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UPTAKE AND TRANSPORT OF IRON IONS (Fe^{+2}, Fe^{+3}) SUPPLIED TO ROOTS OR LEAVES IN SPINACH (*Spinacia oleracea* L.) PLANTS GROWING UNDER DIFFERENT LIGHT CONDITIONS

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Abstract

In experiments carried out in a phytotron using aqueous cultures, there was investigated the effect of root or foliar application of different types of iron salts on spinach plant productivity, leaf and root iron content as well as the rate of transport of iron from the roots to the leaves. Plants were grown in Hoagland's solution with a single concentration at two fluorescent light intensities: 290 and 95 µmol × m^{-2} × s^{-1} PAR. To fertilize the plants, iron was supplied at a dose of 25 mg Fe in the nutrient solution or as foliar sprays using the following salts: 1 – Fe 0; 2 – $FeCl_2 \times 4H_2O$; 3 – $FeCl_3 \times 4H_2O$; 4 – $FeSO_4 \times 7H_2O$; 5 – $Fe_2(SO_4)_3 \times nH_2O$; 6 – Fe-Cit.

The obtained results showed that the productivity of spinach plants treated with $FeCl_2$ and $FeSO_4$ using foliar sprays and of those fed with Fe-citrate (Fe-Cit) through the roots was significantly higher than in the case of the other salts used. Root application of the salts used had a significant effect on root iron content, whereas their foliar application significantly affected leaf iron content. In this respect, ferrous salts were generally the most beneficial, while ferric salts were the least beneficial. The rate of transport of iron to the leaves, irrespective of the method of its application, was clearly higher for ferrous salts and Fe-Cit than for ferric salts. The free proline content in the leaves of plants not fertilized with Fe was 2–4 times lower than in plants supplied with this nutrient. An irradiance of 290 µmol × m^{-2} × s^{-1} had a positive effect on plant productivity and root Fe content.

Key words: *Spinacia oleracea*, ferrous salts, ferric salts, Fe-Cit, productivity, Fe – leaves, Fe – roots, transport rate, proline

INTRODUCTION

After aluminium, iron is the second most abundant metal in the Earth's crust (Sieńko and Plane, 1980). Despite this, iron deficiency occurs in many plant species grown in soils with high pH and it appears earliest in young leaves in the form of the so-called "iron chlorosis". Fe deficiency is of significant economic importance, because the quality and amount of yield can be clearly reduced and therefore it is necessary to use expensive treatments to correct iron deficiency (Alvarez-Fernández et al. 2003). Correction of iron deficiency in plants with chlorosis symptoms by soil application of iron generally does not bring expected effects (Mortvedt, 1991). That is why iron ions are applied to leaves by spraying the above-ground organs with an aqueous solution of Fe salts (Reed et al. 1988; Rombola et al. 2000; Alvarez-Fernández et al. 2003; Fernandez et al. 2005; Fernandez et al. 2006; Borowski and Michałek, 2010). Relatively cheap inorganic ferrous salts with Fe^{+2} and ferric salts with Fe^{+3} as well as much more expensive iron chelates (Fe-citrate, Fe-EDTA, Fe-EDDHA, Fe-DTPA, Fe-IDHA, Fe-AM4) with the Fe^{+3} ion are available on the market. Aqueous solutions of inorganic iron salts are not very stable (Silver, 1993) and therefore in foliar fertilization they are most frequently replaced with much more stable iron chelates (Brüggeman et al. 1993; Fernandez et al. 2006). However, a question arises whether this is justified in the light of the present knowledge on iron uptake by plants. The existing research shows that dicotyledonous plants and non-grass monocotyledonous species take up iron as Fe^{+2} and that Fe^{3+} ions supplied to plants, irrespective whether by root or foliar application, must be first reduced to Fe^{2+} (Longnecker and Weich, 1990; Rombola et al. 2002). This process takes place in the root plasmalemma (Bienfait et al. 1983; Römheld and Marschner, 1986; Sijmon et al. 1984; Cacmak et al. 1987) or in the mesophyll and on the epidermis surface (Larbi et al. 2001). In the case of application of iron chelates, ligands are not absorbed by isolated leaf cells (Kannan and Wittwer, 1965). Thus, after the ligand is separated from the Fe^{+3} ion, it is subsequently reduced to Fe^{+2} and taken up in this form. On this basis, it should presumed that the application of inorganic ferrous salts (Fe^{2+}) will be more effective in foliar iron fertilization of plants than the application of inorganic ferric salts or chelates of this metal. But the existing research does not provide clear answers. Fernandez et al. (2006) as well as Borowski and Michałek (2010) found ferrous salts [$FeSO_4$, $Fe(NO_3)_2$] to show higher effectiveness than ferric salts and iron chelates, whereas Reed et al. (1988) and Rombola et al. (2000) observed similar effectiveness of $Fe^{II}SO_4$, Fe^{III}-citrate, Fe^{III}-malate, and Fe^{III}-DTPA.

