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Influence of water relations and growth rate on plant element uptake and distribution

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Summary

Plant uptake of Ni, Sr, Mo, Cs, La, Th, Se, Cl and I was examined to determine how plant water relations and growth rate influence the uptake and distribution of these elements in the studied plants. The specific questions were how water uptake and growth rate influenced the uptake of various nuclides and how transpiration influenced translocation to the shoot. The knowledge gained will be used in future modelling of radionuclide leakage from nuclear waste deposits entering the ecosystem via plants. The plant studied was willow, *Salix viminalis*, a common plant in the areas suggested for waste disposal; since there can be clone variation, two different clones having different uptake properties for several other heavy metals were used. The plants were grown in nutrient solution and the experiments on 3-month-old plants were run for 3 days. Polyethylene glycol was added to the medium to decrease the water uptake rate, a fan was used to increase the transpiration rate, and different light intensities were used to produce different growth rates. Element concentration was analysed in roots and shoots.

The results show that both the uptake and distribution of various elements are influenced in different ways and to various extents by water flow and plant growth rate, and that it is not possible from the chemical properties of these elements to know how they will react. However, in most cases increased growth rate diluted the concentration of the element in the tissue, reduced water uptake reduced the element uptake, while transpiration had no effect on the translocation of elements to the shoot. The clones did not differ in terms of either the uptake or translocation of the elements, except that I was not taken up and translocated to the shoot in one of the clones when the plant water flow or growth rate was too low. Not all of the elements were found in the plant in the same proportions as they had been added to the nutrient solution.

Sammanfattning

I detta projekt undersöktes upptag och fördelning i växten av elementen Ni, Sr, Mo, Cs, La, Th, Se, Cl och I vid olika hastigheter av vattenupptagning, transpiration och tillväxthastighet. Syftet var att söka förstå hur vattenupptagningen och tillväxthastigheten påverkar upptag och hur transpirationen påverkar fördelningen till skottet av de nämnda elementen. Kunskapen är sedan tänkt att användas i framtida modellering av transport av radioaktiva nuklider från kärnbränsleavfall som läckt till ekosystemet, där växter ingår som naturlig del. Korgpil, *Salix viminalis,* användes i detta försök då den är vanligt förekommande inte minst på de föreslagna områdena för förvaring av radioaktivt avfall. Eftersom tidigare försök visat att olika sorters korgpil tar upp olika mycket av vissa metaller så användes en låg- och en högupptagande sort i denna undersökning. Växter odlades i vattenkultur och experimenten utfördes på tre månader gamla växter under 3 dagar. Polyetylenglykol tillfördes mediet för att minska vattenupptagningshastigheten. För att få olika transpirationshastigheter sattes växterna på olika avstånd från en fläkt. Olika tillväxthastighet erhölls genom odling vid olika ljusstyrka. Efter avslutat försök analyserades koncentrationen av de nämnda elementen i rötter och skott.

Resultaten visar att vattenupptagning, transpiration och tillväxt påverkade upptag och fördelning av de skilda elementen i växten på olika sätt och olika mycket. Detta kunde inte förklaras med elementens skiftande kemiska egenskaper eftersom element med liknande kemiska egenskaper ofta inte påverkades på samma sätt. I de flesta fall minskade koncentrationen av ämnena i växten med ökad tillväxthastighet och minskad vattenupptagningshastighet. Transpirationen påverkade generellt inte transporten av elementen till skotten. Inga större sortskillnader återfanns, utom att upptaget av I och dess transport hämmades totalt i en av klonerna och det var när vattenflödeshastigheten genom växten och tillväxthastigheten var för låg. Elementen återfanns i växten bara till viss del i de proportioner som de tillsattes till upptagsmediumet.

Contents

1 Introduction

Nuclear power production produces nuclear waste. Systems for taking care of the waste have long been discussed, and of these systems deep repository is the most likely to be used in the future. Sites for deep repository in bedrock are being characterized in several projects run by SKB.

A potential future problem is the leakage of nuclear waste: radionuclides could be translocated via water, ending up in the ecosystems of the earth. An important component in such a transport chain is vegetation, since plants can take up the nuclides and serve as food for both humans and many animals. To predict possible future problems with element leakage from deep repositories of spent nuclear fuel, it is necessary to understand and be able to calculate the influence of plants on radionuclide recirculation in the environment.

1.1 Plant uptake

Uptake by plants is complicated, and even though elements are largely taken up into the plant body by a passive process, this process is more than a simple pump /reviewed by Greger 2004/. Plants themselves determine the uptake, while the soil and sediment determines the availability of the elements to the plants; moreover, the elements themselves can interact with each other, also influencing the uptake. Plants take up all kinds of available elements. The uptake can proceed until a depletion concentration has been obtained, the magnitude of which differs depending on the element and specific situation. According to /Ingestad 1982/ it is not the concentration per se that is important but rather the addition rate.

Uptake works via the water flow; it is driven by the bulk flow, which in turn is driven by the transpiration rate /Marschner 1995/. During uptake, elements follow the water into the plant tissue, where as cations they bind to the negative charges of the cell wall system (apoplast) or as cations and anions are translocated into the xylem vessel in the apoplast /Marschner 1995, Greger 1999/. Elements are also taken up into the cells, where they are bound up, compartmentalized, or are further translocated, symplastically, to the xylem vessel /Marschner 1995, Greger 1999/. Since water is a necessary medium in which elements are solubilized as well as translocated in soil and in plants, it is likely that the water flow regulates the entrance of elements into plant tissue, thus also regulating their concentration in the plant. If there is a genuinely passive intake of elements via the water flow, *all* the molecules of an element contained in the water will be taken up. In addition, the *proportions* of elements in the water will also be mirrored in the plant tissue. The water uptake rate may thus influence element uptake. However, the water uptake rate had been found to have no effect on the uptake of Cd /Perttu et al. 2003/.

In the xylem, elements are translocated upwards via the transpiration stream consisting of water and solubilized elements. On their way upwards, they are also unloaded to cells in contact with the vessels. The xylem translocation of cations functions via interaction with non-diffusible anions of the cell walls of the xylem vessels, which leads to a separation of cation transport from the water flow /Wolterbeek 1987/. The xylem is thought to act as an ion-exchange column for cations that has the potential to impede the movement of cations up the stem /Bell and Biddulph 1963, Momoshima and Bondietti 1990/. This is not the case with anions, which probably follow the flow without any interactions with the vessels. The

translocation of cations can be enhanced if they form complexes with organic compounds, thus reducing their affinity for the fixed negative charges in the cell walls /White et al. 1981, Cataldo et al. 1988/, thereby it is likely that the transpiration stream influences the translocation of cation-organic complexes but not of free cations. Various cations, due to their differing affinities for the negative charges, are translocated to varying degrees to the shoot. Moreover, anions are translocated to the shoot to higher degree due to repellence to the negative charges.

The transpiration stream is driven by transpiration in mature plants while in seedlings it is the root pressure that drives the xylem stream upwards /Marschner 1995/, a difference arising from the absence of sufficient leaf area in seedlings. Element translocation should therefore be influenced by the transpiration in mature plants, this, however, is not the case for at least Cd /Perttu et al. 2003/.

Another important factor influencing the accumulation of elements in plants is the growth rate and thus the biomass production of the plant. The root biomass as well as the number of root tips, where most of the water and elements are taken up, can influence the uptake parameter. The greater the biomass, the greater the uptake in relation to the external concentration. This is probably due to the density of uptake sites in the apoplast of the root tissue and the availability of the sites. This means that the greater the biomass, the more the internal element concentration is diluted; this results in low tissue concentration, even though total uptake increases with increasing biomass /Ekvall and Greger 2003/. Furthermore, a great shoot biomass may enhance the translocation of elements from root to shoot. In addition, the amount translocated to the shoot depends on the specific plant species and element in question. Most elements with high mass have a very restricted translocation to the shoot /Greger 2004/. In addition to biomass, the translocation of an element to the shoot also depends on factors such as interactions with other elements in the tissue, transpiration stream, leaf size and shape, cuticle permeability, and humidity.

1.2 Elements of interest

Caesium (Cs), strontium (Sr), chlorine (Cl), molybdenum (Mo), iodine (I), nickel (Ni), selenium (Se), lanthanum (La), and thorium (Th) are important elements in the context of nuclear waste leakage. These elements, some of which are essential to plants, encompass a broad spectrum of chemical properties.

The essential elements are Cl, Mo, and Ni. Chlorine is an essential element for plants, predominantly in the form of an inorganic anion (Cl^-), and is used for metabolic processes involved in maintaining electrochemical potentials in the plant cell tissue. Root-absorbed Cl readily translocates to both stems and leaves /Coughtrey and Thorne 1983/. Molybdenum, also a nutrient element, is taken up in anionic form as molybdate /Marschner 1995/. The rate of molybdate uptake by roots is closely related to metabolic activity /Kannan and Ramani 1978/. Molybdenum is moderately mobile in plants and it has been suggested that it could be translocated as a Mo-S amino acid complex in the xylem /Tiffin 1972/. Molybdenum has a necessary function related to valence change, since it is a transition element and is thus involved in redox reactions. Nickel is the most recently discovered plant nutrient /Marschner 1995/. Like other divalent cations, Ni^{2+} is known to form organic compounds and complexes. Nickel has been found bound to anionic organic complexes in xylem exudates /Tiffin 1977/, such as Ni-histidine complex in hyperaccumulator plants /Krämer et al. 1996/. Nickel is an essential component of the enzyme urease required by nodulated legumes that translocate N from roots to shoot in the form of ureide componds /Marschner 1995/.

