	4.9
300	3.27	22.7	26.1	3.6
400	3.06	22.2	25.0	3.4
Significance	NS	L***	NS	L**
Marmalade				
50	2.73	32.8	30.9	7.3
75	3.77	34.8	35.7	7.6
100	3.20	34.2	33.5	7.9
200	2.80	32.9	31.3	7.2
300	3.17	32.1	31.9	6.1
400	3.43	33.2	33.6	6.0
Significance	NS	NS	NS	NS
Peppermint Spice				
50	1.70	31.4	26.6	6.6
75	2.07	31.0	27.6	13.1
100	1.73	32.5	27.5	10.8
200	2.20	28.7	26.4	10.6
300	1.93	25.1	23.3	9.1
400	2.17	30.1	27.3	9.1
Significance	NS	NS	NS	L*

[z]Plant height (ht) measured from the substrate surface to the apical meristem.
[y]Plant diameter (diam) determined by measuring the widest dimension and the axis perpendicular to the widest dimension and averaged.
[x]Growth index (GI) = (plant height + plant diameter) ÷ 2].
[w]Total plant dry mass (TDM) = young plant dry mass (YDM) + plant dry mass (PDM).
[v]Linear (L) response for nitrogen (N) concentration. [NS, *, **, ***]Not significant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

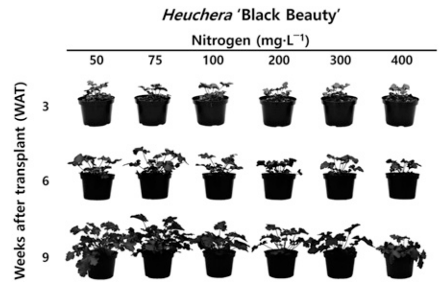

Fig. 1. Depiction of coral bells (*Heuchera hybrida* L. ‘Black Beauty’) fertilized with one of six constant liquid fertilizer concentrations [50, 75, 100, 200, 300, or 400 $mg \cdot L^{-1}$ nitrogen (N)], based on balanced ratios of N–phosphorous (P)–potassium (K) supplied by 15N–1.7P–12.5K containing 1.9% ammoniacal-N and 13.1% nitrate-N with a constant level of water-soluble micronutrient blend at 3, 9, and 9 weeks after transplant (WAT).

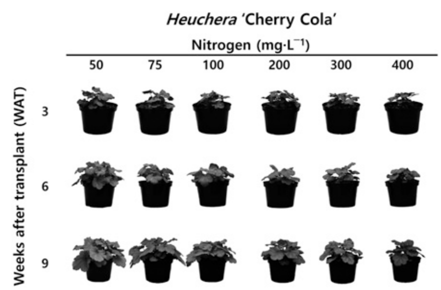

Fig. 2. Depiction of coral bells (*Heuchera hybrida* L. ‘Cherry Cola’) fertilized with one of six constant liquid fertilizer concentrations [50, 75, 100, 200, 300, or 400 $mg \cdot L^{-1}$ nitrogen (N)], based on balanced ratios of N–phosphorous (P)–potassium (K) supplied by 15N–1.7P–12.5K containing 1.9% ammoniacal-N and 13.1% nitrate-N with a constant level of water-soluble micronutrient blend at 3, 6, and 9 weeks after transplant (WAT).

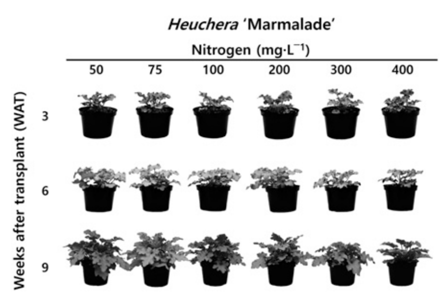

Fig. 3. Depiction of coral bells (*Heuchera hybrida* L. ‘Marmalade’) fertilized with one of six constant liquid fertilizer concentrations [50, 75, 100, 200, 300, or 400 $mg \cdot L^{-1}$ nitrogen (N)], based on balanced ratios of N–phosphorous (P)–potassium (K) supplied by 15N–1.7P–12.5K containing 1.9% ammoniacal-N and 13.1% nitrate-N with a constant level of water-soluble micronutrient blend at 3, 6, and 9 weeks after transplant (WAT).

