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Zinc Mobility in Wheat: Uptake and Distribution of Zinc Applied to Leaves or Roots

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Little is known about transport of Zn from leaves to other plant organs. The present study tested a range of Zn forms applied foliarly for their suitability to provide adequate Zn nutrition to wheat (*Triticum aestivum* L.). Transport of ^{65}Zn applied either to leaves or to one side of the root system was also studied. Inorganic (ZnO, $ZnSO_4$) and chelated sources of Zn (ZnEDTA, glycine-chelated Biomin Zn) applied foliarly provided sufficient Zn for vigorous growth. Zinc concentrations in roots and shoots were in the sufficiency range, except in the −Zn control. Foliar treatments with $ZnSO_4$ and chelated Zn forms resulted in shoot Zn concentrations in 7-week-old plants being about two-fold greater than those in plants supplied with Zn in the root environment or via foliar spray of ZnO. Adding surfactant to foliar sprays containing chelated forms of Zn did not cause negative growth effects, but surfactant added to ZnO or $ZnSO_4$ foliar sprays decreased shoot growth. Adding urea to the ZnO foliar spray had no effect on shoot growth. Foliarly-applied ^{65}Zn was translocated to leaves above and below the treated leaf as well as to the root tips. Stem girdling confirmed that ^{65}Zn transport toward lower leaves and roots was via the phloem. Split-root experiments showed intensive accumulation of ^{65}Zn in the stem and transport to all leaves as well as to the root tips in the non-labelled side of the root system. Foliar application of Zn in inorganic or organic form is equally suitable for providing adequate Zn nutrition to wheat. Phloem transport of Zn from leaves to roots was demonstrated.

Key words: Foliar spraying, phloem, surfactant, urea, xylem, wheat, zinc.

INTRODUCTION

Knowledge of zinc transport in the plant is inadequate (for reviews see Longnecker and Robson, 1993; Grusak *et al.*, 1999; Rengel, 1999). While it was shown that Zn can be transported in phloem in tobacco trees (*Nicotiana glauca*) (Hocking, 1980) and grape vines (Volschenk *et al.*, 1999), it has been claimed that such transport does not occur in wheat, leaving roots starved of Zn if not supplied in the root environment (Webb and Loneragan, 1990). However, more recent studies with wheat showed good transport of Zn from stem and leaves to developing grain (Pearson and Rengel, 1994, 1995*a*; Pearson *et al.*, 1995, 1996), as well as from one root to another (Pearson and Rengel, 1995*b*), indicating involvement of phloem transport. However, the movement of foliarly-applied Zn to wheat roots has not yet been demonstrated.

In foliar application of nutrients, the leaf cuticle is the first obstacle in nutrient absorption (Kannan, 1990). Surfactants can increase penetration of many substances through the cuticle (e.g. Stock and Holloway, 1993). In addition, urea has an uptake rate up to 20-times greater than other nutrients; it can aid absorption of nutrients, including foliarly-applied Zn (see Mortvedt and Gilkes, 1993). However, older reports (Wallace and Bedrice, 1958) described decreased uptake of Zn when urea was combined with foliar sprays of Zn sulphate or ZnEDTA. Resolving this controversy regarding the effects of urea may have practical implications in foliar nutrition of crops.

The aims of the present study were to assess suitability of various forms of Zn applied as foliar sprays, to test effects of urea and surfactants on foliar Zn nutrition and to decipher transport pathways for Zn applied to leaves or to one side of the root system.

MATERIALS AND METHODS

Seeds of wheat (*Triticum aestivum* L.) 'Aroona' were surface-sterilized in 1·5 % (v/v) sodium hypochlorite for 10 min, rinsed thoroughly in deionized water (resistivity $\geqslant$ 15 MOhm cm^{-2}) and imbibed in a Petri dish containing a shallow layer of water at 4 °C overnight. Imbibed seeds were germinated on a filter paper pre-soaked with 0·2 mM $CaCl_2$ at room temperature. The seed Zn concentration was 12·2 ± 0·4 mg kg^{-1} seed (equivalent to a seed Zn content of 0·39 ± 0·04 µg zinc per seed) (mean ± s.e., $n = 4$).

Ten 4-d-old seedlings were mounted in holes drilled in PVC lids that fitted tightly over 3·5-l ceramic pots. Sufficient blu-tack® was applied around the stem to provide a waterproof, yet flexible seal.