Also, in the literature there is no clear answer concerning the effect of light intensity on iron uptake by plants. Intense light increases the thickness of the cuticle covering the leaf surface, which inhibits the penetration of ions, but on the other hand, it increases ferric-chelate reductase activity, which promotes iron absorption (Brüggeman et al. 1993; Fernandez et al. 2005).

In view of the above considerations, it seemed interesting to conduct a study on the effect of root or foliar fertilization of spinach plants with ferrous and ferric iron salts as well as with Fe-citrate on productivity, leaf and root Fe content as well as on the transport of supplied Fe ions to the leaf mesophyll. The investigations were conducted at two distinctly different light intensities, for determination effect of that factor on studded processes.

MATERIALS AND METHODS

Two plant growth experiments were conducted in a phytotron of the University of Life Sciences in Lublin during the period from 11 April to 23 May and from 28 September to 9 November 2011. Both experiments were carried out using the same experimental design and under the same conditions. Seedlings of spinach cv. 'Matador' grown in quartz sand were transferred at the cotyledon stage to $1 dm^3$ plastic containers (2 seedlings in each) filled with Hoagland's medium with the addition of the micronutrient solution (A–Z), solution not containing iron. For a period of one week, i.e. until the 3 true leaf stage, the plants grew under full fluorescent light at a PPFD of 290 $\mu mol \times m^{-2} \times s^{-1}$, air temperature of 20°C, and with a photoperiod of 11/13h (light/dark). After this time, 6 experimental series were created by random selection which differed in the form of iron salts used: 1 – Fe 0 (control); 2 – $FeCl_2 \times 4H_2O$; 3 – $FeCl_3 \times 4H_2O$; 4 – $FeSO_4 \times 7H_2O$; 5 – $Fe_2(SO_4)_3 \times nH_2O$; 6 – Fe-citrate. Subsequently, in the part of the experiment with root application, the solutions of all tested salts were added to the nutrient solution and half of the plants from each experimental series, comprising 12 containers, were placed under light with three times lower intensity, i.e. about 95 $\mu mol \times m^{-2} \times s^{-1}$. In the part of the experiment with foliar application, the plants were sprayed with 0.2% solutions of the salts, containing equivalent amounts of iron, with the addition of an adjuvant (Suprem 10AL) and the same procedure was followed. Each 2 plants growing in a container received 25 mg Fe.

During later plant growth, in both experiments the nutrient solution was replaced at a weekly interval, setting its pH at 6.5. At the same time, the same amounts of iron in the form of the salts were added to the nutrient solution or supplied to the leaves, each time using freshly prepared solutions. After a week from the last application, proline content was determined in leaf samples taken from the middle part of plant rosette, following the method described in the paper by Bates et al. (1973). Next, the leaves were separated from the roots and after their fresh weight was determined; subsequently, after leaves treated with the solutions of iron salts were washed twice in distilled water, they were all dried. After mineralization of the leaves, iron content in leaf dry matter was determined by atomic absorption spectrometry (AAS).

On the basis of dry matter yield of leaves and roots as well as the iron content in them, the transport rate (TR) of this metal from the roots to the leaves as well as from the leaf surface to the mesophyll was calculated using the following formula (Baligar et al. 1993):

$$TR=[(SU_2 - SU_1)/ (t_2 - t_1)] \times [(\ln SW_2 - \ln SW_1)/ (SW_2 - SW_1)]$$

where: SU_1 and SU_2 – leaf iron content (nmol $\times g^{-1} \times h^{-1}$); SW_1 and SW_2 – dry weight of leaf rosette (g x $plant^{-1}$) at time t_1 and t_2; the following values were accepted: $t_1=7$, $t_2=42$ days (840 hours); $SU_1=0$; $SW_1=0.01g$.

The results presented in this paper are means from the two experiments. They were subjected to analysis of variance for two-way classification, while the significance of differences was determined by Tukey's confidence intervals at the =0.05 level of significance.