232% (1.71–2.95 $mS \cdot cm^{-1}$) higher than average substrate EC values determined for plants fertilized at 50–75 $mg \cdot L^{-1}$ N, respectively. Additionally, average substrate pH decreased by 19% (1.1 pH units), from 5.8 to 4.7 pH units, as fertilizer concentration increased from 50 to 400 $mg \cdot L^{-1}$ N, respectively. Therefore, based on these results and visual observations, it was concluded that plants fertilized with ≥100 $mg \cdot L^{-1}$ N were entering a situation of luxury to detrimental nutrient consumption, and the additional fertilizer was not beneficial to plant quality (Jeong et al., 2009; Krug et al., 2010; Owen, 2019; Papineau and Krug, 2014). When plant growth and substrate pH and EC data are taken together, 75 $mg \cdot L^{-1}$ N was determined to be the upper nutritional range limit, and plants fertilized with 100 to 400 $mg \cdot L^{-1}$ N were excluded from further statistical analyses. Thus, the optimal sufficiency range for all four *Heuchera* cultivars in this study was 50 to 75 $mg \cdot L^{-1}$ N.

Sufficiency ranges for all four *Heuchera* cultivars were used to determine recommend leaf tissue concentrations of eleven elements by chronological age. Similar to Owen (2019), lower and upper limits of recommended leaf tissue concentration ranges were defined by analyzing data for each *Heuchera* cultivar grown at 50 to 75 $mg \cdot L^{-1}$ N over a 9-week crop cycle. Nutrient concentrations differed among cultivars with black- (‘Black Beauty’), red- (‘Cherry Cola’), orange- (‘Marmalade’), and green-colored leaves (‘Peppermint Spice’). No leaf tissue concentration limits have been published for *H. hybrida*, but survey measurements taken from botanical garden or arboretum- (*H. micrantha* Douglas ex Lindl. ‘Palace Purple’) and nursery-grown (*H. sanguinea* Engelm.) coral bell plants are reported by Bryson and Mills (2014; Table 2). These tissue concentration ranges will be referred to as the genera *Heuchera*.

Nitrogen. Total N [NO_3^- and NH_4^+] concentration of *Heuchera* cultivars in this study harvested at 3, 6, and 9 WAT (Table 3) resulted in higher and broader sufficiency ranges than those previously reported for *H. micrantha* (1.46% to 1.77% N) and *H. sanguinea* (1.26% to 1.45% N; Bryson and Mills, 2014)—but not *H. sanguinea* ‘Firefly’ (5.5% N; Biernbaum and Morrison, 2000; Table 2). At all stages of growth, total N concentration was higher in plants fertilized with 75 $mg \cdot L^{-1}$ N than with 50 $mg \cdot L^{-1}$ N. In young growth (3 WAT), total N concentration of ‘Black Beauty’, ‘Cherry Cola’, ‘Marmalade’, and

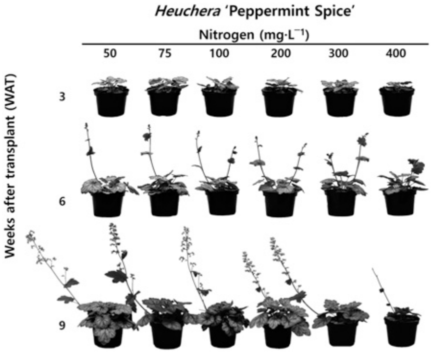

Fig. 4. Depiction of coral bells (*Heuchera hybrida* L. 'Peppermint Spice') fertilized with one of six constant liquid fertilizer concentrations [50, 75, 100, 200, 300, or 400 mg·L^{-1} nitrogen (N)], based on balanced ratios of N–phosphorous (P)–potassium (K) supplied by 15N–1.7P–12.5K containing 1.9% ammoniacal-N and 13.1% nitrate-N with a constant level of water-soluble micronutrient blend at 3, 6, and 9 weeks after transplant (WAT).