Pots contained continuously aerated standard −Zn solution of the following composition (in µM, according to Rengel *et al.*, 1994): Ca, 2000; Mg, 500; K, 2100; NO_3-N, 4000; H_2PO_4-P, 100; SO_4-S, 1504; FeEDTA [ethylenediaminetetraacetic acid], 20; B, 9·06; Na, 5·48; Cu, 0·90; Co,

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0·08; Mo, 0·13; and Cl, 5·48. This solution was used for the −Zn control as well as for growing plants in all foliar spraying treatments in expts 1 and 2. In contrast, Zn control plants in expts 1 and 2 received the above solution supplemented with 1 μM $ZnCl_2$. In the third group of experiments (phloem transport), the standard −Zn solution was used for the −Zn treatment, and was supplemented with 1 μM labelled Zn (see below) or with 1 μM of non-labelled $ZnCl_2$ as specified. Solutions were changed weekly.

Possible contamination by Zn was assessed by concentrating the nutrient solution 20 times and determining Zn by inductively coupled plasma emission spectrometry (ICP). Contamination was minimal (concentration of Zn was 0·03 μM) in freshly prepared solution, although it increased (0·25–0·29 μM Zn) when the solution was aerated for 7 d (this being the period between solution changes in the experiments) in the same experimental set-up as used in the present study, but without plants.

In expt 1, four different types of foliar spray ($ZnSO_4$, ZnO, ZnEDTA and Biomin Zn) were tested; all had a Zn concentration equivalent to 3·5 mM. Biomin Zn is a commercial product that contains Zn atoms chelated by two glycine molecules (I. Safi, Ferticom Pty Ltd, Adelaide, Australia, pers. comm.). Foliar sprays were applied twice on days 27 and 36 after the commencement of the experiment. Sprays were applied until all leaves on the target plants were wet. Care was taken to avoid contact between the Zn-containing spray and the nutrient solutions that had no Zn.

In expt 2, nine combinations of Zn sources, urea and surfactant were compared with the root-supplied Zn (Zn control). Surfactant (Agrol-600, a commercial grade) was added at a rate of 0·01 % (v/v) (commercially recommended rate). Urea (low biuret, 0·4 % w/w) was added to selected sprays at a rate that would not cause any leaf damage (0·5 % w/v) (e.g. Boaretto *et al*., 1998). For the first spraying (24-d-old plants), Zn concentration in all sprays was 1·74 mM, and 40 ml of the spray was applied in each treatment. For the second spraying (43-d-old plants), Zn concentration was raised to 3·5 mM, with 65 ml of spray being applied in each treatment. The volume sprayed was adjusted for the two sprayings so that all leaf surfaces were thoroughly wet.

Plants in expt 1 were grown in a glasshouse during early spring [average mid-day photosynthetically active radiation (PAR) was 1200 μmol m^{-2} s^{-1}], with temperatures ranging from the daily maximum of 27 °C to nightly minimum of 7 °C. For expt 2 conducted in early summer, PAR was decreased to 400 μmol m^{-2} s^{-1} because shade-cloth was used to prevent temperature increases. Hence, during expt 2, the temperature maximum was maintained at 27 °C during the day, while the nightly minimum was 10 °C. In both experiments, the position of the pots in the glasshouse was changed periodically to minimize the influence of any potential gradients in environmental parameters.

In expts 1 and 2, plants were harvested when they were 5, 6 and 7 weeks old. Roots were washed under running tap water and rinsed in deionized water. Shoots were washed under running tap water, rinsed in two lots of 1 % (v/v) acetic acid (to remove any traces of Zn that might have adhered to the shoot surface), with a final rinse in deionized water. After washing, roots and shoots were separated (tillers were also separated in expt 2), dried at 80 °C and weighed. Dried samples were digested and analysed for mineral nutrient composition by ICP as described elsewhere (Rengel and Graham, 1995).

In the third set of experiments designed to monitor transport of ^{65}Zn, plants were grown in nutrient solution as described above. During exposure to ^{65}Zn plants were grown on the laboratory bench under a light bank (PAR 35 μmol m^{-2} s^{-1} at plant level) with a 16 h light period. All experiments were performed with intact plants, except in the treatment where a leaf tip was cut to allow direct entry of Zn.

A stock solution of 0·71 mM ^{65}Zn, specific activity 50 MBq μmol^{-1}, was used to make up the working solution of 5 μM ^{65}Zn. Application of ^{65}Zn was made by either immersing the cut leaf tip into labelled solution (Penot and Gallou, 1977), or applying a droplet of ^{65}Zn-containing solution to the upper leaf surface, or by adding ^{65}Zn to one side of the split-root pots. When the leaf tip was cut, a section approx. 2 cm long was excised under water to prevent air entering xylem vessels. The cut surface and approx. further 2 cm of the leaf were inserted into the ^{65}Zn-containing solution (5 μM) for 24 h.