Three elements that are closely related to nutrient elements are Cs, Sr, and Se. Caesium is related to the plant nutrient element K and follows the uptake route of K /Cline and Hungate 1960, Erdei and Trivedi 1991, Bunzl et al. 2000/. Plants relatively easily take up Cs^+. Differences between K and Cs are found in the selectivity of the xylem-loading process /Buysee et al. 1995/. Uptake is affected by water stress and osmotic conditions /Van der Borght et al. 1967/, and it is proposed that Cs uptake is controlled by diffusion /Shalhevet 1973/. Caesium is found in areas of cell expansion and active metabolism, and thus is present in plant parts having an increased need for water and nutrients, i.e. nodes, leaf tips, young leaves, and shoot meristems /Vanek et al. 2001/. Strontium is often associated with Ca and sometimes also with Mg, both of which are plant nutrients. Strontium exists largely as immobile complexes with glutauronic acids and pectate in the plant tissue /Mortensen and Marcusiu 1963, Myttenaere and Masset 1965/. It mainly occurs as Sr^{2+} ions or in chelated forms /Coughtrey and Thorne 1983/. Selenium is taken up in plants in the form of SeO_4^{2-}, SeO_3^{2-} but also as selenomethionine /Abrams et al. 1990/. Selenate is taken up in strong preference to selenite and competes for the same uptake site as sulphate /Asher et al. 1977/. Selenium competes with sulphur and is able to take the place of sulphur in amino acids and thus in proteins and thereby changing their functions.

Other non-essential elements are I, La, and Th. The most common forms of I are I^- and IO_3^- /Garrels and Christ 1965/, both of which are easily available to plants. Lanthanium is the most studied of the lanthanides, and according to /Menzel 1965/ lanthanides are strongly excluded by plants. Accumulation of La in wheat decreases with high fertilization /Zhang and Shan 2001/, as is also the case with the actinide Th /Whicker et al. 1999/, which may be due to the increased growth rate shown for other metals /Göthberg et al. 2004/.

1.3 The aim of the willow uptake study

Salix viminalis is a plant species commonly found at suggested sites for nuclear waste deposits. Its roots can grow deep and take up a huge amount of water /Lindroth and Cienciala 1996/. It is also found to have huge intraspecies variation in terms of the uptake and translocation of metals to the shoot, i.e. between clones (genotypes) of *S. viminalis* /Landberg and Greger 1994, Landberg and Greger 1996, Greger and Landberg 1999, Greger et al. 2001/.

The aim of this work was to investigate the influence of water uptake, transpiration, and growth, on the uptake and translocation (i.e. distribution to the shoot) of Ni, Sr, Mo, Cs, La, Th, Se, Cl, and I (Figure 1-1). These elements were chosen since they figure prominently in nuclear waste and represent a wide range of elements (in both their anion and cation forms), both essential and non-essential to plants. Our hypotheses were that depressed water uptake would decrease element uptake, increased transpiration would increase the translocation of elements to the shoot, and increased growth would diminish total uptake due to dilution of the elements in the plant tissue. The same effects are likely found for all elements and both clone types, though to different degrees.

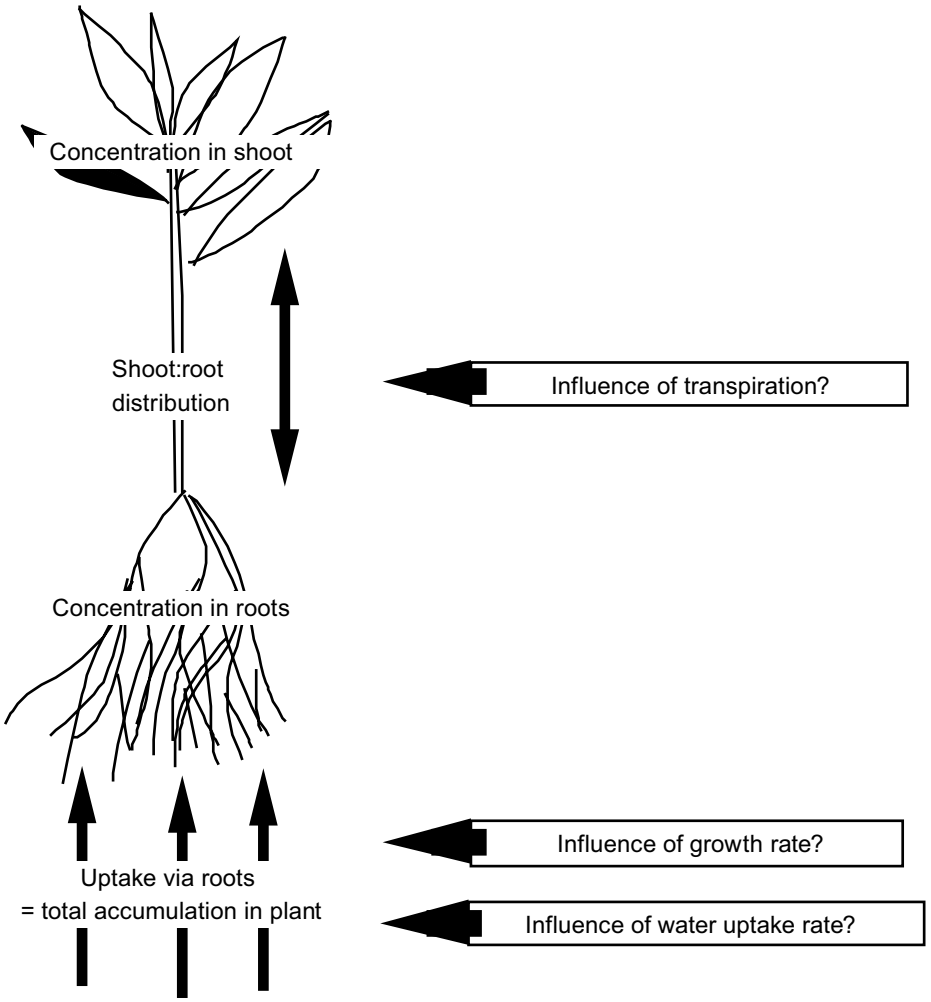

Figure 1-1. *The system studied.*

2 Materials and methods

2.1 Plant materials and growth conditions

Two clones of *Salix viminalis* were used in this investigation. Clone 88-31-1 (called 31-1) is a clone with as high an uptake and root accumulation as possible of Zn, Cu, and Cd, while clone 88-4-2 (called 4-2) has as low an uptake and root accumulation as possible of these three elements (see Table 2-1) /Landberg and Greger 1994, 1996, Greger and Landberg 1999, Greger et al. 2001/.

One-year-old stems of each clone were cut into 15-cm pieces and then placed in water for 48 hours to initiate growth and resprouting. Thereafter, three cuttings were placed in each of the black Styrofoam discs, which were placed in one-litre black plastic pots containing 100 µM $CaNO_3$. Two weeks later the solution was replaced by a complete nutrient medium that contained (in µM) the following: 163 KNO_3, 51 KH_2PO_4, 76 $MgSO_4$, 310 $Mg(NO_3)_2$, 295 $Ca(NO_3)_2$, 2.7 $FeCl_3$, 1.6 K_2EDTA, 1.21 $MnSO_4$, 2.34 H_3BO_3, 0.082 $CuCl_2$, 0.063 $ZnCl_2$, 0.015 Na_2SiO_4 and 0.0092 $SiCl_4$; this solution was replaced once a week and later on twice a week. The initial pH was 6.1 and was not adjusted during the experiment. Two weeks before the experiment began the plants were individually transplanted to 1-litre pots.

Except as specified otherwise, plants were grown for 3 months in a growth chamber under the following conditions: 16 hours light and 8 hours darkness, 260 µmol $m^{-2}s^{-1}$ during the light period, and 60–70% humidity.

Table 2-1. Heavy metal accumulation properties of the two *Salix viminalis* clones used in this research as well as lowest and highest values found among about 200 different *Salix* clones /Landberg and Greger 1994, 1996, Greger and Landberg 1999, Greger et al. 2001/.

	Clone 88-4-2			Clone 88-31-1			Min-Max		
	Cu	Cd	Zn	Cu	Cd	Zn	Cu	Cd	Zn
Net uptake, mg in plant (kg DW root)$^{-1}$	0.62	0.40	6.43	2.60	0.82	56.4	0.21–5.84	0.08–15.42	1.86–156
Concentration in roots, mg (kg DW)$^{-1}$	56	16	72	211	35	1,643	6.9–284	4.1–297	72–2,410

2.2 Elements tested

The elements investigated in this work were Ni, Sr, Mo, Cs, La, Th, Se, Cl, and I, which were all added at the same time as CsCl, $NiCl_2$, $SrCl_2$, $Th(NO_3)_4$ (3.93 kBq g^{-1}), $LaCl_3$, KI, Na_2MoO_4, and Na_2SeO_4. The concentration of each added element was 0.05 µM, meaning that in total the nutrient solution contained 0.05 µM Ni, Sr, Cs, Th, La, Se and I, and due to their prior presence in the nutrient medium, 0.063 µM Mo and 18.05 µM Cl. The concentration of the elements in the nutrient medium was not toxic to the plants; this was tested prior to the investigation by measuring growth parameters, chlorophyll content, and superoxide dismutase activity according to /Landberg and Greger 2002/ and /Greger and Ögren 1991/.

2.3 Effect of growth rate on element uptake

Various biomass production rates were achieved by growing plants under two different light conditions, 40 and 260 µmol m^{-2} s^{-1}, both a week prior to and during the experiment. Experiments on Cu, Cd, and Zn showed that the various light intensities had no influence on the uptake /Perttu et al. 2003/. In addition, pre-tests of the effects of light on uptake of the 9 elements showed no effect. The growth rates of the various clones under the different light conditions prior to the experiment were measured by weighing the plants every third day. The experiment started when the growth rate had stabilized. At the start of the experiment, the initial growth medium was replaced with one containing the 9 elements in the concentrations mentioned above. The experiment was run for 72 hours.