'Peppermint Spice' ranged from 3.43% to 3.83%, 3.82% to 3.96%, 3.24% to 3.27%, and 2.87% to 3.15% N, respectively (Table 3). Increased total N concentration occurred at 6 WAT (active growth), but decreased onward as plants matured. Total N concentration of mature growth (9 WAT) ranged from 3.45% to 3.63%, 3.92% to 4.18%, 2.98% to 3.25%, and 2.78% to 3.23% N for 'Black Beauty', 'Cherry Cola', 'Marmalade', and 'Peppermint Spice', respectively. These results are consistent with Krug et al. (2010), who reported decreasing N concentration of geranium cultivars fertilized with 100 to 300 mg·L^{-1} N at young to mature growth stages (2 to 12 WAT). Interestingly, in this study, phenotypes with black- ('Black Beauty') or red-colored leaves ('Cherry Cola') had generally higher leaf tissue N concentration than orange- ('Marmalade') or green-colored leaves ('Peppermint Spice'). Similarly, in the Krug et al. (2010) study, N concentration of geranium 'Tango Dark Red', with dark-colored leaves, was higher (3.99% to 4.15% N) than the range reported for 'Rocky Mountain Red' (3.62% to 4.02% N), with light-colored leaves. However, no correlation between N concentration and leaf color were determined nor the focus of this study. Urban (1918) reports a correlation between beet (*Beta vulgaris* L.) leaf color and N concentration, the darker leaves containing the most N and the lighter the least. Furthermore, Judkins and Wander (1949) found a significant correlation between increasing N application rate, leaf tissue N content, and leaf color in apple (*Malus* sp. Mill. 'Delicious', 'Cortland', and 'Stayman Winesap'), grape (*Vitis* sp. L. 'Concord' and 'Delaware'), and peach [*Prunus persica* (L.) Batsch 'Halehaven']. Based on the work of Urban (1918) and Judkins and Wander (1949), it is speculated that 'Black Beauty' and 'Cherry Cola' had higher leaf tissue N concentration than 'Marmalade' and 'Peppermint Spice', due to their darker-colored leaves.

Phosphorus. The recommended range for leaf tissue P concentration for the genera *Heuchera* is between 0.20% and 0.29% P (Bryson and Mills, 2014; Table 2). In the current study, P concentrations for all *Heuchera* cultivars were higher and broader than those previously published by Bryson and Mills (2014), with the exception of mature growth of 'Peppermint Spice'. Phosphorus uptake is greater in younger plants and decreases with maturity (Bryson and Mills, 2014), and this trend was observed in the current study. In general, for all cultivars grown with 50 to 75 mg·L^{-1} N, leaf tissue P concentration increased by 6 WAT (active growth) and then decreased at maturity (9 WAT; Table 3). This trend is consistent with those of gerbera (Jeong et al., 2009) and geranium 'Tango Dark Red' (Krug et al., 2010). Jeong et al. (2009) report that the P concentration of gerbera increased by 5 WAT and decreased at 8 WAT (bloom). At maturity (9 WAT), P concentrations of 'Black Beauty', 'Cherry Cola', 'Marmalade', and 'Peppermint Spice' were between 0.52% to 0.55%, 0.64% to 0.68%, 0.37% to 0.39%, and 0.22% to 0.30% P, respectively (Table 3). Furthermore, P concentrations were higher in 'Black Beauty' and 'Cherry Cola' than in 'Marmalade' and 'Peppermint Spice' at all stages of growth, while Krug et al. (2010) report higher P concentration only in young growth (2 WAT) of geranium 'Tango Dark Red' than 'Rocky Mountain Dark Red'. The variation in P concentration among cultivars is likely attributed to genetics, because P uptake is genetically determined and differs between species and cultivars (Bryson and Mills, 2014).

Potassium. The recommended range for leaf tissue K concentration for the genera *Heuchera* is between 1.09% and 2.88% K (Bryson and Mills, 2014; Table 2).