For surface application of ^{65}Zn, a well described method by Kannan (1987) was found too cumbersome in preliminary experiments, and only a single droplet (10 and 12 μl for the surfactant-free and surfactant-containing treatments, respectively) of the ^{65}Zn-containing solution was applied to the upper surface of the leaf that was restrained in a horizontal position. The solution to be applied was made by mixing 5 μl of the 0·71 mM stock solution of ^{65}Zn in 10 mM HCl plus 5 μl of 10 mM NaOH in 2 mM MES buffer. When surfactant was added, the above mix was supplemented with an additional 2 μl of Agrol-600 surfactant of the same concentration as used in expt 2. The labelled solution applied was buffered despite Zhang and Brown (1999*a*) showing no effects of pH in the range of 3·5–8·5 on absorption of foliarly-applied Zn at high concentrations (7·5–15 mM) to walnut (*Juglans regia* L.). In the present study, the ^{65}Zn-containing solutions were applied to the mid-section of the second leaf of the 5-week-old wheat plants. The exposure lasted for 48 h.

Steam girdling of the stem was used to differentiate between xylem transport (unaffected by girdling) and phloem transport (blocked completely by girdling) (Jenner, 1985; see also Pearson *et al*., 1995). Stems of 9-week-old plants were girdled just below the attachment point of the leaf to whose surface ^{65}Zn was applied. Steam was applied to replicate plants for 20, 30 or 60 s to test the optimal time for the procedure. After being exposed to ^{65}Zn for 48 h, plants were sectioned as described above. Ungirdled plants were used as controls to estimate transpiration by weighing before and after the treatment.

The 7-week-old plants pre-grown in standard nutrient solution (see above) containing 1 μM Zn were used for the split-root experiment. Roots were divided equally between the two pots, one of which was labelled with ^{65}Zn (1 μM) as above. Two treatments were tested: the non-labelled compartment contained either −Zn solution or solution

supplemented with 1 μM Zn. Treated plants were grown under the light bank (see above) for 24 h.

For experiments with radiolabelled Zn, activity of ^{65}Zn was determined by placing segments directly into scintillant for measurement by a Beckmas LS 3801 Liquid Scintillation counter as described elsewhere (Reid *et al.*, 1996). ^{65}Zn has strong positron and gamma emissions; therefore quenching was not a problem at the tissue density used. Upon termination of the leaf-labelling and split-root experiments, plant roots and leaves were washed, cut into 2 cm segments and analysed for radioactivity. For the stem tissue, sheaths were removed prior to analysis. Aliquots of labelled experimental solutions were also measured.

Experiments 1 and 2 were set up in a completely randomized design with three replicates. Data were analysed by analysis of variance, with post-hoc pairwise comparisons (Tukey-Kramer) of means. Experiments with ^{65}Zn were repeated three times.

RESULTS

Experiment 1: foliar Zn nutrition

Symptoms of Zn deficiency were observed only in the −Zn control. These symptoms included yellow chlorotic areas that developed between the mid-vein and leaf margin of the second and subsequent leaves and became necrotic in the central leaf area, while the leaf tip, base and margins remained green (cf. Rengel and Graham, 1995).

Plants supplied with Zn in the nutrient solution (Zn control) had a somewhat greater shoot dry mass than plants supplied with Zn foliarly, but grew significantly better than plants in the −Zn control (Fig. 1). For the first harvest after 5 weeks, pairwise comparisons revealed significantly better growth of plants treated with the inorganic foliar sprays (Zn sulphate and ZnO) than the −Zn control plants, while the treatments with chelated Zn were not significantly different from the −Zn control. The two foliar treatments with inorganic Zn resulted in significantly better shoot growth than the two treatments with chelated Zn after 6 weeks, but the difference was not significant after 7 weeks. Shoot growth after 7 weeks was as good in the ZnO foliar treatment as in the Zn control treatment in which Zn was supplied in the root environment.

Shoot Zn concentrations were highest in the Biomin Zn treatment, followed closely by the Zn sulphate and ZnEDTA treatments, and were significantly lower in the treatments with root-supplied Zn (Zn control), ZnO and the −Zn control (Fig. 2). Except in the −Zn control treatment, shoot Zn concentrations in all other treatments were in the sufficiency range.

Root Zn concentrations were highest in the Biomin Zn treatment throughout the study. At the middle harvest (6-week-old plants), root Zn concentrations in the ZnEDTA and ZnO treatments were higher than in the Zn sulphate, Zn control (with Zn supplied to the nutrient solution) and the −Zn treatments (data not shown). However, it should be stressed that root Zn concentrations in all treatments and for all three harvests were in the range considered sufficient for wheat.