2.4 Influence of water uptake rate on element uptake

The influence by water uptake on element uptake could be gauged by using increased levels of polyethylene glycol (PEG) in the growth medium to prevent and hence reduce water uptake by the plants. Polyethylene glycol increases the osmotic potential of the surrounding medium since this molecule is big and does not enter the root cells. Therefore, the water will be kept outside the roots and the water uptake will decrease with increasing PEG concentration. Polyethylene glycol has been used elsewhere to control water uptake /see Larsson 1992, Perttu et al. 2003/. At the start of the experiment, the growth medium was replaced with a growth medium containing the 9 elements in the concentrations mentioned above, as well as 0, 8, or 16% (w:v) of PEG. This means that plants were not acclimatized to the different PEG concentrations prior to the experiment. The experiment was run for 72 hours, and the fresh weight of the plants was measured before and at the end of the experiment to enable calculation of the growth rate during the uptake experiment.

2.5 Transpiration effect

Plants were exposed to various wind speeds to adjust the transpiration rate, in order to determine the influence of the transpiration stream rate on the distribution of the 9 elements to the shoot. Ten plants of each clone were placed various distances from a fan creating wind speeds of 0–0.8 m s^{-1}; this created differences in transpiration of 0.09–0.12 and 0.13–0.16 g m^{-2} d^{-1} for clones 4-2 and 31-1, respectively, by the plant shoot without the closing of the leaf stomata. The latter was confirmed by making casts of some test-plant leaves using nail polish, which was painted on the leaf surface, dried, pulled off, and then

studied under a microscope. The nutrient solution was replaced with the one containing the test elements after one day of acclimation under different wind speeds. The experiment was run for 72 hours. Plants and pots together were weighed at the beginning and end of the experiment to enable calculation of the transpiration rate. Furthermore, pots without plants were also weighed at the same times to enable measurement of evaporation from the pots, which then was subtracted from the transpiration data. Also, plants alone were weighed prior to and at the end of the experiment to enable calculation of the plant growth rate.

2.6 Harvest and analysis

Plants were harvested and the roots were cleaned in redistilled water and EDTA according to the method of /Landberg and Greger 1996/; the harvested plants were finally divided into root and shoot portions. This was also done with the control plants, which had been cultivated in parallel with the experimental plants but without addition of the nine elements. Plant materials were weighed to determine the fresh weight, dried at 45°C for 72 hours, and thereafter analysed for element content by SGAB Analytica AB (Luleå, Sweden) using ICP-SMS (analyses L0304516 and L0304517).

2.7 Calculations and statistical treatment

The concentration of elements in roots and shoots is presented in mg $kgDW^{-1}$ (it should be noted that the "dry weight" was measured at 45°C and is not a formal dry weight measured after treatment in an oven at 105°C). To determine the distribution of elements between shoot and root, and thereby measure the change in translocation according to treatment, the ratio between $[element]_{shoot}$: $[element]_{root}$ was calculated. The total accumulated elements in the entire plant at the end of the experiment were calculated according to formula (1) and related to the plant root dry weight:

$$\textbf{Total accumulated element} = \frac{\textbf{total amount of the element (µg)}}{\textbf{gDW root}} \quad (1)$$

Plant growth was calculated as the increase in fresh weight (FW) of the plant over 72 hours, according to formula (2):

$$\textbf{Growth, \% per day} = \frac{(W_{Tx} - W_{T0})}{W_{Tx}} \quad (2)$$

where W_{T0} and W_{Tx} are the weight at time zero and after 72 hours, respectively. Also, the relationship between dry and fresh weight was calculated (gDW : gFW) to determine whether the dry matter production of the plant had been influenced. Furthermore, to determine whether the distribution of dry mass between shoot and roots had been influenced, the shoot dry weight : root dry weight ratio was calculated.

To calculate transpiration over 72 hours, the following calculation was performed:

$$\textbf{Transpiration, g } H_2O\ d^{-1} = \frac{\textbf{WD – EV + GI}}{\textbf{days of experiment}} \quad (3)$$

where WD is the weight decrease of plants in pots, EV is evaporation (i.e. weight decrease of pots without plants), and GI is the growth increase over three days. Transpiration was also calculated in relation to the leaf area of the shoot, giving g H_2O $m^{-2}d^{-1}$. The leaf area was measured by copying the leaves using a photocopy machine, cutting out the paper leaves, weighing them, and relating the result to the known weight of the paper per cm^2.

The removal of an element (E) from the solution by the plant was estimated based on the assumption that the entire amount of the element contained in a given amount of water (with a specific element concentration) that had been taken up over three days had been removed from the solution according to the formula (4):

$$\text{µg E removed at T3} = \frac{\text{µg E at T0} \times \text{ml } H_2O \text{ taken up at T3}}{\text{ml } H_2O \text{ in pot at T0}} \quad (4)$$

where E is the element in question, and T0 and T3 are time zero and 72 hours, respectively. The removal of the element was also calculated based on the actual net element uptake by the plant from the pot over the three days (5):

$$\text{µg E removed at T3} = ([E]_{\text{plant at T3}} - [E]_{\text{control plant}}) \times \text{g plant in pot} \quad (5)$$

Element (E) net uptake, i.e. that had been taken up via roots and stayed in the plant during the experiment period (T3) of 3 days was calculated after had subtracting the background concentration of the element according to (6):

$$\text{Net uptake} = \frac{\text{µg E at T3 in shoot} + \text{µg E at T3 in roots}}{\text{gDW root at T3}} \quad (6)$$

and the translocation of the element(E) to the shoot of what has been taken up during the 3 days of experiment (T3) was calculated according to the formula (7):

$$\text{Translocation to the shoot} = \frac{\text{µg E at T3 in shoot}}{\text{µg E at T3 in shoot} + \text{µg E at T3 in roots}} \quad (7)$$

All experiments, except that of transpiration influence, were run in 3 and 4 replicates for the growth-rate influence and water-uptake influence experiments, respectively. In the transpiration-influence test, 10 points (i.e. different transpiration rates) were used per each regression line. The data were statistically tested using linear regression (where $r = \pm 0.600$, giving $p = 0.05$) with Excel 2001 (Microsoft). One-way ANOVA, the Student's t-test, and the Tukey-Kramer test were tested at the $\alpha = 0.05$ and $p = 0.05$ level using JMP 2.02 (SAS Institute Inc.).

3 Results

3.1 Uptake and distribution of the elements

The plants took up all nine elements (Table 3-1), and these were also translocated to the shoots, except for I in clone 4-2 in most cases (Figures 3-5, 3-11, and 3-15). The concentration of Mo, Cs, Th, La, and Cl was of the same order of magnitude as in the reference plant /Markert 1992, 1994/, while *Salix* seems to accumulate much less Ni, Sr, and I and much more Se than the reference plant does (Table 3-1). The concentration accumulated, however, greatly depended on the amount of the element supplied in the nutrient medium, and cannot be directly related to the reference plant per se.

Table 3-1. Concentration ranges of the various elements in shoots and roots (mg kgDW^{-1}), the shoot:root concentration ratio, and the total accumulated elements (mg in a whole plant [kgDWroot]$^{-1}$) from each of the three studies and clones. Also indicated are concentrations (mg kgDW^{-1}) of the elements in the photosynthetically active parts of the reference plant, according to /Markert 1992, 1994/.

	Ni	Sr	Mo	Cs	Th	La	Se	Cl	I
Reference plant conc.	1.5	50	0.5	0.2	0.005	0.2	0.02	2,000	3
Growth-rate influence study									
31-1									
Root conc.	0.8–2.1	2.5–4.0	9–24	0.3–1.2	1.35–2.67	0.87–2.06	0.8–1.0	1,985–4,323	1–2
Shoot conc.	0.2	1.1–3.4	0.3–1.4	0.1–0.2	0.001–0.003	0.03–0.19	0.2–0.5	978–1,160	0.14
Shoot:root	0.1–0.3	0.5–0.8	0 –0.1	0.2–0.6	0.001	0.03–0.08	0.2–0.5	0.3–0.6	0.1–0.2
Total acc.	1.5–3.5	9–23	11–32	1.3–2.1	1.5–2.7	1.1–3.2	1.9–3.5	5,348–10,104	1.8–2.8
4-2									
Root conc.	0.8–1.3	2.8–3.7	9–19	0.3–1.2	1.35–2.67	0.87–2.10	0.8–0.9	2,415–4,393	0.4–1.1
Shoot conc.	0.1–0.4	1.3–3.6	0.4–1.8	0.1	0.002	0.02–0.17	0.2–0.4	617–1,155	0–0.1
Shoot:root	0.1–0.3	0.5–1.0	0–0.1	0.2–0.7	0.001	0.02–0.09	0.2–0.8	0.3	0–0.1
Total acc.	1.4–3.9	11–26	11–30	0.9–2.0	1.6–2.1	1.2–2.9	2.0–3.0	6,211–11,107	0.6–1.5
Water-uptake influence study									
31-1									
Root conc.	0.8–1.3	2.5–2.8	8.7–11.1	0.2–1.2	0.24–1.35	0.72–1.16	0.8–1.0	1,985–3,493	0.4–1.0
Shoot conc.	0.1–0.2	0.9–1.5	0.3–0.4	0–0.1	0.002–0.003	0.01–0.03	0.1–0.2	938–1,160	0.1
Shoot:root	0.1–0.3	0.4–0.6	0.03	0.2–0.4	0.002–0.008	0.01–0.03	0.2–0.3	0.3–0.6	0–0.2
Total acc.	1.5–2.3	6–12	11–13	0.3–2.1	0.2–1.5	0.7–1.3	1.2–2.3	5,348–9,144	0.4–1.8
4-2									
Root conc.	0.8–1.1	2.4–2.8	8.7–9.1	0.1–1.3	0.33–1.61	0.70–1.11	0.5–0.9	2,415–3,540	0.3–1.1
Shoot conc.	0.1–0.1	1.0–1.3	0.3–0.4	0–0.1	0.001–0.003	0.01–0.02	0.1–0.2	617–857	0–0.1
Shoot:root	0.1–0.1	0.4–0.5	0.04	0.2–0.4	0.001–0.004	0.01–0.02	0.2	0.3–0.4	0–0.1
Total acc.	1.3–1.8	7–11	10–11	0.3–2.0	0.3–1.6	0.8–1.2	1.1–2.0	6,211–8,126	0.3–1.5
Transpiration-influence study									
31-1									
Root conc.	0.4–1.1	2.0–2.9	4–14	0.5–2.8	0.8–2.8	0.5–1.5	0.4–1.0	1,310–4,100	0.7–1.7
Shoot conc.	0.1–0.1	0.8–1.2	0.2–0.3	0.1	0.001–0.002	0.01–0.02	0.1–0.2	410–1,220	0–0.1
Shoot:root	0.1–0.3	0.3–0.4	0–0.1	0–0.2	0–0.002	0.01–0.03	0.2–0.4	0.1–0.7	0–0.1
Total acc.	0.6–1.5	5–11	6–15	1.0–3.6	0.9–2.8	0.6–1.6	0.9–2.5	3,000–11,700	0.7–2.3
4-2									
Root conc.	0.9–1.0	1.7–3.1	4–10	0.2–0.5	1.0–4.2	0.2–1.7	0.3–1.5	1,470–3,460	0.3–1.4
Shoot conc.	0.0–0.1	0.7–0.9	0.2–0.3	0.1	0.001–0.004	0.01–0.02	0.1–0.2	440–1,650	0–0.1
Shoot:root	0.1–0.3	0.3–0.5	0–0.1	0.2–0.5	0–0.001	0.01–0.03	0.1–0.4	0.2–1.1	0–0.2
Total acc.	0.4–2.1	5.7–9.6	6–15	0.5–1.1	1.0–4.2	0.3–1.8	0.8–3.0	4,800–9,900	0.6–1.6