Young leaf tissue K concentrations for 'Black Beauty', 'Marmalade', and 'Peppermint Spice' were similar to those reported by Bryson and Mills (2014), while K concentration of 'Cherry Cola' were higher and broader. For instance, at 3 WAT, K concentrations of 'Black Beauty', 'Cherry Cola', 'Marmalade', and 'Peppermint Spice' were between 2.40% to 2.68%, 2.80% to 3.29%, 1.92% to 2.27%, and 1.64% to 1.70% K, respectively (Table 3). As plants matured, K concentration increased by 6 WAT and decreased at 9 WAT (mature growth/bloom), which is similar to osteospermum (Papineau and Krug, 2014), gerbera (Jeong et al., 2009), and perennial hibiscus (Owen, 2019). Leaf tissue K concentrations of 'Black Beauty', 'Cherry Cola', 'Marmalade', and 'Peppermint Spice' at 9 WAT were between 2.21% to 2.27%, 2.68% to 3.03%, 1.45% to 1.58%, and 1.10% to 1.35% K, respectively. Lower and upper range limits at 9 WAT were narrower and within the recommended range limit for all cultivars except 'Cherry Cola', which was 5% higher than the upper limit reported by Bryson and Mills (2014). Similarly, Krug et al. (2010) reported increased K concentration of geranium 'Tango Dark Red', the dark-colored leaf at maturity. The higher range limit for 'Cherry Cola' may indicate that plants fertilized with 75 mg·L^{-1} N were supplied with more K than needed for their metabolic requirements (luxury consumption), thus K recommendations may be lower than observed in the current study. However, no K toxicity symptoms were observed in 'Cherry Cola' (personal observation).

Calcium. The recommended range for leaf tissue Ca concentration for the genera *Heuchera* is between 1.26% and 2.23% Ca (Bryson and Mills, 2014; Table 2). The previously published Ca concentration range for *Heuchera* is higher than those observed for 'Black Beauty', 'Marmalade', and 'Peppermint Spice', but not 'Cherry Cola' (Table 3). Calcium concentrations in young growth (3 WAT) were between 1.01% to 1.10%, 1.14% to 1.34%, 0.70% to 0.72%, and 0.89% to 0.94% Ca for 'Black Beauty', 'Cherry Cola', 'Marmalade', and 'Peppermint Spice', respectively (Table 3). While Ca concentration should increase as plants mature (Krug et al., 2010), leaf tissue Ca concentrations of 'Black Beauty', 'Cherry Cola', 'Marmalade', and 'Peppermint Spice' at 9 WAT decreased and were between 0.88% to 0.95%, 1.36% to 1.66%, 0.73% to 0.77%, and 1.15% to 1.21% Ca, respectively. The observed trend of increased Ca by 6 WAT (active growth) and decrease at maturity and bloom (9 WAT) is consistent with zonal geranium 'Rocky Mountain Dark Red' (Krug et al., 2010) and perennial hibiscus (Owen, 2019)—but not gerbera (Jeong et al., 2009) or osteospermum (Papineau and Krug, 2014). The increased Ca concentration at 6 WAT may be attributed to the increased amount of NO_3^- (13.1%) than NH_4^+ (1.9%) N provided by the fertilizer, because NO_3^- usually increases Ca uptake (Bryson and Mills, 2014). The decrease in Ca concentration from 6 to 9 WAT (active to mature growth/bloom) may be attributed to the antagonism and competitive uptake of K or high relative humidity in the greenhouse, thus limiting Ca movement to meristematic tissues (Bryson and Mills, 2014; Owen, 2019); however, no Ca deficiency symptoms were observed. Furthermore, the average substrate pH of plants fertilized with 50 to 75 mg·L^{-1} N was 5.8, which is optimal for Ca availability and noted by Owen (2019) for *Hibiscus* production.

Magnesium. The recommended range for leaf tissue Mg concentration for the genera *Heuchera* is between 0.20% and 0.45% Mg (Bryson and Mills, 2014; Table 2). The magnesium concentration range for all *Heuchera* cultivars in this study were narrower but within range previously reported by Bryson and Mills (2014; Table 3). Magnesium concentration in young leaf tissue of 'Black Beauty', 'Cherry Cola', 'Marmalade', and 'Peppermint Spice' at 3 WAT ranged between 0.39% to 0.41%, 0.41% to 0.44%, 0.25% to 0.27%, and 0.27% to 0.30% Mg, respectively. In mature plants (9 WAT), Mg concentration ranged between 0.31% to 0.33%, 0.35% to 0.37%, 0.23% to 0.24%, and 0.29% to 0.33% Mg for 'Black Beauty', 'Cherry Cola', 'Marmalade', and 'Peppermint Spice', respectively. Over time, an increase in Mg concentration by 6 WAT occurred and then decreased for both lower and upper range limits. Krug et al. (2010) and Papineau and Krug (2014) reported similar trends for the lower range limits (100 mg·L^{-1} N)

Table 2. Recommended leaf tissue ranges for *Heuchera micrantha* 'Palace Purple' and *H. sanguinea* previously published by Bryson and Mills (2014) and values reported for *H. sanguinea* 'Firefly' by Biernbaum and Morrison (2000).

