

Growth and Yield of Iron-deficient Chile Peppers in Sand Culture

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ABSTRACT. Growth and yield responses of ‘New Mexico 6-4’ and ‘NuMex R Naky’ chile pepper [*Capsicum annuum* L. var. *annuum* (Longum Group)] to four Fe levels were studied under sand culture. A balanced nutrient solution (total nutrient concentration <2 mmol·L⁻¹) was recirculated continuously to plants potted in acid-washed sand from the seedling stage to red fruit harvest. Plants received 1, 3, 10 or 30 μM Fe as ferric ethylenediamine di-(o-hydroxyphenyl-acetate). Plant growth was determined by leaf area, specific leaf area [(SLA), leaf area per unit dry weight of leaves], instantaneous leaf photosynthetic rates, and dry matter partitioning. Low Fe (1 or 3 μM Fe) in the nutrient solution was associated with lower relative growth rates (RGR), increased SLA, and higher root to shoot ratios (3 μM Fe plants only) at final harvest. High Fe levels (10 or 30 μM Fe) in the nutrient solution were associated with an increased yield of red fruit and total plant dry matter. RGR of low-Fe young chile plants was reduced before any chlorotic symptoms appeared.

Iron deficiency occurs frequently in many crops cultivated in calcareous soils. These soils are distributed worldwide (Guerinot and Yi, 1994) and cover large areas of the southwestern United States and northern Mexico. Although chile pepper [*Capsicum annuum* L. var. *annuum* (Longum Group)] has evolved some biochemical and root morphological adaptations such as H⁺ extrusion, reduction of ferric Fe, release of organic acids in an expanded subapical root zone, and discharge of riboflavin (Landsberg, 1986; Welkie, 1993) to deal with low Fe availability, Fe deficiency problems have been reported (Shifriss and Eidelman, 1983; Welkie, 1993). Temporary chlorosis, that was corrected with foliar applied Fe, had been observed during the fast growth phase of chile peppers in our experimental plots in New Mexico.

To achieve maximum growth rates, plants balance their dry matter partitioning (Gutschick, 1987). Restriction of relative growth rates can reduce the internal requirement for mineral nutrients (Gutschick, 1993). Changes in dry matter partitioning have practical application because they have allowed for development of high yielding crops (Ericsson, 1995). Changes in root to shoot (R:S) ratios are element-specific (Marschner et al., 1996). Göransson (1993) found that European white birch (*Betula pendula* Roth.) seedlings had increased their R:S ratio when subjected to low relative rates of Fe.

The present research sought to evaluate plant growth and yield of chile peppers grown in sand culture at low Fe levels. The sand culture system used relatively large volumes of dilute nutrient solution and fine silica sand to simulate some mechanical soil properties. Root hair abundance may explain the lower Fe con-

centration required by chile pepper and other crops grown in rockwool than in nutrient film technique (Sonneveld and Voogt, 1985). Sand culture was chosen to reduce root medium heterogeneity (Asher and Edwards, 1983), control nutrient concentrations, and allow ready separation of roots from the growing medium.

Materials and Methods

PLANT MATERIAL AND ROOT SUBSTRATE. Seeds of ‘New Mexico 6-4’ and ‘NuMex R Naky’, two chile pepper cultivars with different yield potential, were surface disinfested with 2.6% sodium hypochlorite (50% Clorox) solution for 30 min, rinsed, and germinated at approximately 23 °C in paper towels moistened with a solution of CaSO₄ at 0.1 mol·m⁻³ to preserve membrane function (Gutschick, 1993). After 9 d, the germinated seeds were transferred to 192-cell plastic trays (cell size 2.8 × 2.8 cm) filled with 40-mesh (0.635-mm) white silica sand, which had been washed with HCl to remove Fe and other micronutrients.