The concentrations of the various elements in the plants differed between elements and plant part (Table 3-2). The highest total accumulated level was found for Cl, which was higher than those of Sr and Mo, which in turn were higher than those of Ni, Cs, Th, La, I, and Se. The high concentration of Cl was probably because much more Cl than any of the other elements was added to the solution. Except in some cases, the roots always had a higher Cl concentration than the shoots, thus the shoot:root ratio was lower than 1. The lowest distribution of an element to the shoots was that of Th; it was approximately 10 times higher for La and approximately 100 times higher for the other elements.

Differences between the two clones could not generally be found, except in a few specific cases (Table 3-1). In the study of water-uptake influence, the concentration of Cl in the shoots of 4-2 was found to be significantly less than in the shoots of 31-1. In the growth-rate influence study, the total accumulated I, and thus also the concentration in roots and the shoot:root concentration ratio, was significantly less in 4-2 than in 31-1. A similar trend was found for Cs in the transpiration-influence study.

The uptake of the various elements from the nutrient solution was estimated to run parallel to the uptake of water. Thus, the amount of Ni initially added was 2.935 µg 1,000 ml^{-1} solution, and since 400 ml of solution was taken up over 3 days, the estimated amount of Ni removed from the solution should be 1.174 µg. This was, however, not the case: much less Ni was actually taken up, 0.118 and 0.309 for 31:1 and 4:2, respectively, meaning that the solution after uptake would have a higher concentration of Ni than at start of the experiment. This was the case for all elements (Figure 3-1). This means that 18, 16, 40, 26, 26, 16, 58, 34, and 16% of the estimated uptake was actually taken up in the case of Ni, Sr, Mo, Cs, Th, La, Se, Cl, and I, respectively. The concentration in the solution therefore increased by 1.3 to 1.6 times.

Table 3-2. Concentration range of the various elements in shoots and roots, the shoot: root concentration ratio, and the total accumulated elements in all studies and clones in this investigation. The total amounts of the elements added are also indicated.

Element	Concentration, mg $kgDW^{-1}$		Shoot:root concentration	Total accumulated	Added concentration	
	Shoot	Root	ratio	mg $(kgDW_{root})^{-1}$	µmol L^{-1}	µg L^{-1}
Ni	0–0.4	0.4–2.1	0.1–0.3	0.4–3.9	0.05	2.94
Sr	0.7–3.6	1.7–4.0	0.3–1.0	5–26	0.05	4.38
Mo	0.2–1.8	4–24	0–0.1	6–32	0.06	6.04
Cs	0–0.2	0.1–2.8	0–0.7	0.3–3.6	0.05	6.65
Th	0.001–0.004	0.2–4.2	0–0.008	0.2–4.2	0.05	11.60
La	0.01–0.19	0.2–2.1	0.01–0.09	0.3–3.2	0.05	6.95
Se	0.1–0.5	0.3–1.5	0.1–0.8	0.8–3.5	0.05	3.95
Cl	410–1,650	1,310–4,393	0.1–1.1	3,000–11,700	18.10	647.00
I	0–0.14	0.3–2.0	0–0.2	0.3–2.8	0.05	6.45

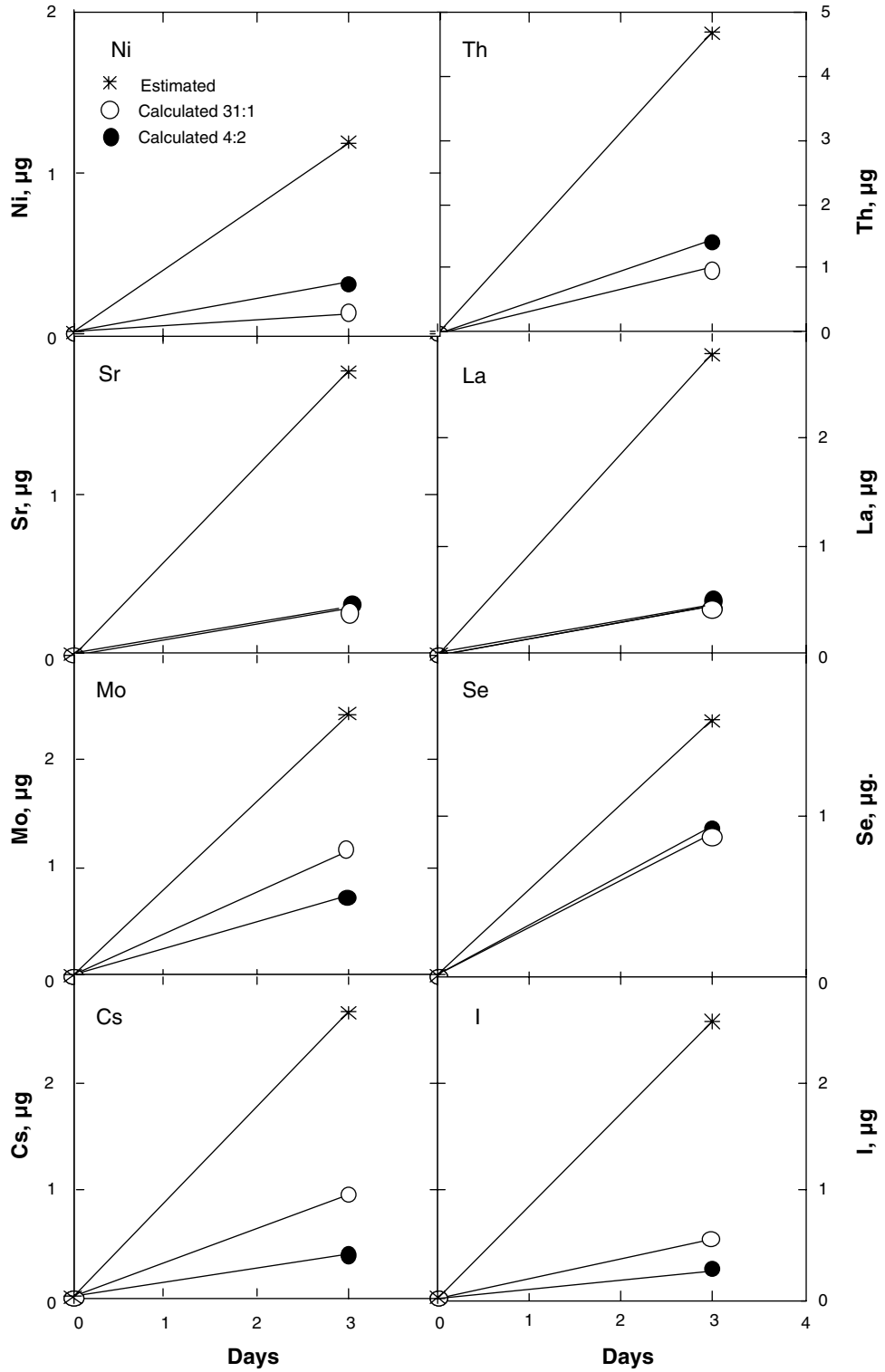

Figure 3-1. *Estimated element uptake, i.e. passive and following the water uptake, and calculated actual uptake from the solution by two Salix clones over 3 days.*

3.2 Influence of water uptake on element uptake

Plants were grown in different concentrations of PEG to decrease the water uptake, thereby enabling us to study the influence of water uptake on element uptake. The water uptake decrease also decreased the transpiration rate in both clones by approximately a factor of 4 with addition of 16% PEG (Figure 3-2). Since the water content in the plants in all cases was 82% ± 2% (SE) and did not change with PEG treatments, the change in water uptake rate was estimated to decrease in line with the transpiration rate, i.e. by a factor of 4 with 16% PEG (Figure 3-2). These findings were also shown previously (Ekvall and Greger unpublished results). Plant growth was not affected by the diminished water-uptake rate; however, the highest PEG concentration completely eliminated growth in plants (Figure 3-3a, b), likely due to depressed photosynthetic activity. Since the water uptake decreased with increasing PEG concentration, the gDW:gFW ratio could have been increased due to lower water levels in the tissue. However, no difference in the water content of the plants was found. Instead, this ratio could have decreased due to diminished photosynthetic activity, i.e. production of the building blocks of growth, and this was the case in clone 4-2 but was only as a tendency in the other clone (Figure 3-3c). The shoot:root dry weight ratio decreased with increasing PEG concentration, indicating that shoot growth was more depressed, at least at the highest PEG concentration (Figure 3-3d). However, the plant weight (DW) was not changed by PEG treatment (Figure 3-3a).