Elemental nutrients	Unit of measure	Bryson and Mills (2014)[z] *Heuchera micrantha* 'Palace Purple'[x]	Bryson and Mills (2014)[z] *Heuchera sanguinea*[w]	Biernbaum and Morrison (2000)[y] *Heuchera sanguinea* 'Firefly'[v]
Macronutrients				
Total nitrogen	%	1.46–1.77	1.26–1.45	5.5
Phosphorus		0.20–0.29	0.16–0.28	0.4
Potassium		1.49–2.88	1.09–1.28	2.1
Calcium		1.26–1.88	1.47–2.23	1.1
Magnesium		0.32–0.45	0.20–0.29	0.6
Sulfur		0.13–0.25	0.10–0.14	0.2
Micronutrients				
Iron	$mg \cdot kg^{-1}$	35–77	30–53	57
Manganese		34–77	13–26	78
Zinc		20–34	15–32	45
Copper		3–12	1–4	7
Boron		22–47	21–39	32
Sodium		—[u]	—	258

[z]Recommended leaf tissue range for *Heuchera micrantha* 'Palace Purple' and *H. sanguinea* previously published by Bryson and Mills (2014).
[y]Leaf tissue values reported for *Heuchera sanguinea* 'Firefly' previously published by Biernbaum and Morrison (2000).
[x]Tissue sample from botanical garden/arboretum plants.
[w]Tissue sampled from container production nursery and botanical garden/arboretum plants.
[v]Tissue samples from plants grown in a soilless substrate.
[u]No previously reported recommended leaf tissue range for the genera *Heuchera* by Bryson and Mills (2014).

Table 3. Sufficiency ranges of 11 essential elemental nutrients determined at 3 (young growth), 6 (active growth), and 9 (mature growth and/or bloom) weeks after transplant (WAT) for coral bells (*Heuchera hybrida* L.) with black- ('Black Beauty'), red- ('Cherry Cola'), orange- ('Marmalade'), and green-colored leaves ('Peppermint Spice') grown (n = 6) under 50–75 $mg \cdot L^{-1}$ nitrogen (N), based on balanced ratios of N–phosphorous (P)–potassium (K) supplied by 15N–1.7P–12.5K containing 1.9% ammoniacal-N and 13.1% nitrate-N with a constant level of water-soluble micronutrient blend.