RESULTS

The results in Table 1 show that, control plants produced the significantly lowest biomass yield. The mean productivity of plants fertilized with iron salts through the roots and leaves was similar, but the response of the plants to the salts used was different. In the case of root application of iron in the form of ferrous and ferric salts, biomass yields were similar and did not differ significantly from each other. However, plants fertilized with iron citrate (Fe-Cit) showed considerably higher productivity.

Table 1
Effect of Fe^{+2} and Fe^{+3} supplied in the nutrient solution or as foliar sprays to plants grown at different light intensities on productivity of spinach plants (g $plant^{-1}$)

Iron salts	Root application		Mean	Foliar sprays		Mean
	Light intensity – (μmol × m^{-2} × s^{-1})			Light intensity – (μmol × m^{-2} × s^{-1})		
	290	95		290	95	
Control	3.77	2.09	2.93	5.21	2.21	3.71
$FeCl_2 \times 4H_2O$	15.18	8.80	11.99	18.95	6.92	14.43
$FeCl_3 \times 4H_2O$	14.27	9.43	11.85	16.61	4.43	10.52
$FeSO_4 \times 7H_2O$	14.10	8.17	11.13	18.52	6.52	12.52
$Fe_2(SO_4)_3 \times nH_2O$	14.86	8.33	11.59	15.80	2.81	9.30
Fe-Cit	17.17	11.26	14.21	15.57	4.85	10.21
Mean	13.22	8.01		15.11	5.12	
$LSD_{0.05}$ for Fe			1.87			1.26
$LSD_{0.05}$ for light			0.78			0.49
$LSD_{0.05}$ for Fe × light			3.12			2.01

Biomass yields of plants supplied with iron through the leaves differed more clearly. Plants fertilized with ferric salts and Fe-citrate were characterized by significantly lower productivity than those fertilized with ferrous salts ($FeCl_2$, $FeSO_4$). Irrespective of the type of salts used and the method of their application, plants grown at the higher light intensity produced significantly higher biomass yield.

Leaf Fe content in spinach plants supplied with this nutrient through the roots was nearly 3.5 times higher than root iron content. However, iron content in both investigated organs was dependent on the type of salts used. Plants fertilized with Fe-Cit contained the highest amount of iron, while those supplied with $FeSO_4$ and $FeCl_2$ were found to have distinctly less iron, but these differences were not significant. The leaves of plants fed with $FeCl_3$ and $Fe_2(SO_4)_3$ were characterized by significantly lower content of this metal (Table 2). As regards the roots, plants fertilized with $FeCl_2$ and $FeSO_4$ contained the highest amount of iron, while those fertilized with the other salts [$FeCl_3$, $Fe_2(SO_4)_3$ and Fe-Cit] were found to have significantly less iron. Trace amounts of Fe were found in both studied organs of control plants.

Light had a significant effect on iron uptake by spinach, since plants grown at the higher light intensity contained significantly less Fe in the leaves and significantly more iron in the roots (Table 2).

Table 2
Effect of Fe^{+2} and Fe^{+3} supplied in the nutrient solution to plants grown at different light intensities on iron content in spinach leaves and roots (mg kg^{-1} d.w.)

Iron salts	Light intensity (μmol × m^{-2} × s^{-1})		Mean	Light intensity (μmol × m^{-2} × s^{-1})		Mean
	290	95		290	95	
	leaves			roots		
Control	14.1	24.1	19.1	4.1	6.4	5.2
$FeCl_2 \times 4H_2O$	132.0	203.0	167.5	91.1	48.6	69.8
$FeCl_3 \times 4H_2O$	120.0	157.0	138.5	36.2	28.0	32.1
$FeSO_4 \times 7H_2O$	148.0	217.0	182.5	91.8	48.8	70.3
$Fe_2(SO_4)_3 \times nH_2O$	136.0	173.0	154.5	58.3	30.1	44.2
Fe-Cit	212.0	223.0	217.5	46.5	24.5	35.5
Mean	127.0	166.2		54.7	31.1	
$LSD_{0.05}$ for Fe			50.6			14.4
$LSD_{0.05}$ for light			19.5			6.1
$LSD_{0.05}$ for Fe × light			83.5			27.8

When plants were foliar fertilized with iron, the leaves contained on average 57.8% of iron more than in the case of root application. Fe content in the leaves sprayed with iron salt solutions was significantly dependent on the type of salt. The leaves treated with $FeCl_2$ and $FeSO_4$ contained the highest amount of Fe, those treated with Fe-Cit and $Fe_2(SO_4)_3$ significantly less, while the lowest amount was found in the leaves sprayed with $FeCl_3$. The content of this nutrient in the roots was nearly 12 times lower than in the leaves and it was not significantly dependent on the type of salts used. Likewise in the case of iron fertilization through the roots, plants grown at the higher light intensity contained significantly less Fe in the leaves and significantly more Fe in the roots (Table 3).