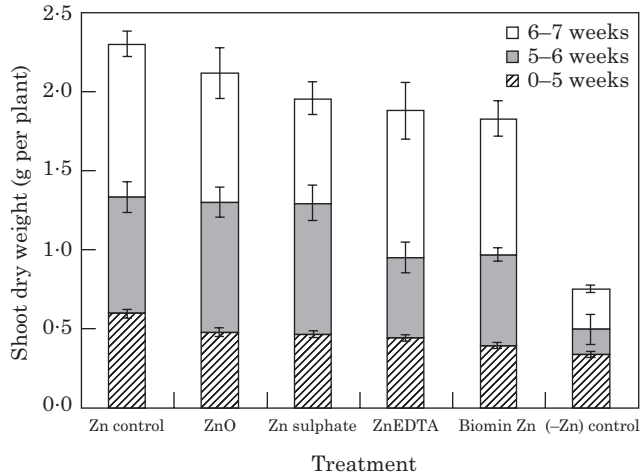

FIG. 1. Accumulation of shoot dry matter by wheat plants grown in expt 1 in nutrient solution for 7 weeks either without Zn supply (−Zn control) or with Zn supplied in the root environment (Zn control) or foliarly (the remaining four treatments). Vertical bars denote ± s.e.

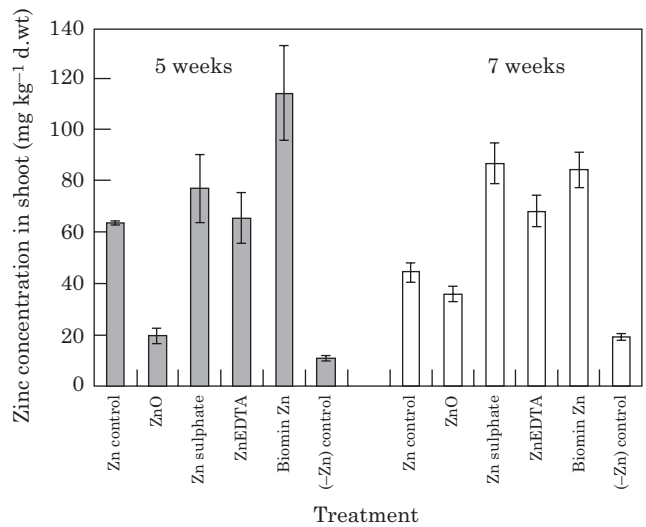

FIG. 2. Zinc concentration in shoot tissue of wheat grown in expt 1 in nutrient solution for various periods of time (5–7 weeks) either without Zn supply (−Zn control) or with Zn supplied in the root environment (Zn control) or foliarly (the remaining four treatments). The treatment effects on shoot Zn concentration of 6-week-old plants were not shown because they were similar to those for 7-week-old plants. Vertical bars denote ± s.e.

The ratio of root-to-shoot Zn concentrations was greater in the −Zn and +Zn controls than in the Zn sulphate and ZnEDTA treatments (Fig. 3). Such a high ratio in the −Zn control indicates that transport of Zn from roots to shoots was limited during Zn deficiency.

Experiment 2: role of urea and surfactants in foliar Zn nutrition

Surfactant Agrol, used in commercial foliar applications, caused a decrease in shoot growth when added to the foliar sprays containing inorganic Zn (ZnO and $ZnSO_4$), but not

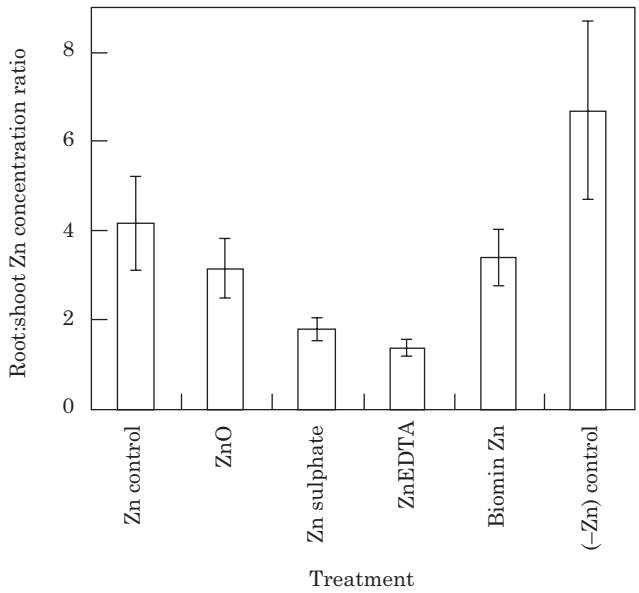

FIG. 3. The ratio of Zn concentration in root *vs.* shoot tissues of wheat plants grown in expt 1 in nutrient solution for 7 weeks either without Zn supply (−Zn control) or with Zn supplied in the root environment (Zn control) or foliarly (the remaining four treatments). Vertical bars denote ± s.e.

when added to sprays with chelated forms of Zn (ZnEDTA and Biomin Zn) (Fig. 4). This growth reduction was especially prominent in the case of ZnO mixed with the surfactant. Adding urea to ZnO spray had no effect on shoot growth and could not alleviate the growth reduction caused by the surfactant.