Cultivar and weeks after transplant (WAT)	Total nitrogen (%)	Phosphorus (%)	Potassium (%)	Calcium (%)	Magnesium (%)	Sulfur (%)	Iron ($mg \cdot kg^{-1}$)	Manganese ($mg \cdot kg^{-1}$)	Zinc ($mg \cdot kg^{-1}$)	Copper ($mg \cdot kg^{-1}$)	Boron ($mg \cdot kg^{-1}$)
Black Beauty											
3	3.43–3.83	0.55–0.58	2.40–2.68	1.01–1.10	0.39–0.41	0.38–0.39	105.2–155.0	61.9–72.2	34.9–39.4	6.3–7.1	28.0–28.5
6	3.79–4.00	0.72–0.75	3.00–3.06	1.07–1.26	0.37–0.40	0.40–0.45	128.5–189.6	57.2–67.5	54.6–56.1	7.1–7.2	29.9–33.5
9	3.45–3.63	0.52–0.55	2.21–2.27	0.88–0.95	0.31–0.33	0.45–0.57	124.2–145.5	43.7–44.7	56.4–59.4	9.7–9.8	41.3–46.2
Cherry Cola											
3	3.82–3.96	0.57–0.60	2.80–3.29	1.14–1.34	0.41–0.44	0.41–0.47	116.6–137.1	67.2–70.7	38.6–41.6	6.0–7.9	36.6–38.2
6	4.26–4.35	0.64–0.72	2.87–2.92	1.83–1.91	0.46–0.45	0.47–0.56	115.9–117.2	58.1–68.4	41.6–48.9	8.3–9.2	48.6–55.5
9	3.92–4.18	0.64–0.68	2.68–3.03	1.36–1.66	0.35–0.37	0.59–0.66	106.8–111.7	58.4–65.7	58.5–71.8	9.9–10.3	65.3–67.5
Marmalade											
3	3.24–3.27	0.47–0.50	1.92–2.27	0.70–0.72	0.25–0.27	0.45–0.52	137.5–154.2	62.6–73.5	41.7–47.8	6.4–7.1	30.8–33.6
6	3.98–4.09	0.57–0.61	2.60–2.66	0.89–1.07	0.32–0.34	0.47–0.48	197.0–209.0	62.6–73.5	49.2–50.8	7.4–8.4	34.8–36.8
9	2.98–3.25	0.37–0.39	1.45–1.58	0.73–0.77	0.23–0.24	0.45–0.59	146.7–203.4	44.3–46.0	69.0–70.8	10.3–10.9	37.8–37.9
Peppermint Spice											
3	2.87–3.15	0.37–0.44	1.64–1.70	0.89–0.94	0.27–0.30	0.39–0.41	50.3–58.4	54.2–65.5	35.1–35.9	5.5–5.8	30.3–30.6
6	3.58–3.74	0.39–0.40	2.01–2.15	1.22–1.26	0.32–0.33	0.35–0.43	65.5–73.4	48.4–50.2	36.1–38.8	6.0–6.2	34.5–34.7
9	2.78–3.23	0.22–0.30	1.10–1.35	1.15–1.21	0.29–0.33	0.36–0.38	51.6–65.4	45.5–51.6	45.6–47.7	6.4–8.1	36.1–36.4

of geranium 'Tango Dark Red' and ostespermum from 2 to 12 WAT. A lower Mg concentration at 9 WAT in comparison with Mg concentration at 3 WAT may be attributed to the antagonistic effect of K from the fertilizer source, reduced residual effect of the dolomitic limestone used to adjust substrate pH, or a dilution effect of dry mass and a consistent volume of $MgSO_4$ applied (Owen, 2019). Though leaf tissue Mg concentrations were within the recommended range, symptoms of Mg deficiency such as interveinal chlorosis would be difficult to observed because of the color and venation pattern of *Heuchera* leaves.

Sulfur. The recommended range for leaf tissue S concentration for the genera *Heuchera* is between 0.10% and 0.25% S (Bryson and Mills, 2014; Table 2). Unlike previous reports by Krug et al. (2010) and Papineau and Krug (2014), S concentration for all *Heuchera* cultivars in this study were higher and narrower than those previously reported by Bryson and Mills (2014; Table 3). In young plants (3 WAT), S concentration ranged between 0.38% to 0.39%, 0.41% to 0.47%, 0.45% to 0.52%, and 0.39% to 0.41% S for 'Black Beauty', 'Cherry Cola', 'Marmalade', and 'Peppermint Spice', respectively (Table 3). As plants matured (9 WAT), S concentration for 'Black Beauty', 'Cherry Cola', 'Marmalade', and 'Peppermint Spice' ranged between 0.45% to 0.57%, 0.59% to 0.66%, 0.45% to 0.59%, and 0.36% to 0.48% S, respectively. At 9 WAT, the lower range limits for 'Black Beauty', 'Cherry Cola', 'Marmalade', and 'Peppermint Spice' were 350%, 490%, 350%, and 260% higher, respectively, than ranges previously published by Bryson and Mills (2014). Upper range limits at 9 WAT for 'Black Beauty', 'Cherry Cola', 'Marmalade', and 'Peppermint Spice' were 128%, 164%, 136%, and 52% higher, respectively, than ranges previously published by Bryson and Mills (2014). Leaf tissue S concentration was generally lower for 'Peppermint Spice' than 'Cherry Cola', which may be attributed to a dilution effect of dry mass because TDM was 0.2 to 7.7 g greater for 'Peppermint Spice' than 'Cherry Cola' fertilized with 50 to 75 $mg \cdot L^{-1}$ N—though S deficiency was not observed.