Table 3
Effect of Fe^{+2} and Fe^{+3} supplied as foliar sprays to plants grown at different light intensities on iron content in spinach leaves and roots (mg × kg^{-1} × d.w.)

Iron salts	Light intensity (μmol × m^{-2} × s^{-1})		Mean	Light intensity (μmol × m^{-2} × s^{-1})		Mean
	290	95		290	95	
	leaves			roots		
Control	10.5	19.5	15.0	4.1	3.1	3.6
$FeCl_2$ × $4H_2O$	238.0	466.0	352.0	23.6	17.6	20.6
$FeCl_3$ × $4H_2O$	182.5	175.0	178.7	32.0	20.5	26.2
$FeSO_4$ × $7H_2O$	280.0	417.0	348.5	32.5	16.8	24.6
$Fe_2(SO_4)_3$ × nH_2O	228.0	225.0	226.5	24.8	24.2	24.5
Fe-Cit	264.0	270.0	267.0	23.8	16.8	20.3
Mean	200.5	262.1		23.5	16.5	
$LSD_{0.05}$ for Fe			46.5			6.0
$LSD_{0.05}$ for light			18.2			2.6
$LSD_{0.05}$ for Fe × light			77.6			9.1

The mean value of the transport rate (TR) of Fe supplied to the leaf surface to the leaf mesophyll was 52% higher than the value of TR in the case of translocation of iron from the roots to the leaves. In the case of root fertilization, the value of TR for all the iron salts used was higher, except for Fe-Cit, at the lower light intensity compared to the higher one. Ions supplied as Fe-Cit were transported most intensely, to be followed by those supplied as $FeSO_4$, $FeCl_2$, $Fe_2(SO_4)_3$, and $FeCl_3$ (Table 4).

Under the conditions of foliar application, the value of TR was more variable Fe ions supplied as ferrous salts were transported twice more efficiently than it was in the case of ferric salts. The lower light intensity increased the value of the transport rate of iron supplied as ferrous salts and decreased this rate in the case of ferric salts. The value of TR for Fe-Cit was at a medium level and the higher light intensity had a beneficial effect on the process in question (Table 4).

Table 4
Effect of Fe^{+2} and Fe^{+3} supplied in the nutrient solution or as foliar sprays to plants grown at different light intensities on the transport rate (TR) of iron to the leaf mesophyll (nmol × g^{-1} × h^{-1})

Iron salts	Root application		Foliar sprays	
	Light intensity (μmol × m^{-2} × s^{-1})			
	290	95	290	95
Control	1.30	1.84	0.99	1.50
$FeCl_2$ × $4H_2O$	15.04	21.04	28.21	45.70
$FeCl_3$ × $4H_2O$	13.51	16.21	21.15	15.75
$FeSO_4 \cdot 7H_2O$	16.50	22.05	33.17	40.94
$Fe_2(SO_4)_3$ × nH_2O	15.55	17.56	26.14	17.90
Fe-Cit	24.97	24.05	30.50	25.03
Mean	14.48	17.12	23.36	24.47

Free proline content in the leaves of plants supplied with Fe by foliar application was on average 72.9% higher than in the case of root fertilization (Table 5). Control plants contained the least amount of proline in both methods of iron fertilization. Root application of iron increased leaf proline content 2–4 times. The content of this amino acid increased the least when plants were fertilized with Fe-Cit and $FeCl_2$, whereas this increase was higher in the case of fertilization with the salts $FeCl_3$ and $FeSO_4$ and the highest when $Fe_2(SO_4)_3$ was applied. Under the conditions of foliar iron application to plants, control plants and those fertilized with $FeSO_4$ contained the least proline, plants fertilized with Fe-Cit and $Fe_2(SO_4)_3$ showed significantly higher amounts of proline, while those fertilized with $FeCl_3$ had the highest amount. Irrespective of the method of iron application, the higher light intensity significantly decreased the leaf content of this amino acid (Table 5).