The trays were placed in a greenhouse and watered as needed during the 34 d of initial growth. The greenhouse conditions and the nutrient solution for the seedlings were the same as later in the sand culture, including their corresponding iron treatment, as described below. From these trays, 24 seedlings (43 d old) from each cultivar were randomly selected and transplanted individually into 15.7-L plastic pots filled with acid-washed silica sand. The pots were painted white to reduce heat loading. At 1500 HR on a typical day (day 108), air temperature was 31 °C and the temperature of the nutrient solution in the reservoirs was 24 °C.

To eliminate Fe, each 10-L quantity of sand was rinsed several times with reverse osmosis (RO) water mixed with 4 L concentrated HCl (commercial grade) and shaken within a manual, plastic tumbler (19 L) for 20 min. After standing 2 to 3 d, the acid/sand mixture was drained, rinsed several times with RO water, neutralized with KOH, and rinsed again. Control of the washing process was achieved by sampling, extraction with diethylene-triamine penta-acetic acid (DTPA), and analysis of the sand

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batches for Fe with an inductively coupled plasma (ICP) spectrophotometer (JY70; Jovin Yvon, Edison, N.J.).

Each 15.7-L pot was watered continuously with nutrient solution through one surface drip-emitter (75 mL·min⁻¹) until red fruit were harvested (231 d after germination). The emitters, as well as the drain outputs on the bottom of the pots, were connected to return lines leading to reservoirs housing a nutrient solution. This solution was pumped continuously back to the emitters.

HYDROPONIC SYSTEM AND NUTRIENT SOLUTION. The hydroponic system was located in a greenhouse at the Fabian García Agricultural Science Center of the New Mexico State University, Las Cruces. The greenhouse had natural light with a transmission factor near 70% for photosynthetically active radiation (*PAR*) at plant height (photosynthetic photon flux of 1010 mmol·m⁻²·s⁻¹ at 1200 HR on day 151). Temperature was controlled within a range of 18 to 37 °C (12 to 37 °C beginning on day 125, to favor fruit set) by evaporative cooling and natural gas heating. The latter raised atmosphere CO₂ episodically to as high as 450 mmol·mol⁻¹.

Four, 200-L plastic drums contained the nutrient solution for the 48 potted plants of the experiment. Each drum served a set of 12 randomly placed, 15.7-L pots, half of which were planted to each cultivar. The nutrient solution was recirculated between the drums and the pots by 1/40 horsepower submersible pumps (Little Giant, Oklahoma City, Okla.). Every drum contained the same nutrient solution, plus one of four different Fe concentrations [1, 3, 10, or 30 μM Fe-EDDHA (ferric ethylenediamine di-(*o*-hydroxyphenyl-acetate) as Sequestrene-138 (Ciba-Geigy, Greensboro, N.C.)].

The composition of the nutrient solution reflected the elemental composition of chile pepper (Winsor and Adams, 1987), and the overall concentration was planned to support the expected growth rate of the crop, taking into account the replacement schedule of the nutrient solution. The low strength of the nutrient solution was intended to resemble the diluted concentrations of macronutrients often found in natural, high-fertility soils (Clarkson, 1985; Gutschick, 1987).

The nutrient solution was prepared with RO water and contained 1 mM KNO₃, 125 μM Ca(H₂PO₄)₂, 250 μM MgSO₄, 250 μM CaSO₄, 20 μM KCl, 25 μM H₃BO₃, 10 μM MnSO₄, 3 μM ZnSO₄, 1 μM CuSO₄, 0.5 μM Na₂MoO₄, and four levels of Fe (1, 3, 10, or 30 μM Fe-EDDHA), that represented the four treatments of the experiment.

The pH of the nutrient solution was maintained at 6.5 ± 0.3 by addition of HNO₃. Both N and K, as well as pH, were adjusted manually every day after monitoring with ion selective electrodes and combination electrodes, respectively. Iron concentrations in the nutrient solution were not adjusted between replenishments, because the solution volume was large enough to account for depletion. The nutrient solution was discarded and replaced with fresh solution every 2 weeks at the beginning of the season, and at 1-week intervals when plants were larger, to avoid element depletion.