Iron. The recommended range for leaf Fe concentration for the genera *Heuchera* is between 30 and 75 $mg \cdot kg^{-1}$ Fe (Bryson and Mills, 2014; Table 2). Iron concentrations were higher than those published by Bryson and Mills (2014) for 'Black Beauty', 'Cherry Cola', and 'Marmalade', but not 'Peppermint Spice'. The observed higher range for 'Black Beauty', 'Cherry Cola', and 'Marmalade' may likely be attributed to high K, which increases the mobility and solubility of Fe in plants (Bryson and Mills, 2014) than Fe toxicity, which is associated with a substrate pH <5.4. In the current study, substrate pH ranged from 5.7 ± 0.1 to 5.8 ± 0.2 for plants fertilized with 50 to 75 $mg \cdot L^{-1}$ N at 3 to 9 WAT, respectively; no Fe toxicity symptoms, such as lower leaf bronzing or necrosis, were observed. In young plants (3 WAT), Fe concentration ranged between 105 to 155, 117 to 137, 138 to 154, and 50 to 58 mg·kg^{-1} Fe for 'Black Beauty', 'Cherry Cola', 'Marmalade', and 'Peppermint Spice', respectively (Table 3). Similar to studies of gerbera (Jeong et al., 2009), perennial hibiscus (Owen, 2019), and osteospermum (Papineau and Krug, 2014), Fe concentration increased slightly from 3 to 6 WAT, but decreased onward as plants matured. At maturity/bloom (9 WAT), leaf tissue Fe concentration for 'Black Beauty', 'Cherry Cola', 'Marmalade', and 'Peppermint Spice' ranged between 124 to 146, 107 to 112, 148 to 203, and 52 to 65 mg·kg^{-1} Fe, respectively.

Manganese. The recommended range for Mn concentration for the genera *Heuchera* is between 13 and 77 mg·kg^{-1} Mn (Bryson and Mills, 2014; Table 2). In the current study, Mn concentrations were within a narrower range than previously published by Bryson and Mills (2014). Manganese concentrations for 'Black Beauty', 'Cherry Cola', 'Marmalade', and 'Peppermint Spice' grown with 50 mg·L^{-1} N decreased by 29%, 13%, 29%, and 16% (18.2, 8.8, 18.3, and 8.7 mg·kg^{-1} Mn) beginning at 3 to 9 WAT, respectively (Table 3). Although Mn concentrations were narrower than previously published ranges, visual Mn deficiency symptomology was not observed in any of the *Heuchera* cultivars trialed. A similar response occurred for the upper optimal Mn range. Leaf tissue Mn concentration of 'Black Beauty', 'Cherry Cola', 'Marmalade', and 'Peppermint Spice' grown with 75 mg·L^{-1} N decreased by 38%, 7%, 37%, and 21% (27.5, 5, 27.5 and 13.9 mg·kg^{-1} Mn) beginning at 3 to 9 WAT, respectively. This is consistent with trends reported for geranium 'Rocky Mountain Red' (Krug et al., 2010), gerbera (Jeong, et al., 2009), perennial hibiscus (Owen, 2019), and osteospermum cultivars (Papineau and Krug, 2014).

Zinc. The recommended range for Zn concentration for the genera *Heuchera* is between 15 and 34 mg·kg^{-1} Zn (Bryson and Mills, 2014; Table 2). Zinc tissue concentrations in the current study were higher at all stages of growth for all *Heuchera* cultivars than those previously published. Lower and upper limits increased over time, similar to studies of gerbera (Jeong et al., 2009), perennial hibiscus (Owen, 2019), and osteospermum (Papineau and Krug, 2014). Zinc concentrations of young growth for 'Black Beauty', 'Cherry Cola', 'Marmalade', and 'Peppermint Spice' range between 34.9 to 39.4, 38.6 to 41.6, 41.7 to 47.8, and 35.1 to 35.9 mg·kg^{-1} Zn, respectively (Table 3). Bryson and Mills (2014) indicated that high levels of available P and Fe in soils can adversely affect plant uptake of Zn, which may attribute to lower concentrations observed at 3 WAT. Furthermore, lower Zn tissue concentration in young growth may be related to plant age, when plants lack extensive root systems, and thus diffusion of available Zn is limited (Owen, 2019). As plants matured, leaf tissue Zn concentration for 'Black Beauty', 'Cherry Cola', 'Marmalade', and 'Peppermint Spice' increased to ranges between 56.4 to 59.4, 58.5 to 71.8, 69.0 to 70.8, and 45.6 to 47.7 mg·kg^{-1} Zn, respectively (Table 3).