Experiments on ^{65}Zn transport

In the cut-leaf experiment, ^{65}Zn taken up and exported from the leaf was directed toward the stem (which contained 34 % of the applied isotope), youngest leaf (8 %) and roots (6 % of the applied isotope). The old leaves received little ^{65}Zn (0·1 % of the applied amount).

Preliminary experiments into leaf surface application of ^{65}Zn showed that the addition of surfactant improved Zn uptake by about 15 %; therefore, subsequent experiments involving surface application used the solution mixed with surfactant. Most of the surface-applied ^{65}Zn moved toward the tip of the leaf to which it was applied (about 85 % of the amount applied, omitting the section to which ^{65}Zn application was made), with the remainder being distributed among stem, leaves, roots and, to a considerably lesser extent, older leaves (Fig. 5).

Stem girdling was effective in decreasing Zn transport: only 0·7 and 0·2 % of the applied Zn passed the girdling point after 20 and 60 s of steam application, respectively, compared with 8 % in the ungirdled control (Fig. 6). In contrast, xylem was left intact by girdling as the transpiration rates (between 0·32 and 0·46 ml H_2O g^{-1} plant fresh weight h^{-1}) were slightly higher in the girdled compared with ungirdled plants.

When only half of the roots were exposed to ^{65}Zn in the split-root system containing 1 μM Zn on both sides, about 60 % of ^{65}Zn exported out of labelled roots ended up in the

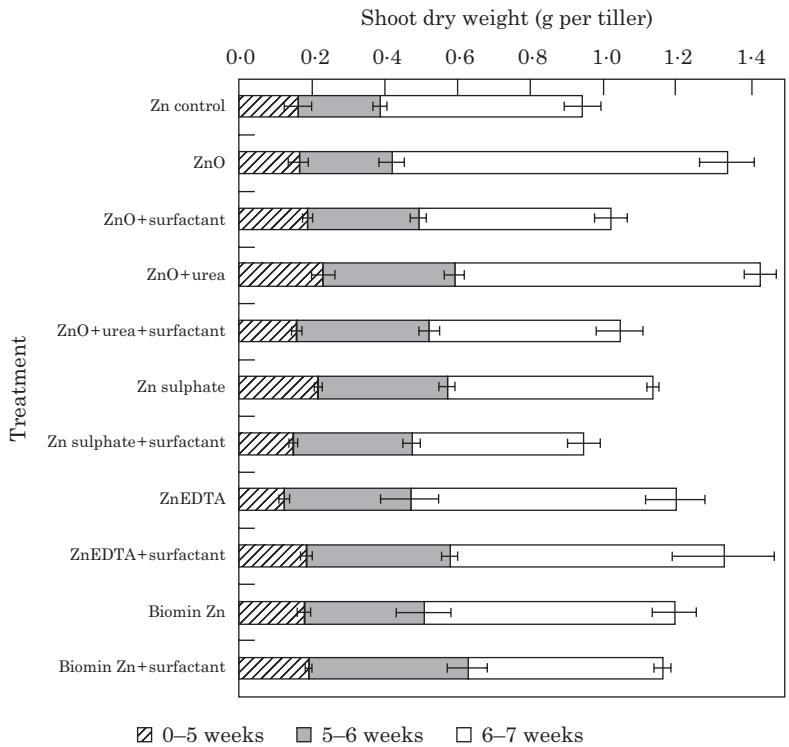

FIG. 4. Accumulation of shoot dry matter by wheat plants grown in expt 2 in nutrient solution for 7 weeks with Zn supplied either in the root environment (Zn control) or foliarly (the remaining treatments). Vertical bars denote ±s.e.