The water uptake influences the uptake (i.e. total accumulation) of Ni, Sr, Cs, Th, La, Se, and I, but not that of Mo and Cl (Figures 3-4 to 3-6). The uptake of elements decreased progressively with decreasing water uptake in the case of clone 4-2 for Ni, La, and Sr and in both clones for Cs, Th, and I. In clone 31-1 for Ni, La, and Sr and in both clones for Se only the very lowest water uptake level decreased the uptake of these elements. The concentration of Ni and Cs in the shoots in both clones, of Sr and La in clone 4-2, and of I in clone 31-1 decreased with decreasing water uptake. Only at the lowest water uptake did the concentration of La in the shoots in clone 31-1 and of Se in both clones decrease. In the shoots, I was detected in clone 31-1 and only at the highest water-uptake rate in clone 4-2. The concentration of Ni in the roots increased, while that of Cs, Th, and I decreased with decreasing water-uptake rate. The shoot:root concentration ratio decreased for Ni and I, whereas it increased for Th.

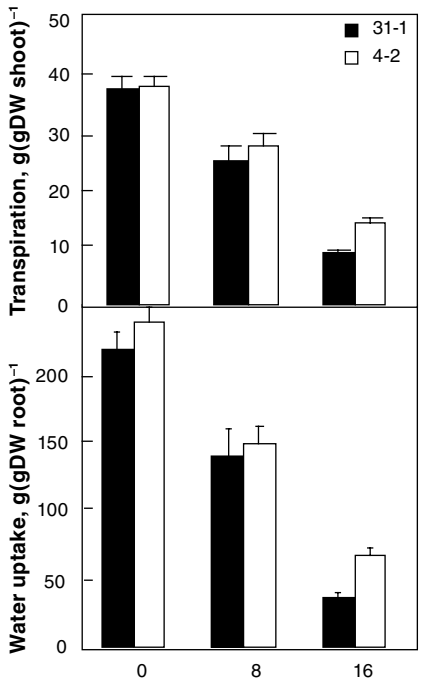

Figure 3-2. *Influence of water uptake (PEG treatment) on transpiration (upper) and water uptake (lower) of two Salix clones over 3 days.*

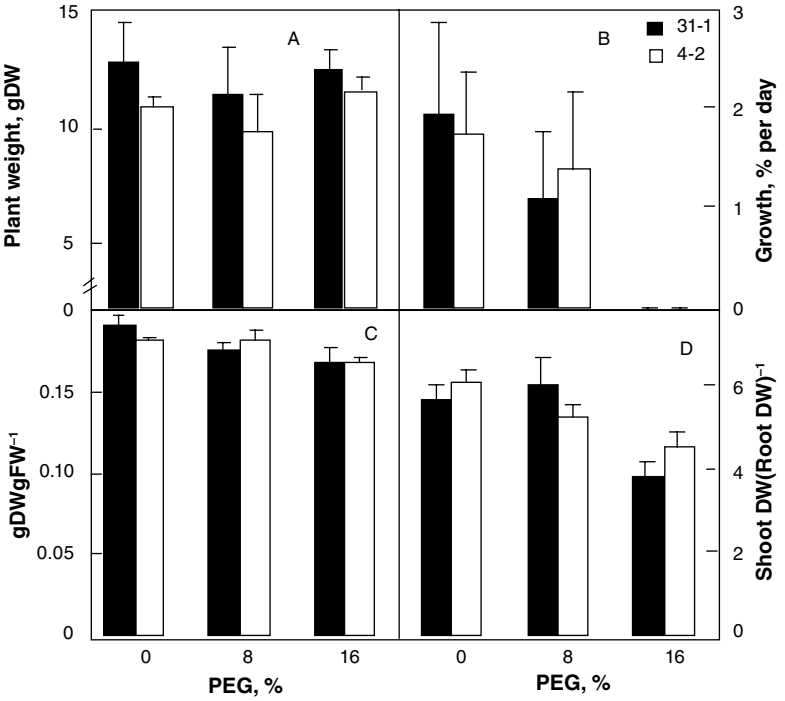

Figure 3-3. *Influence of water uptake (PEG treatment) on plant weight (A), growth rate (B), DW:FW ratio (C) and shoot:root ratio (D) of two Salix clones over 3 days.*

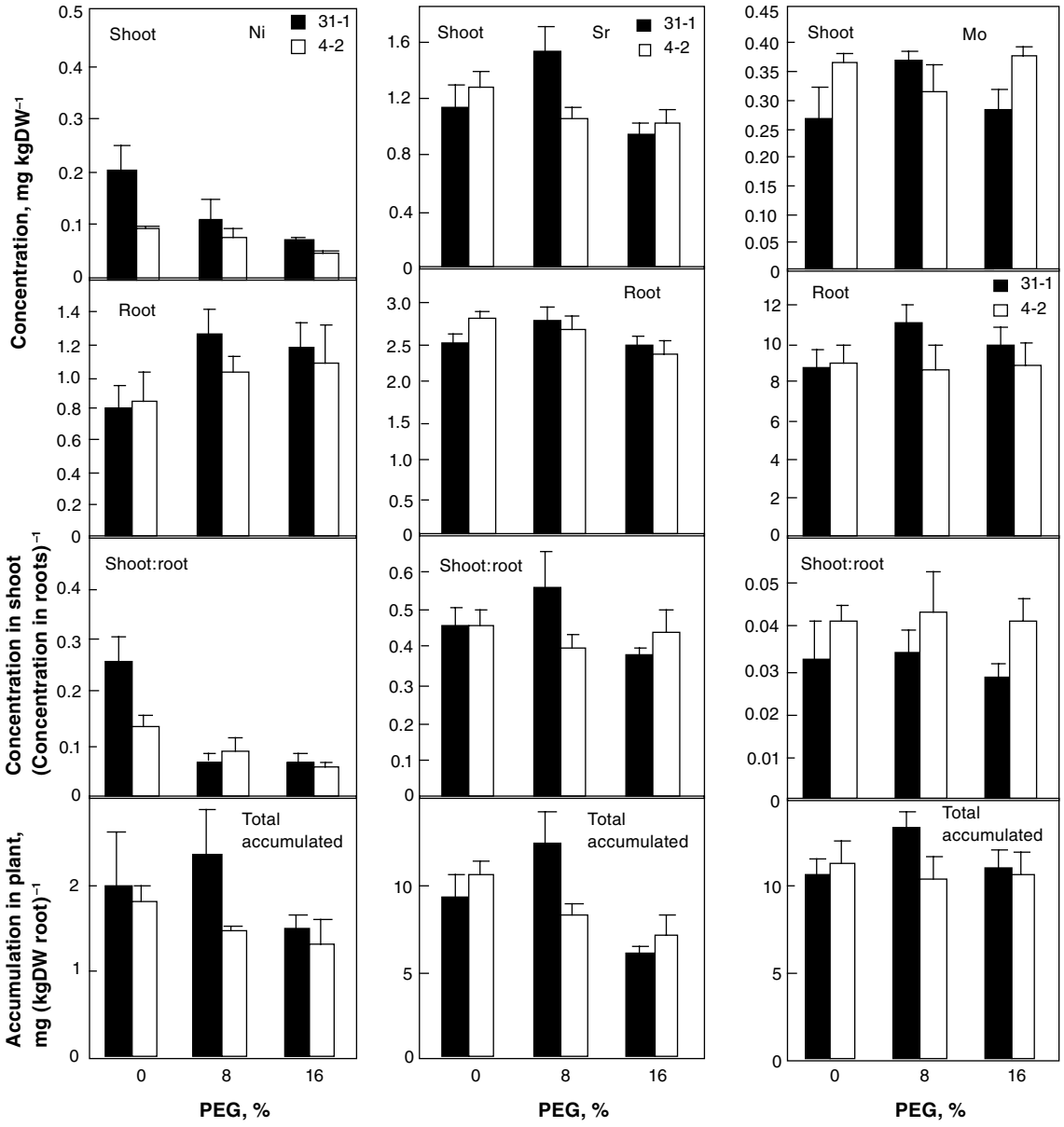

Figure 3-4. *Influence of water uptake (PEG treatment) on total accumulation, concentration in roots and shoot and distribution to shoot of Ni, Sr and Mo in two Salix clones over 3 days.*