Iron was withheld intentionally from a nutrient solution replacement for the 1 and 3 μM Fe treatments from days 96 to 106 when no visible symptoms of Fe deficiency had appeared. Similarly, Fe was not applied to the 10 or 30 μM Fe treatments from days 96 to 100 after a failure of the submersible pumps occurred. The supply and recirculation of water and all other nutrients were unaffected during the Fe shortage.

GROWTH MEASUREMENTS. Leaf area was monitored weekly from days 78 to 108 by measuring length and maximum width of all leaves of all plants during the first two dates, and of all leaves

on the plants of two to five replications thereafter, followed by calibration with a regression model. A smaller number of plants was used in the latter dates due to the time needed to sample a larger number of leaves in a short period of time. To build the model, the leaf area of individual leaves from a sample of eight to 10 leaves from each plant (as determined with a leaf area meter (LI-3000; LI-COR, Lincoln, Nebr.) was regressed against the corresponding products of leaf width and length. Differences in total leaf area between sampling dates were used to obtain weekly means of relative rates of leaf area increase, a surrogate for relative growth rate (RGR). RGR (m²·m⁻²·d⁻¹) was the product of the natural logarithm of the ratio (leaf area at date 1/leaf area at date 2), divided by the number of days elapsed between the two dates [$\ln(A/A_0)/\Delta T$] (Beadle, 1993).

Light-saturated (1300 mmol·m⁻²·s⁻¹, *PAR*) net photosynthetic rates of the youngest fully expanded leaves were measured at 1200 HR with a portable photosynthesis system (LI-6200; LI-COR) five times during the study (93, 106, 127, 151, and 181 d after germination). For the first four dates, a light source was used (a 300-W metal halide lamp). The fourth date included both artificial and natural light measurements. The fifth measurement was done under natural light only, because the natural light increased and eliminated the need for artificial light. Photosynthetic rates were expressed per leaf area, per gram of chlorophyll, and per gram of dry tissue, the latter derived from the specific leaf area (SLA) measurements. For chlorophyll and SLA determinations, two to three young, fully expanded leaves used for photosynthesis determination from each plant were harvested, placed in plastic bags, cooled in an ice chest, and transported to the laboratory. Ten leaf discs (6.5 mm in diameter) were weighed, ground in a mortar with acetone plus CaCO₃ (Abadía and Abadía, 1993), adjusted to 10 mL volume with acetone neutralized with CaCO₃ and centrifuged at 6227 g_n for 5 min. Absorbance of the supernatant was measured at 645, 662, 470 and 730 nm with a spectrophotometer (model 690; Sequoia Turner, Mountain View, Calif.). Absorbance at 730 nm accounted for scattering by fine suspended debris. Chlorophyll a and b were computed from equations based on extinction coefficients (Abadía and Abadía, 1993; Lichtenthaler, 1987). For SLA, another 10-disc subsample from the same leaves was taken and weighed before and after drying at 65 °C, and the results expressed as leaf area per unit dry weight (DW) of leaves (m²·g⁻¹).

When the first mature green fruit began to form (day 151), eight plants (one plant from each cultivar in each of the four iron treatments) were cut at the medium level and the number of leaves, total leaf area per plant, fresh weight (FW) and DW of leaves, stems, flower buds, and fruit per plant were determined. Root DW also was recorded after sand removal. DWs were determined by weighing samples before and after drying in an oven (65 °C) to constant weight.

When the red fruit from the bottom three to five node positions on the plant had begun to dehydrate (day 231, postgermination) the remaining plants were cut at the medium level and the FW and DW of the leaves, stems, green fruit, and red fruit of each plant were recorded as final harvest. Root DWs were obtained after sand removal. Three to five plants were harvested from each cultivar of the initial six plants, because one plant from each cultivar had been sacrificed in the midseason sampling, one plant was lost to virus, and three plants had branches that detached from the weight of fruit a few days before final harvest. In the latter case, these plants were weighed at the time that branches self-detached.