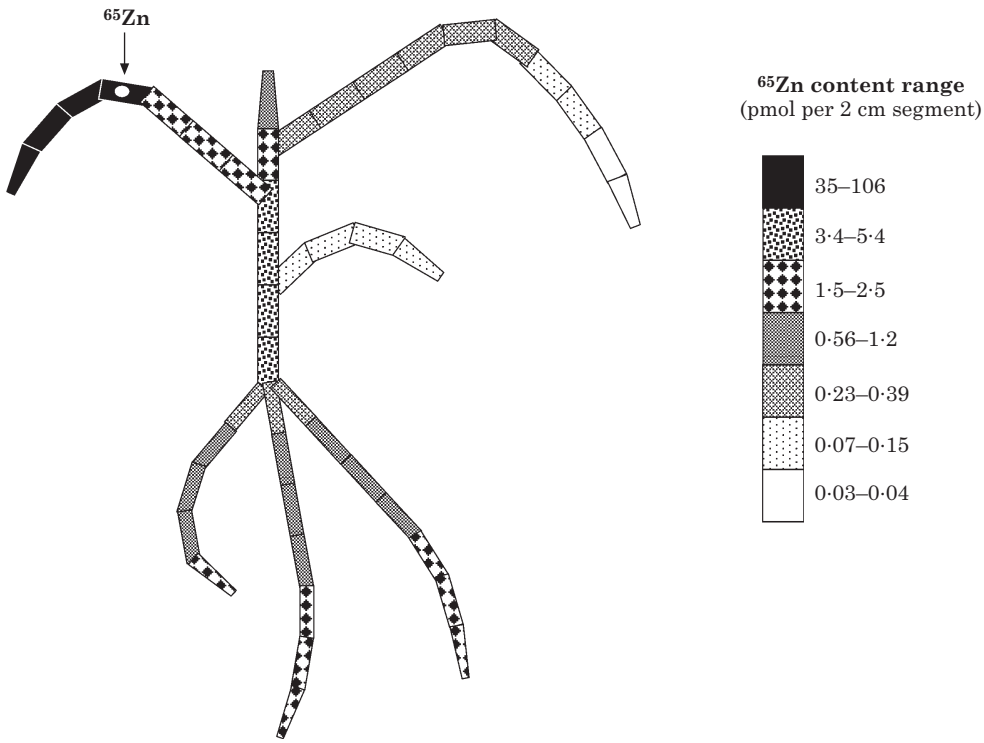

FIG. 5. Schematic presentation of distribution of ^{65}Zn applied to the leaf surface for 48 h. Wheat plants were 5 weeks old at the beginning of treatment. The leaves shown (from top to bottom) represent the youngest fully emerged leaf, the middle leaves and the oldest leaf. Roots were divided into three subsamples.

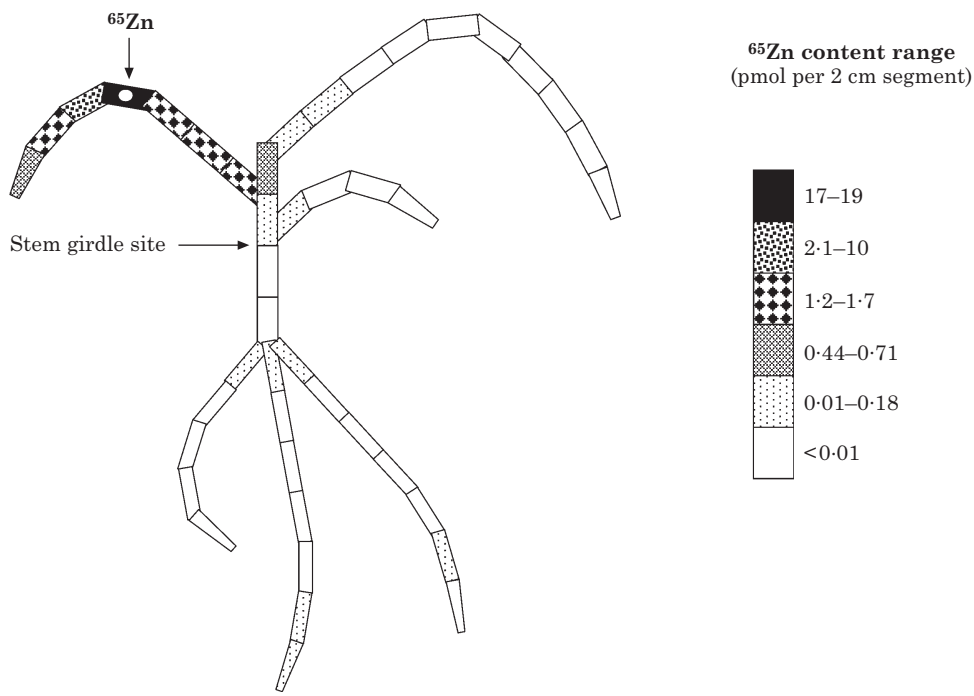

FIG. 6. Distribution of ^{65}Zn applied to the leaf surface for 48 h as influenced by stem girdling (achieved by applying steam for 60 s). Wheat plants were 9 weeks old at the beginning of the treatment. The leaves shown (from top to bottom) represent the youngest fully emerged leaf, the middle leaves and the oldest leaf. Roots were divided into three subsamples.