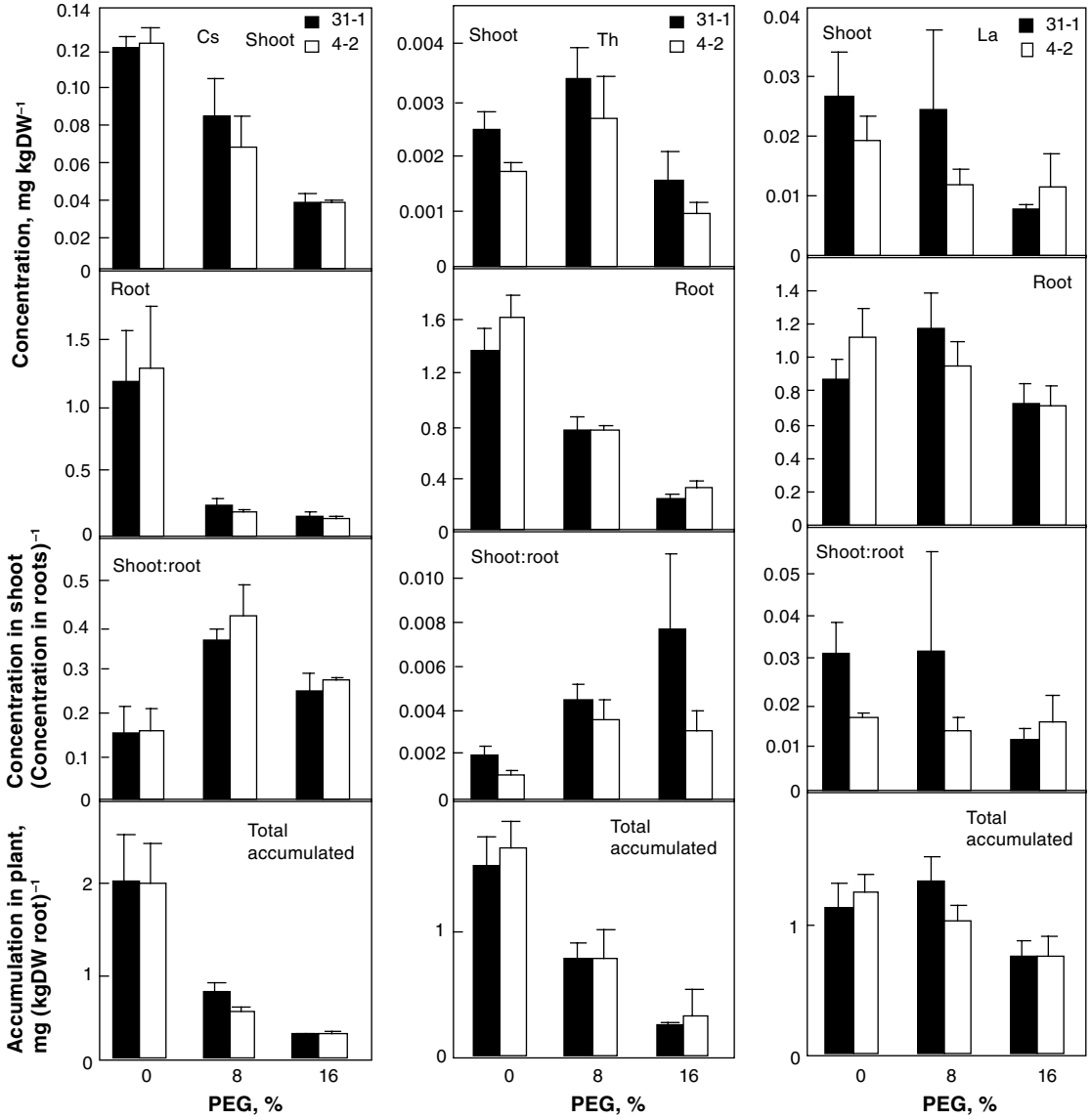

Figure 3-5. *Influence of water uptake (PEG treatment) on total accumulation, concentration in roots and shoot and distribution to shoot of Cs, Th, and La in two Salix clones over 3 days.*

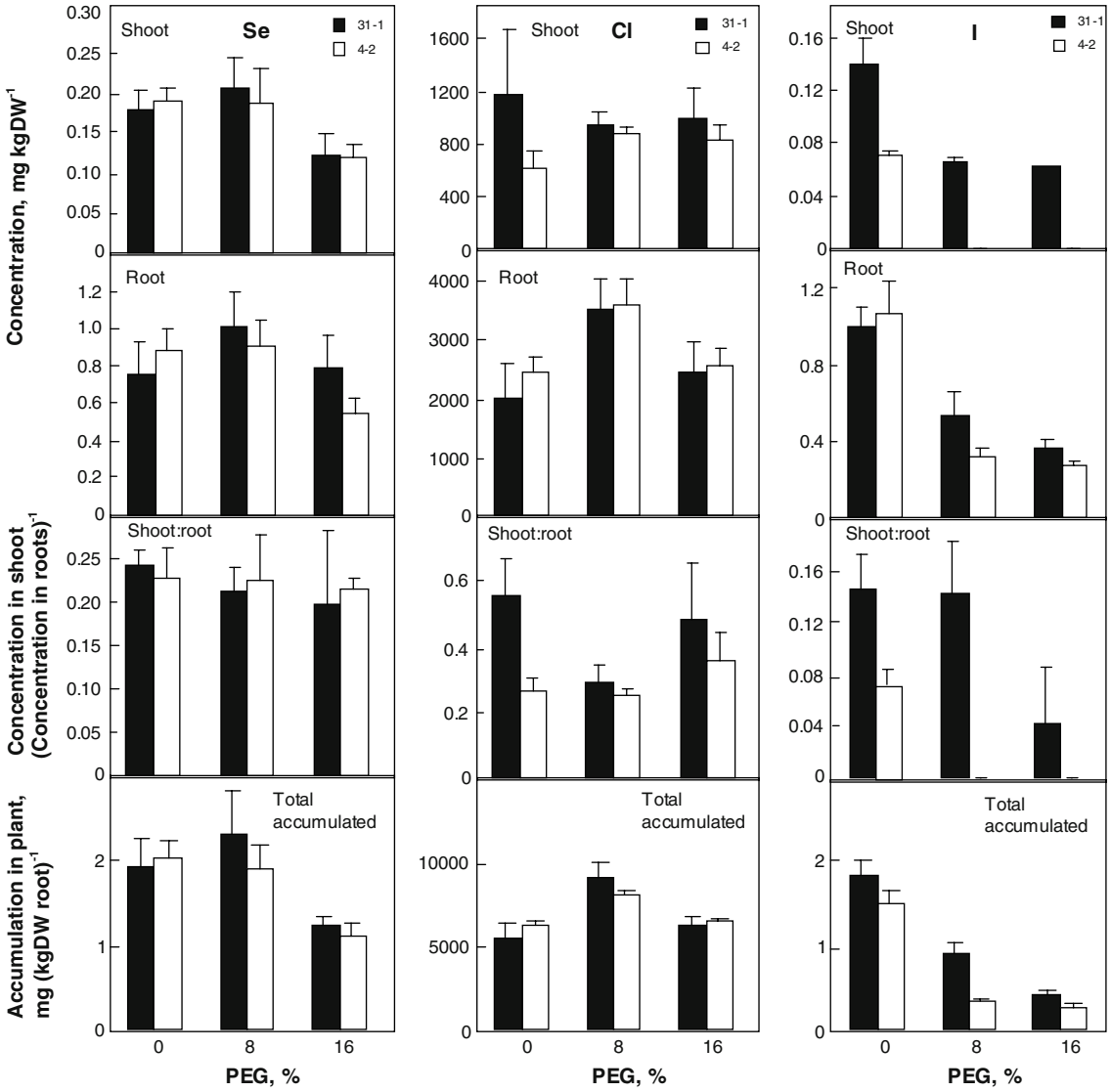

Figure 3-6. *Influence of water uptake (PEG treatment) on total accumulation, concentration in roots and shoot and distribution to shoot of Se, Cl, and I in two Salix clones over 3 days.*

3.3 Influence of transpiration rate on element uptake

In the transpiration study no difference was found in terms of growth between clones 31-1 and 4-2, for which the growth rates (g d^{-1}) were 2.49 ± 0.76 (SE) and 2.12 ± 0.14, respectively. The growth rate did, however, decrease with increasing transpiration rate (Figure 3-7), while there was no difference in growth between roots and shoots (Figure 3-8). The total leaf surface of the plant was positively related to the transpiration, and it was obvious that clone 4-2 had a lower transpiration rate since this clone had a smaller total leaf area than 31-1 had (Figure 3-9). The water uptake was not influenced by the transpiration rate (Figure 3-10).