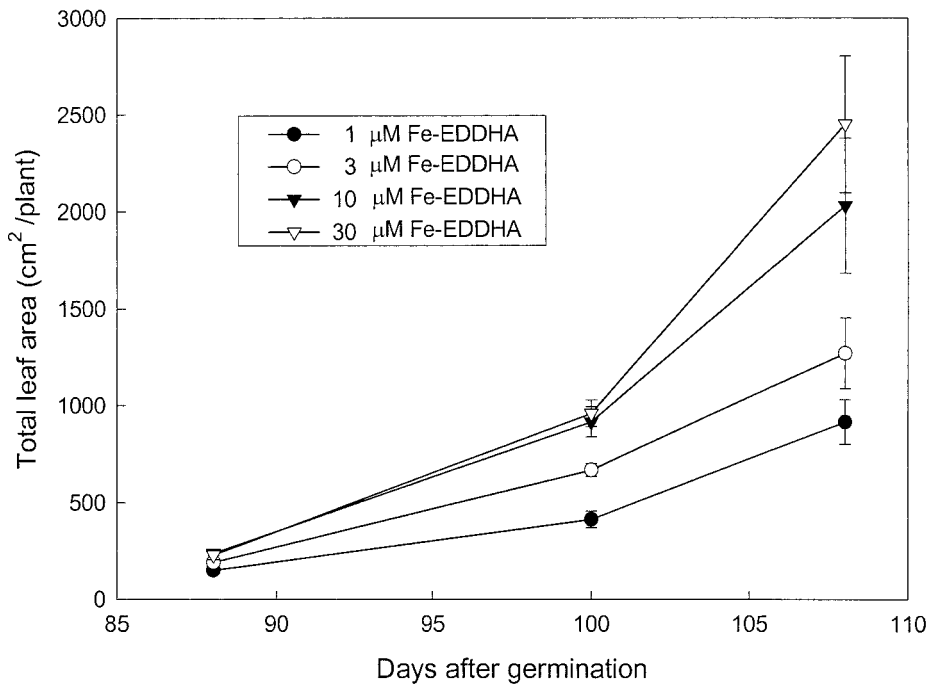


Fig. 1. Total calculated leaf area (cm² per plant) of hydroponically grown chile pepper plants (cultivars 'New Mexico 6-4' and 'NuMex R Naky' combined) at three dates after germination. Each symbol represents the mean of eight (88 and 100 d) or four (108 d) observations. Vertical bars = se.

EXPERIMENTAL DESIGN. Every 15.7-L pot, containing one chile plant, represented an experimental unit. There were 48 pots in the experiment, half of which were planted with 'New Mexico 6-4' and the other 24 pots with 'NuMex R Naky'. Each cultivar received four Fe treatments (1, 3, 10, or 30 mM Fe-EDDHA, the last being the control) in a 2 × 4 factorial arrangement. The six replications were blocked in two directions in a rectangular layout to account for light and temperature gradients across the greenhouse. Analysis of variance (ANOVA) of all variables was performed using the general linear models procedure of SAS (PROC GLM, SAS Inst., Inc., Cary, N.C.), using a randomized complete block statistical model. Mean separation of significant treatment differences was performed following a cluster-based method (Bautista et al., 1997). This method produces an unambiguous separation of treatment means without sharing a given treatment mean with two or more different groups. The analysis begins by testing the hypothesis that the two closest treatment means are equal. If this hypothesis is not rejected by a nested ANOVA, the analysis is gradually expanded to include either the two treatment means with the smallest difference between them or the treatment mean which is more proximal to the average of the means that were just tested, whichever difference is smaller.

Results and Discussion

This study used large volumes of low ionic strength, balanced nutrient solution to resemble the nutrient concentration present in soil solutions. Plants had adequate time for adaptation, because they were grown from seed to harvest in this solution. Also, the use of large pots, filled with fine silica sand, helped to simulate a more realistic root volume and mimic some soil mechanical properties that are absent in many liquid-only hydroponic studies.

Data indicate long-lasting effects of Fe levels on chile pepper

plant growth and yield. The cultivar × treatment interaction was nonsignificant for all growth measurements. Therefore, the Fe effects are reported across cultivars.