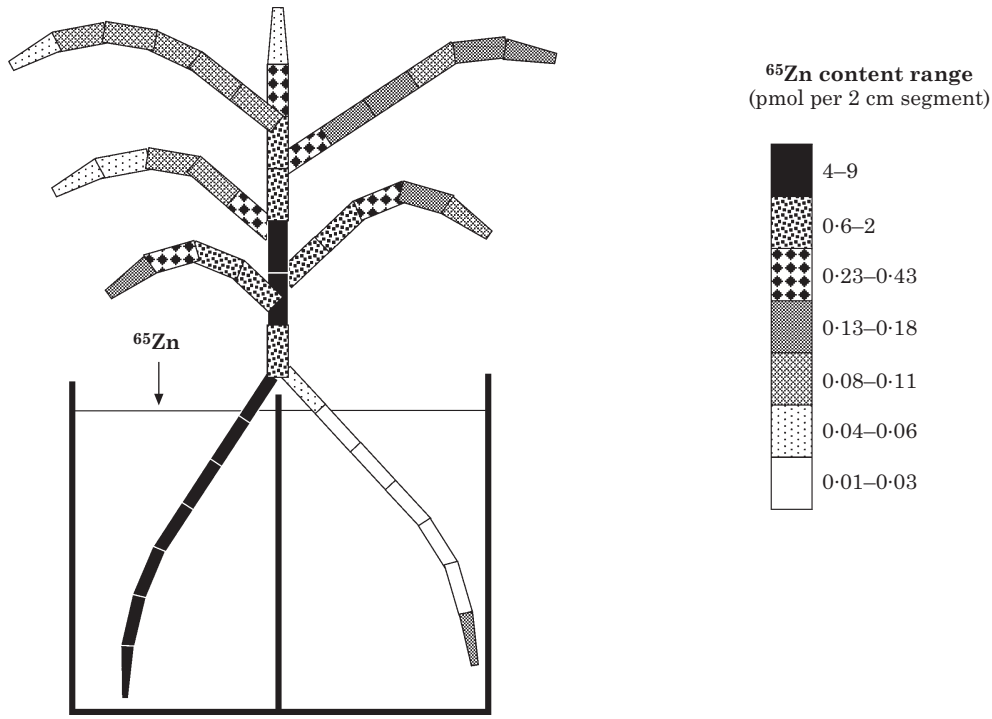

FIG. 7. Distribution of ^{65}Zn applied to one side of the wheat root system for 24 h. Both sides of the root system were bathed in the nutrient solution containing 1 μM Zn. Plants were 7 weeks old at the beginning of the treatment.

stem, with the first and the second leaves also receiving substantial amounts (Fig. 7). Interestingly, a large portion of ^{65}Zn transported from the labelled side of the root system to the unlabelled side accumulated in the root tips. When the unlabelled side of the split-root system was bathed in the −Zn solution, a greater proportion of the translocated ^{65}Zn (8 %) accumulated in the root tip segments compared with the treatment in which 1 μM Zn was supplied to both sides (1·6 %). On a weight basis, such an increase in ^{65}Zn accumulation in −Zn grown roots was three-fold greater than in the case of +Zn roots.

DISCUSSION

Foliarly-applied Zn was effectively absorbed and translocated to other wheat organs and tissues (Figs 1, 2, 5, 6). While the mechanism of Zn absorption by wheat leaf cells was not determined in the present study, in pistachio (*Pistachio vera* L.) and walnut (*Juglans regia* L.) such absorption was via ion exchange and/or ion diffusion, the two processes not requiring direct expenditure of energy (Zhang and Brown, 1999*a*).

Foliar application of Zn, especially of inorganic Zn, may be sufficient for similarly vigorous growth of wheat as in the case of root-supplied Zn (Figs 1, 4). Organic sources of foliarly-applied Zn were more effective in promoting growth in later stages (6–7 weeks compared with 5–6 weeks). The overall difference between Zn sulphate (the most commonly used inorganic Zn spray in horticulture, pomology and agriculture) and ZnEDTA (the most common chelated Zn form) was minimal (Fig. 1), which supports findings in other crops (*Phaseolus vulgaris*, Boaretto *et al*., 1998) as well as in wheat grown in soils in pots (Modaihsh, 1997) and in the field (Brennan, 1991). Therefore, there may not be any justification in preferring more expensive chelated over cheaper inorganic forms of Zn in foliar Zn fertilization.

Despite some earlier reports on a range of crops (for a review see Mortvedt and Gilkes, 1993; Stover *et al*., 1999), addition of urea to foliar sprays containing inorganic Zn in the present study did not influence effectiveness of the spraying or the growth of wheat (Fig. 4), these results being consistent with those on bean (Boaretto *et al*., 1998). However, since no negative growth effects were observed either, addition of urea can still be advocated if improvement of N nutrition via foliar sprays is desired.

Surfactants can increase penetration of many substances through the leaf cuticle (Stock and Holloway, 1993) and they are therefore frequently added to foliar sprays. However, some surfactants may be toxic to plants (Z. Rengel unpubl. res.) and some may not be at all effective in increasing nutrient absorption (Kannan, 1987). The surfactant Agrol-600 used in the present study at the rate recommended by the manufacturer (Fig. 4) had a negative effect on wheat shoot growth when combined with either ZnO or $ZnSO_4$ foliar sprays. It is therefore advisable to test individual combinations of crop-surfactant-nutrient at a range of concentrations before engaging in large scale spraying.