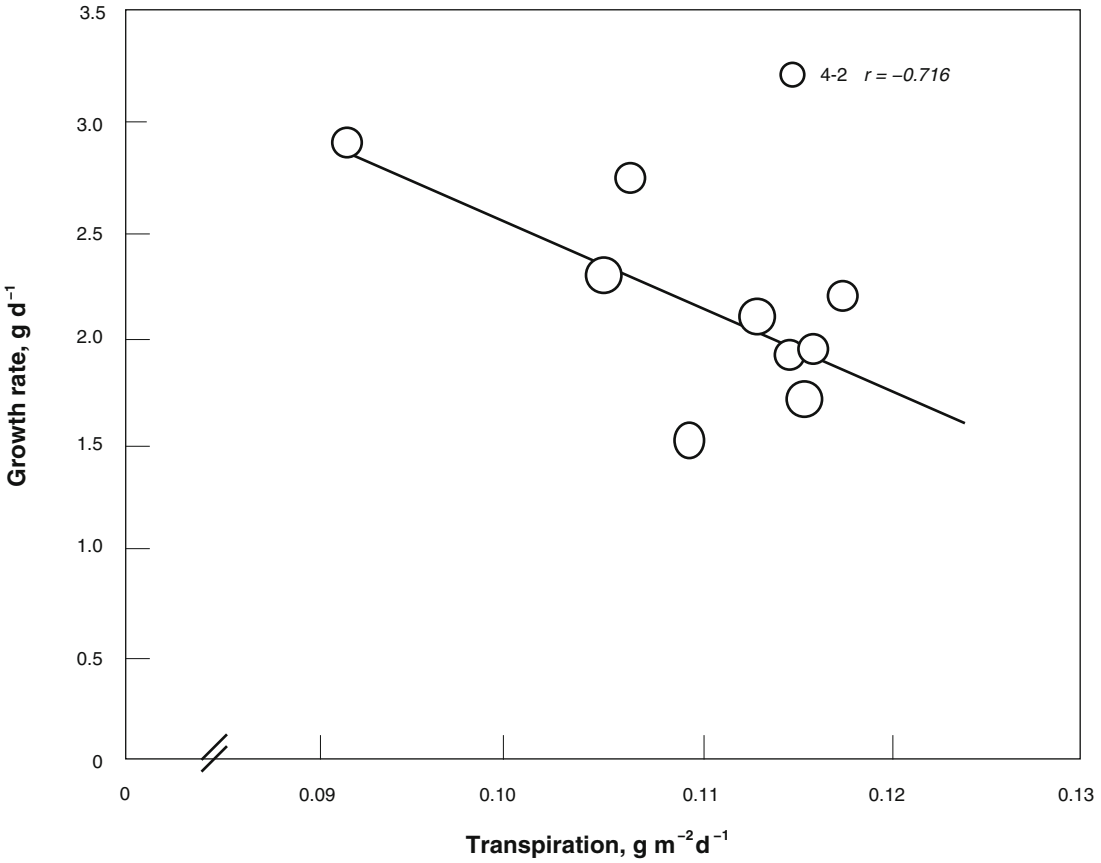

Figure 3-7. *Influence of transpiration rate on growth rate of two Salix clones over 3 days.*

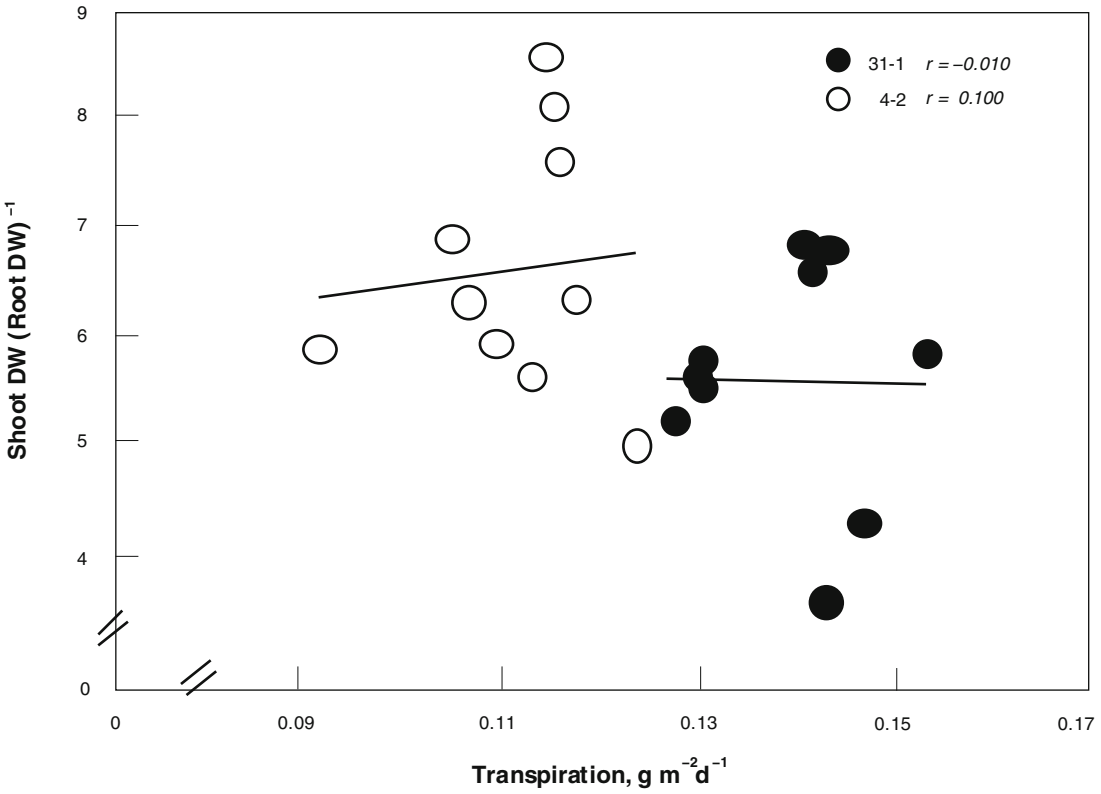

Figure 3-8. *Influence of transpiration rate on shoot:root ratio of two Salix clones over 3 days.*

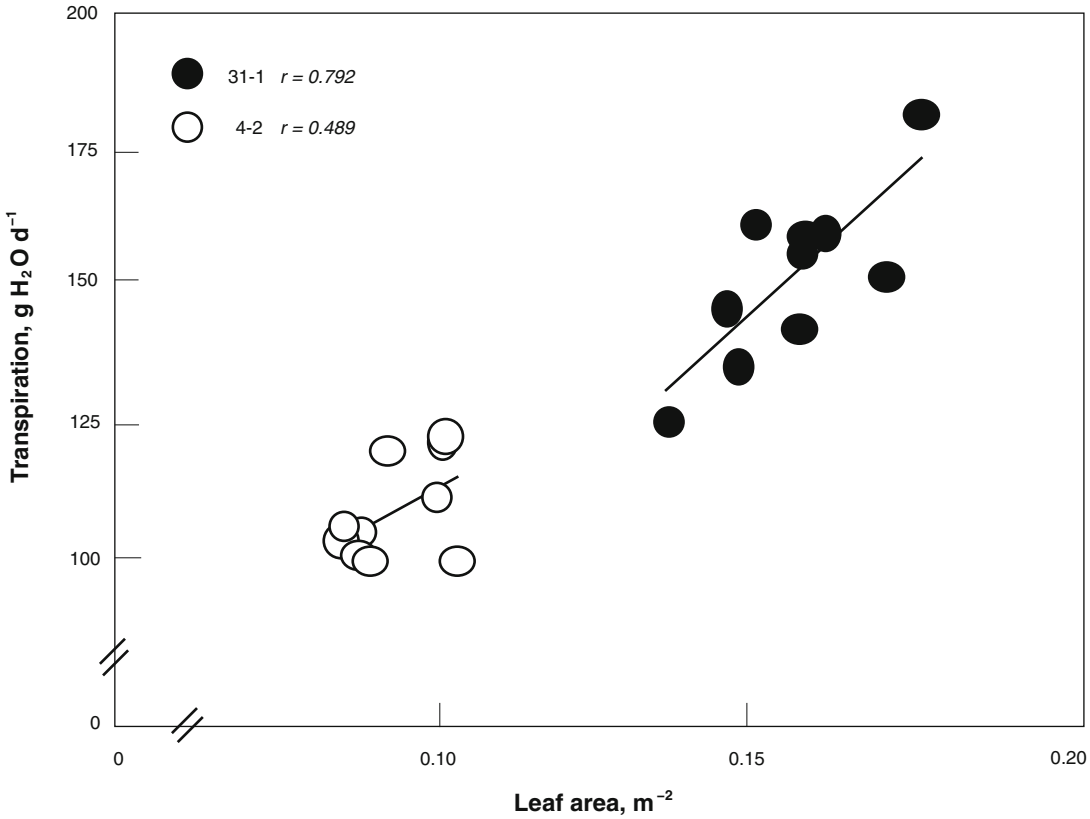

Figure 3-9. *Influence of leaf area on the transpiration rate of two Salix clones during 3 days.*