PLANT GROWTH. Plants grown under low Fe (1 or 3 μM Fe) treatments had smaller total leaf areas at 88 and 100 d after the beginning of the experiment (Fig. 1) than those grown under high Fe (10 or 30 μM Fe) treatments. Differences between low and high Fe treatments continued through day 108 (Fig. 1), when the last periodic foliar area measurements were made.

Iron-stressed plants also tended to produce thinner leaves, as indicated by their higher specific leaf area at day 106 (0.0401 and 0.0419 m²·g⁻¹ for 1 and 3 μM Fe plants, respectively, versus 0.0362 and 0.0359 m²·g⁻¹ for 10 and 30 μM Fe, respectively, *P* = 0.007) and day 127 (0.0303 and 0.0302 m²·g⁻¹ for 1 and 3 μM Fe plants, respectively, versus 0.0278 and 0.0285 m²·g⁻¹ for 10 and 30 μM Fe, respectively, *P* = 0.049).

Later, on day 141, 1 μM plants had the thinnest leaves (0.0261 m²·g⁻¹) of all treatments (0.0247, 0.0231 and 0.0236 m²·g⁻¹ for 3, 10, and 30 μM Fe, respectively; *P* = 0.009). With greater canopy closure, leaf thickness increased for all plants, with no significant differences among treatments (data not presented).

During early growth, production of thinner leaves may have represented a partial compensation in whole-plant photosynthesis for the Fe-deficient plants. Beadle (1993) observed that production of thin leaves requires a smaller investment of photoassimilates per unit foliar area. The strategy of thin leaf production maximizes light interception and photosynthesis per unit dry weight, and still enables the plant to shade competitors (Gutschick and Wiegel, 1988). Photosynthetic rate per total leaf area can be greater for thin leaves when the canopy is sparse, but declines as the canopy closes (Gutschick, 1987; Gutschick and Wiegel, 1988).

Table 1. Average relative growth rates (RGR, m²·m⁻²·d⁻¹)^z calculated using total leaf area of chile pepper plants at different times during the season.^y

Iron treatment (μM Fe-EDDHA)	Time period (d after germination)		
	78–88 ^x	88–100 ^w	100–108 ^v
1	0.122 b ^u	0.082 b	0.081 b
3	0.134 a	0.106 a	0.066 b
10	0.142 a	0.111 a	0.103 a
30	0.143 a	0.110 a	0.110 a
<i>P</i> > <i>F</i>	0.0031	0.0001	0.014

^zRGR (m²·m⁻²·d⁻¹) = [ln(A/A₀)]/ΔT, (Beadle, 1993) where A₀ is initial leaf area, A is final leaf area, and ΔT is elapsed time in days.

^yIron application was suspended to treatments of 1 or 3 μM Fe-EDDHA from days 96 to 106 and to treatments of 10 or 30 μM Fe from days 96 to 100.

^xBased on 6 plants of each cultivar for a total of 12 plants.

^wBased on four to five plants of each cultivar for a total of 8 to 10 plants.

^vBased on two plants of each cultivar for a total of four plants.

^uMean separation within columns by cluster approach, *P* ≤ 0.05.

Smaller leaves resulting from reduced cell expansion have been reported following mineral nutrient deficiency. Leaf growth is reduced under nutrient deficiency (Baker, 1983). Snir and Neumann (1997) cultured young maize (*Zea mays* L.) plants in solutions with low total nutrient concentration. They found that the early leaf expansion rate of nutrient-deficient maize seedlings was more affected by loss of elasticity, rather than by the number of cells produced.

Leaf area increments (Table 1) represent the ability of the plants to maximize RGR. Leaf area was recorded before (day 78) and after (day 100) the sudden Fe stress was imposed on day 96. From days 78 to 88, leaf area of high Fe plants increased 17% more per day than that of the 1 μM Fe plants, and during the 88 to

100 d period, that difference increased to 34% (Table 1). By 100 to 108 d, leaf area expansion rate was 36% greater (on a daily basis) in the high Fe treatments compared to the 1 μM Fe treatment (Table 1).