Copper. The recommended range for Cu concentration for the genera *Hibiscus* is between 1 and 12 mg·kg^{-1} Cu (Bryson and Mills, 2014; Table 2). Lower and upper limits increased over time, similar to both perennial hibiscus cultivars reported by Owen (2019), and were within a narrower range than those previously published for the genera *Heuchera*. In young growth (3 WAT), ranges of Cu concentration for 'Black Beauty', 'Cherry Cola', 'Marmalade', and 'Peppermint Spice' were between 6.3 to 7.1, 6.0 to 7.9, 6.4 to 7.1, and 5.5 to 5.8 mg·kg^{-1} Cu, respectively (Table 3). Though the lowest Cu tissue concentration was observed in 'Peppermint Spice', no deficiency symptoms were observed because Cu deficiency is uncommon in greenhouse production (Jeong et al., 2009). In mature (9 WAT) 'Black Beauty', 'Cherry Cola', 'Marmalade', and 'Peppermint Spice', leaf tissue Cu concentration increased to ranges between 9.7 to 9.8, 9.9 to 10.3, 10.3 to 10.9, and 6.4 to 8.1 mg·kg^{-1} Cu, respectively (Table 3).

Boron. The recommended range for B concentration for the genera *Heuchera* is between 21 and 47 mg·kg^{-1} B (Bryson and Mills, 2014; Table 2). Boron tissue concentrations in this study provide a narrower range limit than values reported by Bryson and Mills (2014), except for 'Cherry Cola', which were higher as plants matured.

Though B concentration at 3 to 9 WAT for 'Cherry Cola' increased from 36.6 to 38.2 mg·L^{-1} B to 65.3 to 67.5 mg·kg^{-1} B, respectively, Bryson and Mills (2014) indicated average B concentration in dry plant tissue can range from 20 to 100 mg·kg^{-1} B. Therefore, B concentrations observed for 'Cherry Cola' are within the general range. Like studies of gerbera (Jeong et al., 2009) and osteospermum (Papineau and Krug, 2014), lower and upper limits for all *Heuchera* cultivars increased over time. In young growth (3 WAT), B concentration for 'Black Beauty', 'Cherry Cola', 'Marmalade', and 'Peppermint Spice' ranges were between 28.0 to 28.5, 36.6 to 38.2, 30.8 to 33.6, and 30.3 to 30.6 mg·kg^{-1} B, respectively (Table 3). For mature (9 WAT) 'Black Beauty', 'Cherry Cola', 'Marmalade', and 'Peppermint Spice' plants, leaf tissue B concentration increased to ranges between 41.3 to 46.2, 65.3 to 67.5, 37.8 to 37.9, and 36.1 to 36.4 mg·kg^{-1} B, respectively (Table 3).

Conclusion

For the four *H. hybrida* cultivars studied, maximum growth occurred when an optimal fertility level of 50 to 75 mg·L^{-1} N and a constant level of micronutrients were provided. Leaf tissue sufficiency ranges for *H. hybrida* 'Black Beauty', 'Cherry Cola', 'Marmalade', and 'Peppermint Spice' by chronological age were determined and established ranges that differentiate between black-, red-, orange-, and green-colored-leaved cultivars. Leaf tissue concentration sufficiency ranges determined in this study are generally narrower or higher than those reported by Bryson and Mills (2014), which is likely due to investigating one cultivar of each leaf color. Therefore, studies investigating multiple cultivars with similar leaf colors and venations and other fertilizer sources is warranted before these values are used for all coral bells. Continued research investigating other popular herbaceous perennial species grown in soilless substrates during container production over time is needed, to thereby establish nutrient sufficiency ranges by chronological age.

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