Table 5
Effect of Fe^{+2} and Fe^{+3} supplied in the nutrient solution or as foliar sprays to plants grown at different light intensities on free proline content in spinach leaves (μg × g^{-1} × f.m.)

Iron salts	Root application		Mean	Foliar sprays		Mean
	Light intensity – (μmol × m^{-2} × s^{-1})			Light intensity – (μmol × m^{-2} × s^{-1})		
	290	95		290	95	
Control	20.6	24.3	22.4	45.3	75.8	60.5
$FeCl_2 \times 4H_2O$	43.3	45.1	44.2	94.7	59.4	77.0
$FeCl_3 \times 4H_2O$	58.7	71.7	65.2	115.3	154.2	134.7
$FeSO_4 \times 7H_2O$	56.2	71.6	63.9	45.6	88.8	67.2
$Fe_2(SO_4)_3 \times nH_2O$	76.1	83.8	79.9	95.0	104.2	99.6
Fe-Citr.	33.3	39.6	36.4	62.3	139.0	100.6
Mean	48.0	56.0		76.4	103.5	
$LSD_{0.05}$ for Fe			18.3			23.5
$LSD_{0.05}$ for light			7.4			9.0
$LSD_{0.05}$ for Fe × light			31.3			38.7

DISCUSSION

The presented research results show very low productivity of spinach not supplied with iron in relation to the other plants. This was undoubtedly attributable to the occurrence of severe iron chlorosis under these conditions, which causes almost complete inhibition of photosynthesis (B o r o w s k i and M i c h a ł e k , 2010). Supply of iron to the plants, irrespective of the method of application and the type of salt used, resulted in a severalfold increase in spinach productivity, which seems to be completely obvious. Nevertheless, it is interesting that fresh weight yield resulted from the type of salt used and did not vary too much in the case of root fertilization, but it varied distinctly when foliar fertilization was applied. However, a comparison of productivity (Table 1) with the mean iron content, in particular in the leaves of root- or foliar--fertilized plants (Tables 2, 3), shows definite relationships. Notably, in the case of root fertilization plants fed with Fe-Cit were characterized by significantly higher productivity in relation to the other experimental series and, at the same time, they contained the highest amount of Fe in their leaves. A similar correlation was found for foliar application, but in this case leaves treated with ferrous chloride and sulphate contained the highest amount of Fe and showed significantly higher productivity than the other ones.

Since numerous earlier studies have shown that iron is taken up as Fe^{+2} ions (B i e n f a i t et al. 1983; S i j m o n s et al. 1984; R o m h e l d and M a r s c h n e r , 1986; C a c m a k et al. 1987; L o n g n e c k e r and W e i c h , 1990; B r ü g g e m a n et al. 1993; L a r b i et al. 2001; R o m b o l a et al. 2002), hence Fe^{+3} ions supplied to spinach plants as ferric salts, that is, $FeCl_3$ and $Fe_2(SO_4)_3$ as well as Fe-Cit, had to be reduced to Fe^{+2} in the roots or leaves by a ferric-chelate reductase before being taken up (B r ü g g e m a n et al. 1993; L a r b i et al. 2001). On this basis, it can be presumed that Fe^{+2} ions supplied as ferrous salts were taken up more quickly by the leaves in the case of foliar fertilization and by the roots under the conditions of root fertilization, since they did not require prior reduction. This line of reasoning is confirmed by the results presented in Tables 2 and 3. However, the absence of such relationship in the leaves of plants fertilized with Fe through the roots probably resulted from the fact that iron taken up through the roots is transported to the leaves as Fe-citrate (B r o w n and J o l l e y , 1986; R o m b o l a et al. 2002). This means that to be metabolized in the leaf cells, Fe^{+3} ions supplied as ferric salts to plants by root application require double reduction, the first one in the root cells and the other one in the leaf cells. The significantly higher leaf content of iron supplied as Fe-Cit found in the case of root fertilization was probably attributable to the fact that this metal was transported most efficiently from the roots to the leaves. Other authors also stress that the use of iron chelates increases the rate of iron translocation in plants (Kannan and Wittwer, 1965; Fernandez et al. 2005). Under the conditions of foliar iron application, the higher transport rate (TR) of this metal for ferrous salts compared to Fe-Cit (Table 4) probably resulted from the omission of the reduction phase.