Leaf area increment is not necessarily linearly related to total RGR, because the thickness of the leaf can vary. Specific leaf area (SLA) measurements on day 93 show a nonsignificant trend toward thinner leaves under low Fe supply (data not presented), and differences became significant by day 106. Thus, plants well supplied with Fe not only had the advantage of greater leaf areas, but also had more weight per unit leaf surface. Reduced RGR has serious disadvantages. For instance, a sustained 8% reduction in RGR during the growing season can result in a plant having only

Table 2. Dry weights (DWs) (mean \pm SE) of dry mass partitioning (g/plant) of sand cultured chile pepper plants at midseason (day 151)².

Variable	Iron treatment (μM Fe-EDDHA)			
	1	3	10	30
DW (g/plant)				
Leaves	30.1 \pm 7.6	34.0 \pm 2.3	64.1 \pm 11.8	67.6 \pm 4.3
Flower and leaf buds	5.5 \pm 2.2	7.6 \pm 0.8	11.1 \pm 2.0	13.0 \pm 1.5
Fruit	2.1 \pm 2.1	2.1 \pm 2.1	11.7 \pm 10.6	14.0 \pm 9.5
Stems	41.6 \pm 11.9	48.5 \pm 2.2	94.2 \pm 8.8	98.2 \pm 2.4
Total shoot	79.2 \pm 23.7	92.1 \pm 5.8	181.2 \pm 33.2	208.7 \pm 30.6
Root	19.8 \pm 6.6	23.2 \pm 2.0	44.0 \pm 9.8	43.1 \pm 7.8
Root to shoot DW ratio	0.25 \pm 0.01	0.25 \pm 0.01	0.24 \pm 0.01	0.21 \pm 0.01
Specific leaf area ($\text{cm}^2\cdot\text{g}^{-1}$)	302.3 \pm 5.5	275.2 \pm 9.6	276.9 \pm 24.7	272.9 \pm 15.0
Average leaf weight (mg/leaf)	81.7 \pm 4.9	93.6 \pm 7.2	108.3 \pm 11.8	97.3 \pm 10.1

²Data shown are the average of one plant each of 'New Mexico 6-4' and 'NuMex RNaky' (cultivars were pooled). Iron was not applied to treatments of 1 or 3 μM Fe-EDDHA from days 96 to 106 and to treatments of 10 or 30 μM Fe-EDDHA from days 96 to 100.

Table 3. Light saturated (1300 $\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, *PAR*) leaf photosynthetic rates of chile peppers cultured on four different Fe concentrations in sand culture at 93 and 106 d after germination.

Iron treatment (μM Fe-EDDHA)	Leaf photosynthetic rates					
	$(\text{CO}_2, \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1})$		$(\mu\text{mol CO}_2/\text{s per g dry tissue})$		$(\mu\text{mol CO}_2/\text{s per g chlorophyll})$	
	93 d	106 d	93 d	106 d	93 d	106 d
1	16.2 b ^z	13.5 a	0.69 b	0.54 a	67.9 a	54.5 a
3	18.7 a	6.6 b	0.80 a	0.26 b	64.0 a	38.0 b
10	19.0 a	18.4 a	0.78 a	0.66 a	51.2 b	43.2 b
30	17.8 a	16.0 a	0.70 b	0.57 a	46.8 b	38.5 b
<i>P</i> > <i>F</i>	0.025	0.0001	0.042	0.001	0.001	0.02

^zData shown are the average of six plants from each of two cultivars (12 plants total). Iron application was withheld to treatments of 1 or 3 μM Fe-EDDHA from days 96 to 106 and to treatments of 10 or 30 μM Fe-EDDHA from days 96 to 100. Mean separation within columns by cluster approach, *P* \leq 0.05.