Contrary to previously published reports on Zn immobility from the position on the apple leaf where application had been made (Orphanos, 1975), movement of foliarly-applied Zn in wheat was rapid and substantial within 24- and 48-h treatments in the present study (Figs 5, 6), supporting field observations (Yilmaz *et al*., 1997, 1998).

In contrast, application of stable isotope ^{68}Zn to leaves of mature pistachio trees resulted in no measurable translocation out of the treated leaves in 10 d, indicating a strong binding of Zn to leaf components (Zhang and Brown, 1999*b*). However, in pistachio seedlings, a small percentage of leaf-applied ^{68}Zn (around 5 % of the applied amount) did move out of the treated leaves (Zhang and Brown, 1999*b*), confirming phloem mobility of Zn in pistachio.

There was little difference in distribution of ^{65}Zn in wheat when applied foliarly or via roots, with the greatest accumulation being in the stem (Figs 5–7). Similar results were reported by Pearson and Rengel (1994, 1995*a*,*b*); Zn accumulated in the wheat stem during Zn supply, and was readily mobilized from it in cases of a diminished external supply. High accumulation of ^{65}Zn was also noted in the meristematic regions at the base of leaves and at the root tips (Figs 5–7), probably because of a large Zn requirement in the rapidly growing tissue of wheat (Pearson and Rengel, 1995*b*) and barley (Welch and Norvell, 1993). Therefore, Zn demand in tissues can influence the pattern of Zn distribution in cereals as well as in bean (see Rodrigues *et al*., 1997). The importance of Zn demand in modifying the pattern of Zn transport was also apparent from the increased transport of ^{65}Zn supplied in the split-pot experiment to roots on the non-labelled side that were Zn deficient compared to the treatment in which they were Zn sufficient (see Results). However, the possibility that greater re-translocation of ^{65}Zn during the labelling period occurred from Zn-sufficient roots than from Zn-deficient ones cannot be excluded, thus resulting in greater ^{65}Zn content in the latter.

Foliar application of ^{65}Zn always resulted in transport of ^{65}Zn to the root tips, regardless of the application method (Figs 3, 5, 6). Such transport does not appear to have been reported in the literature to date. This finding clearly indicates substantial mobility of Zn in the phloem, an assertion frequently made with respect to wheat (Pearson and Rengel, 1994, 1995*a*,*b*; Pearson *et al*., 1995, 1996; Herren and Feller, 1997; Grusak *et al*., 1999). It does, however, contradict the suggestion made by Webb and Loneragan (1990) that Zn does not move from leaves to roots and therefore needs to be supplied in the root environment to prevent root tips from becoming Zn-deficient. A relatively large reservoir of Zn in the stem (Figs 5–7, see also Pearson and Rengel, 1994, 1995*a*,*b*) could also contribute to supply of Zn via remobilization to other parts, including root tips, should external Zn supply diminish.

While ^{65}Zn can clearly move in the phloem, the majority of it (up to 85 % of the applied amount) still moved acropetally toward the tip of the leaf to which it was applied, indicating movement in the xylem. Effective transport of Zn in xylem has been shown previously (Pearson *et al*., 1995, 1996), especially toward the wheat ear. The transfer of Zn from xylem to phloem during transport toward developing wheat grains may occur in either rachis (Pearson *et al*., 1995) or peduncle (Herren and Feller, 1994, 1997; Pearson *et al*., 1995). Xylem-to-phloem transfer may also occur in the crown (where roots meet the stem; Pearson and Rengel, 1995*a*,*b*) as shown by Zn transport from one root to the other in the split-root experiment (Fig. 7). However, transport of ^{65}Zn from labelled roots could have occurred in the xylem all the way up to stem or leaves, with the subsequent transfer to the phloem for downward transport to roots representing a somewhat less direct route from one part of the split-root system to the other. In addition, due to the relatively long labelling period, some of ^{65}Zn transported from leaves to roots via phloem (Fig. 5) could have been re-translocated back to the stem and leaves in the xylem.

Stem-girdled plants had only their phloem transport blocked (Fig. 6), while xylem transport was functioning. Somewhat higher rates of transpiration were observed in girdled compared to ungirdled plants (see Results); this finding is consistent with previously published results on wheat (Jenner, 1985).

In conclusion, it is possible to supply adequate Zn to wheat via foliar sprays. Transport of Zn in phloem from leaves to the stem, lower leaves and roots is substantial. Combined with earlier reports of effective phloem transport of Zn from the stem and leaves to the developing grain, we conclude that Zn is highly mobile in phloem.

ACKNOWLEDGEMENT

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