The increased light intensity had a beneficial effect on plant productivity and root iron content, which seems to be justified due to generally higher metabolic activity of plants under these conditions and the positive effect on ferric-chelate reductase activity (Brüggeman et al. 1993; Fenandez et al. 2005). But it is difficult to explain why the effect of light on leaf Fe content proved to be opposite. If the iron content in leaf yield per plant is calculated it turns out that plants grown at the higher light intensity accumulated nearly 31% and 124% more Fe in their leaves in the case of, respectively, root and foliar application as compared to the lower light intensity.

The obtained results of the study showed low free proline content in spinach leaves. The low light intensity significantly increased the content of this amino acid, which could have been an effect of light deficit stress. But it is more difficult to explain the clearly higher proline content in the case of foliar fertilization compared to root fertilization, which might suggest that the use of foliar sprays induces some kind of mechanical stress in the leaves. However, the greatest differences in the values of the trait in question were found in relation to control plants (Fe – 0) which contained 2–4 times less proline in their leaves than iron-fed plants. This demonstrates that the level of proline is not an indicator of Fe deficiency stress in spinach, which is also confirmed by the studies of Binzel et al. (1987) on tobacco and Ketchum et al. (1991) on grasses. Pardha Saradhi et al. (1993) present a different view with respect to rice plants.

CONCLUSIONS

1. Productivity of spinach plants treated with $FeCl_2$ and $FeSO_4$ using foliar sprays and of those fed with Fe-Cit through the roots is significantly higher than in the case of the other salts used.
2. Root application of the salts used has a significant effect on root iron content, whereas their foliar application significantly affect leaf iron content. In this respect, ferrous salts is generally the most beneficial, while ferric salts is the least beneficial.
3. The rate of transport of iron to the leaves, irrespective of the method of its application, is clearly higher for ferrous salts and Fe-Cit than for ferric salts.
4. Free proline content in the leaves of plants not fertilized with iron is 2–4 times lower than in plants supplied with this metal.
5. The higher light intensity has a positive effect on plant productivity and root iron content, but it has a negative effect on leaf iron and proline content as well as on the rate of transport of iron from the roots to the leaves.

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Pobieranie i transport żelaza (Fe^{+2}, Fe^{+3}) podanych dokorzeniowo lub dolistnie roślinom szpinaku (*Spinacia oleracea* L.) rosnącym w zróżnicowanych warunkach świetlnych

Streszczenie

W doświadczeniach prowadzonych w fitotronie z użyciem kultur wodnych badano wpływ dokorzeniowej lub dolistnej aplikacji różnych rodzajów soli żelaza na produktywność roślin, zawartość żelaza w liściach i korzeniach., a także wartość indeksu transportu Fe do liści. Rośliny rosły w pożywce Hoaglanda o pojedynczej koncentracji przy dwóch intensywnościach światła fluorescencyjnego: 290 i 95 μmol × m^{-2} × s^{-1} w zakresie FAR. W nawożeniu roślin zastosowano żelazo w dawce 25 mg Fe podane do pożywki lub w formie oprysku na liście roślin w postaci następujących soli: 1 – Fe 0, 2 – $FeCl_2 \times 4H_2O$, 3 – $FeCl_3 \times 4H_2O$, 4 – $FeSO_4 \times 7H_2O$, 5 – $Fe_2(SO_4)_3 \times nH_2O$, 6 – Fe-Cytr.

Uzyskane wyniki wykazały, że produktywność roślin szpinaku traktowanych dolistnie $FeCl_2$ i $FeSO_4$, a dokorzeniowo Fe-Cytr. była istotnie wyższa niż w przypadku pozostałych użytych soli. Aplikacja zastosowanych soli drogą dokorzeniową miała istotny wpływ na zawartość Fe w korzeniach, natomiast drogą dolistną na zawartość Fe w liściach. Najkorzystniejsze pod tym względem były na ogół sole żelazawe, najmniej korzystne sole żelazowe. Indeks transportu żelaza do liści niezależnie od sposobu jego aplikacji był wyraźnie wyższy dla soli żelazawych i Fe-Cytr. niż soli żelazowych. Zawartość wolnej proliny w liściach roślin nie nawożonych Fe była 2–4 krotnie niższa niż u roślin zaopatrywanych w ten składnik. Napromienienie 290 μmol × m^{-2} × s^{-1} wpływało pozytywnie tylko na produktywność roślin i zawartość Fe w korzeniach.