Table 4. Dry weight (DW) partitioning (grams per plant) of chile pepper plants at red fruit harvest.^z

Iron treatment (μM Fe)	Green fruit ^y (g)	Red fruit (g)	Total fruit (g)	Shoot ^x (g)	Root (g)	Total DW (g)	Root:shoot ratio
1	113.1 a ^w	26.8 b	140.0 b	321.9	72.3	534.2 b	0.16 b
3	74.0 b	12.4 b	86.3 b	337.6	83.1	506.9 b	0.20 a
10	109.2 a	122.9 a	232.2 a	394.7	93.3	720.1 a	0.15 b
30	143.8 a	71.5 a	215.3 a	413.0	88.9	717.1 a	0.15 b
<i>P</i> > <i>F</i>	0.048	0.005	0.004	0.22	0.45	0.035	0.024

^zData shown are the average of the sample means of 'New Mexico 6-4' and 'NuMex RNaky' chile cultivars. Iron application was withheld to treatments of 1 or 3 μM Fe-EDDHA from days 96 to 106 and to treatments of 10 or 30 μM Fe-EDDHA from days 96 to 100.

^yThree to five plants from each of two cultivars for a total of six to 10 plants for all variables.

^xShoot = leaves plus stems.

^wMean separation within columns by cluster approach, *P* \leq 0.05.

half the weight of a nonstressed plant (Gutschick, 1987).

From the eight plants harvested on day 151 (two from each Fe treatment), significant differences among treatments were detected only for DW of the stems ($P = 0.04$), due to the small number of plants harvested (Table 2). No significant differences were found for leaf area, leaf thickness, and DW of leaves, flower buds, stems, and fruit.

Instantaneous gas exchange measurements during growth (Table 3) showed reduced CO_2 assimilation rates (on a per area basis) for 1 μM Fe plants at 93 d only. However, after the imposed Fe stress, the 3 μM Fe treatment showed the most dramatic reduction in photosynthetic rates (Table 3). These plants could have had low Fe reserves in the leaves so that compensatory increases in root Fe acquisition did not occur. For the remainder of the study (>106 d) no differences in photosynthetic rates were observed among treatments (data not presented).

Photosynthetic capacity tends to be maintained under some mineral nutrient deficiencies, even when shoot growth is severely impaired. For example, under P deficiency, carbon fixation rates can be maintained to allow a flux of photoassimilates to the root for increased root growth (Marschner et al., 1996). When Fe is deficient, it is the number, not the efficiency of the photosynthetic units that is reduced. Although the photosynthetic rates are reduced under Fe-limited growing conditions, photosynthesis per unit chlorophyll is maintained (Spiller and Terry, 1980; Terry, 1980) unless chlorophyll production is impaired (Morales et al., 1992). Chlorophyll and fruit and leaf mineral nutrient concentration data from this study are presented elsewhere (Anchondo et al., 2001).

Photosynthetic rates per unit chlorophyll were higher for the low Fe treatments (1 or 3 μM Fe) on day 93, and also for 1 μM Fe on day 106, whereas the 3 μM Fe plants had a photosynthetic rate comparable to the high Fe treatments (Table 3). When photosynthetic rates were expressed on a per dry matter basis on day 93, the 3 and 10 μM Fe treatments had the highest values. After the Fe shortage, 3 μM Fe plants decreased from 0.80 to 0.26 $\text{mm CO}_2/\text{g per s}$.

Dry matter accumulation and partitioning at harvest were markedly affected by Fe treatment (Table 4). Plants in the 10 and 30 μM Fe treatments yielded more red and total fruit and more total biomass than the low Fe treatments (1 or 3 μM Fe). There was no difference in the yield of green fruit between the lowest Fe treatment (1 μM Fe) and the high Fe treatments (10 or 30 μM Fe) (Table 4). A possible explanation for the similar green fruit yields of 1, 10, or 30 μM Fe is the delayed development of the plants under the 1 or 3 μM Fe treatments (data not presented). Generally, low Fe plants began to bloom, set, develop, and ripen fruit 8 to 9 d later than the high Fe treatments. Thus, as the end of the season approached, the 1 μM Fe plants continued growing new fruit and leaves while the 10 or 30 μM Fe plants had stopped growing, and their branches became so heavy that they began to break.

The smaller yield of green fruit and the higher relative allocation of assimilates to roots of the 3 μM Fe plants, compared to the 1 μM Fe plants (Table 4), could possibly be traced to the 10-d additional Fe stress imposed to both treatments 4 months earlier. Before the Fe interruption, the 3 μM Fe plants had higher RGR (Table 1) and greater biomass than the 1 μM Fe treatments. Thus, the 3 μM Fe plants may have suffered greater reduction in photosynthetic rates immediately after the Fe stress. It follows that critical levels of mineral nutrients needed for growth are not static, but may depend on plant growth rates.

All flowers of the plants receiving 10 or 30 μM Fe were lost to

abortion during the first 8 d of bloom, due to relatively high night temperatures. By the time the problem was corrected, the low Fe plants (1 or 3 μM Fe) had totally escaped fruit abortion because of their phenological delay. High Fe treatments yielded more total fruit and DW than low Fe treatments even with early-season flower abortion.

The interrelationship between mineral nutrient concentration, growth rate, and nutrient deficiency has been reported by Marcelis and Ho (1999), who linked the incidence of blossom-end rot of sweet pepper (*Capsicum annuum* L.) fruit to both low Ca concentration and high growth rates of the fruit. The interdependence between nutrient concentration and growth is used in Ingestad's (1982) relative addition rates approach for the study of plant nutrition. In this approach, the nutrient supply in the nutrient solution is adjusted to the growth rate of the plants in such a way that a constant growth rate and an internal steady-state nutrient concentration are attained (Ericsson, 1995; Ingestad, 1982). Göransson (1993) observed that RGR of European white birch seedlings was linearly dependent ($r^2 = 0.87$) on the internal Fe concentration.

Although root DW at final harvest did not vary among Fe treatments, the root to shoot (R:S) dry matter partitioning of 3 μM Fe plants inhibited shoot growth (Table 4). Increases in the R:S ratio frequently occur under nutrient deficiency, although they are dependent on elemental species (Ericsson, 1995; Gutschick 1987; Marschner et al., 1996). No increase in the R:S ratio of Fe-deficient corn was found (Clark, 1982), but an increase in the R:S total biomass ratio has been reported for European white birch seedlings grown on low Fe nutrient solution (Göransson, 1993).

Low R:S ratios indeed have benefits, because more photoassimilates and mineral nutrients are used in the shoot for more aerial biomass, resulting in higher light interception, which in turn favors higher relative growth rates (Gutschick, 1987). A small R:S ratio is not crucial in nutrient solutions or in soil conditions early in the season, but has the advantage of postponing the formation of nutrient depletion zones around the roots (Gutschick, 1993). However, a limitation of an early-season low R:S ratio is that an unexpected deficiency can severely reduce future relative growth rates (Gutschick, 1987).

Conclusions

Results presented herein indicate a strong and persistent effect of Fe supply on chile pepper plant growth and fruit yield, even without visible chlorotic symptoms, when plants are grown in sand culture. Plants of 'New Mexico 6-4' and 'NuMex R Naky' chile peppers receiving high Fe treatments had increased total leaf area, photosynthesis (early season), red and green fruit production, and total dry matter. Withholding of Fe for 10 d in the 1 or 3 μM Fe treatments (days 96 to 106) seemed to have a long-lasting effect on growth and dry matter partitioning, supporting the hypothesis that critical mineral nutrient concentrations are actually dependent on relative growth rates. Chile pepper had the ability to acclimate to low Fe in the nutrient solution, without exhibiting chlorotic symptoms, by reducing its growth rate. However, when Fe was suddenly withheld from the nutrient solution below the critical level needed to sustain current relative growth rates, a transient chlorosis was induced on 3 μM Fe plants (Anchondo et al., 2001). This dependence of critical nutrient levels on relative growth rates may explain the temporary symptoms of Fe deficiency that have been observed in chile peppers grown in calcareous soils following irrigation or heavy rain.

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