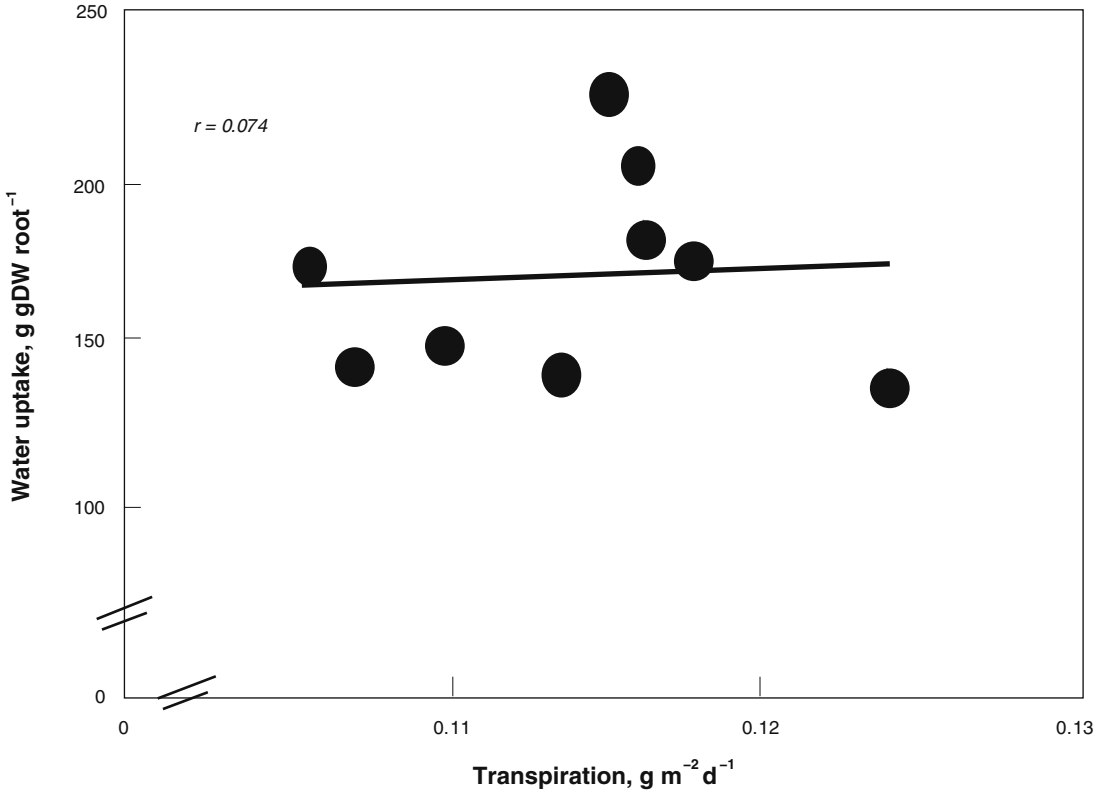

Figure 3-10. *Influence of transpiration rate on water uptake.*

The transpiration rate influenced the total accumulation, concentration in roots and shoots, and shoot:root concentration ratio differently depending on the element. A significant influence was found only in the case of Mo, where total accumulation decreased with increasing transpiration rate (Figures 3-11 to 3-13); similar *tendencies* were, however, found for Sr, Th, La, and I (clone 31-1). I was found in only a few samples of clone 4-2, independently of transpiration rate. The relationship between transpiration rate and concentration in roots was significantly negative for Mo, and the similar tendency was found for La, Se, Cl, Sr and Th. The transpiration rate significantly decreased Sr concentration in shoots. Similarly, an insignificant negative trend was found in the case of Mo, while insignificant increases were found for Se and Ni. When dealing with the shoot:root concentration ratio it is obvious that in the significant cases (i.e. La and Se), as well as in those with strong tendencies (i.e. Ni and Cs for clone 4-2, and Mo), the ratio increases with increasing transpiration rate. One exception to this strong tendency was a decrease in the Cs shoot:root ratio with increasing transpiration in clone 31-1.

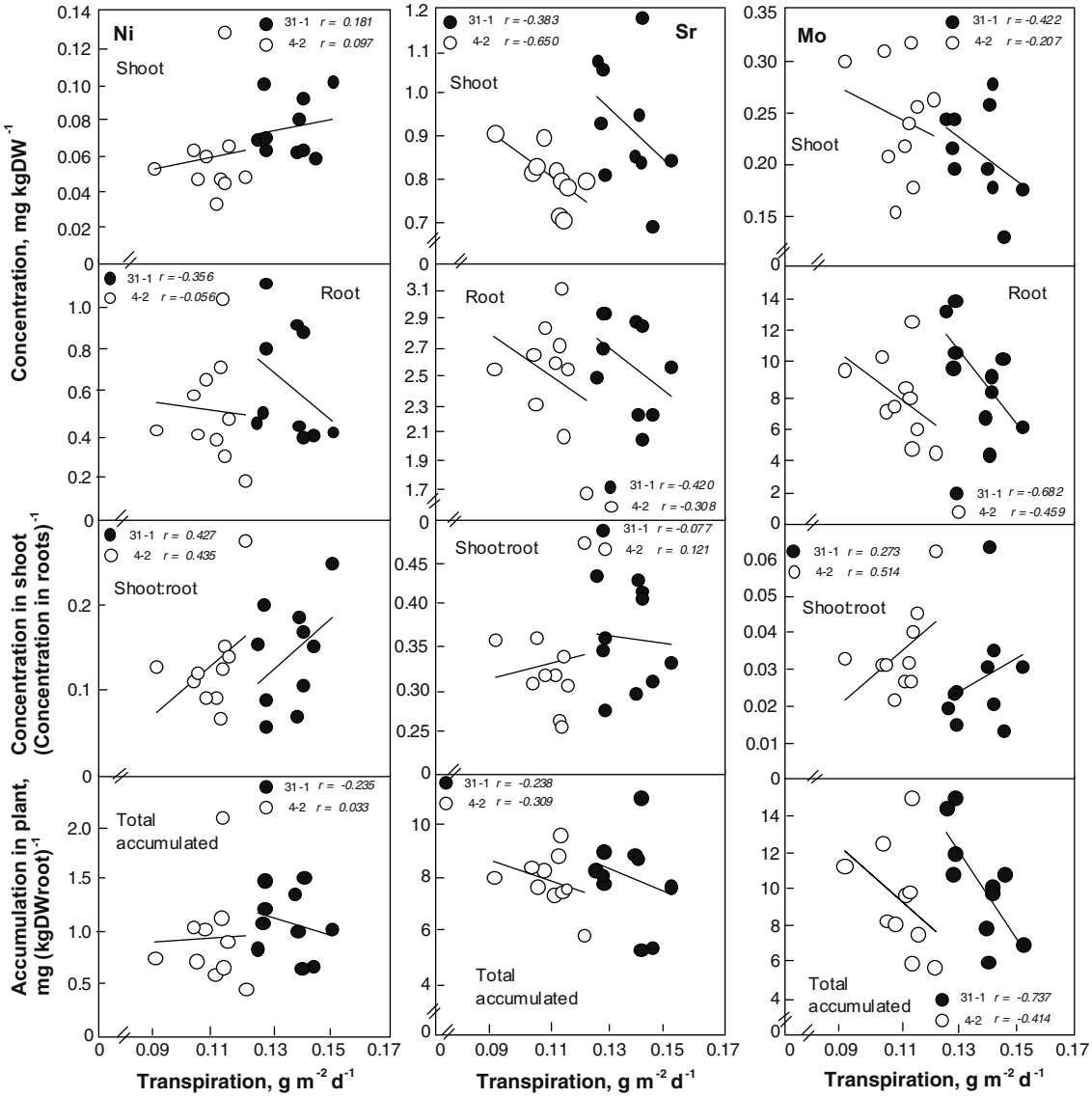

Figure 3-11. *Influence of transpiration rate on total accumulation, concentration in roots and shoots and distribution to shoot of Ni, Sr, and Mo in two Salix clones over 3 days.*

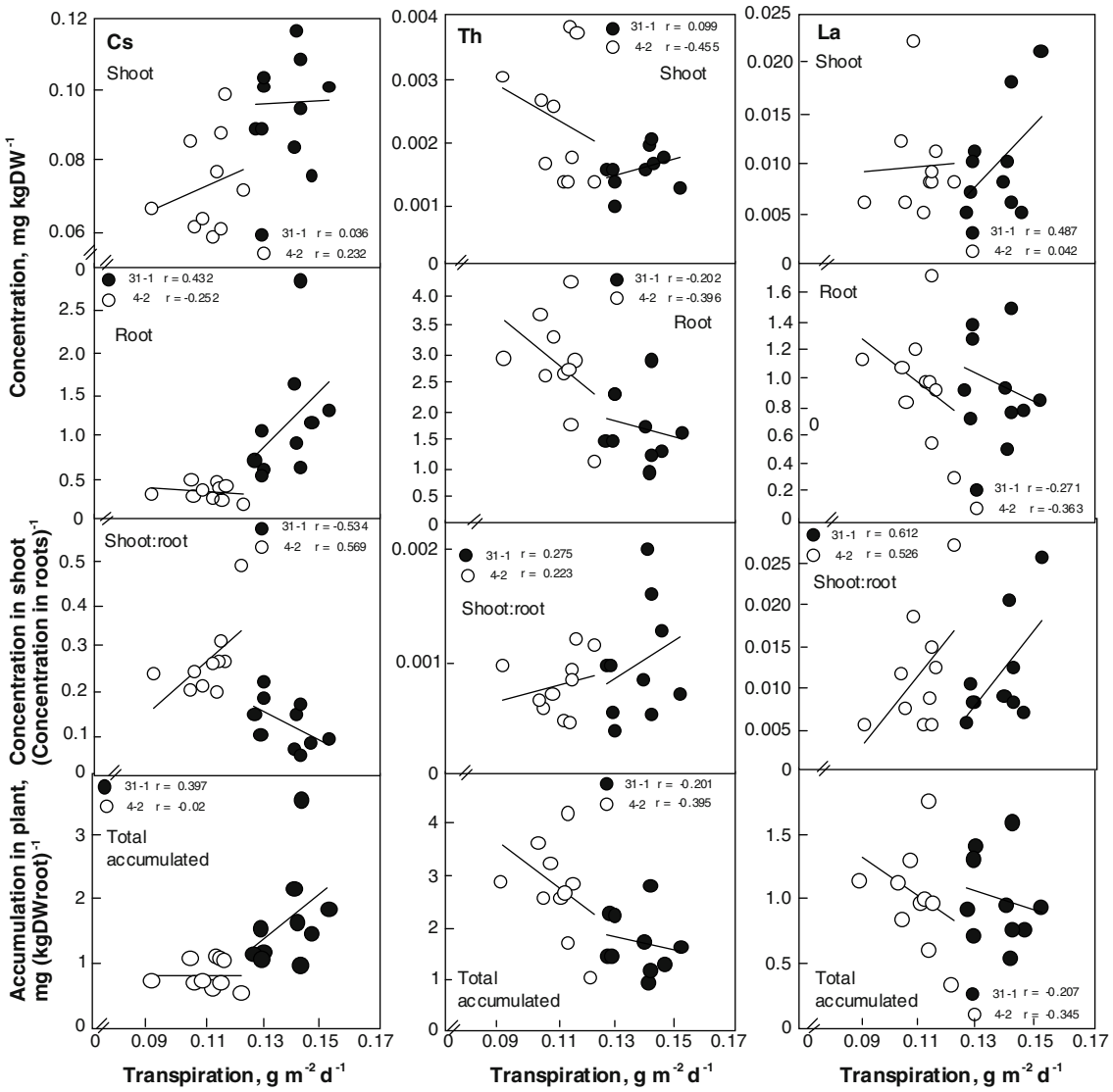

Figure 3-12. *Influence of transpiration rate on total accumulation, concentration in roots and shoots and distribution to shoot of Cs, Th, and La in two Salix clones over 3 days.*

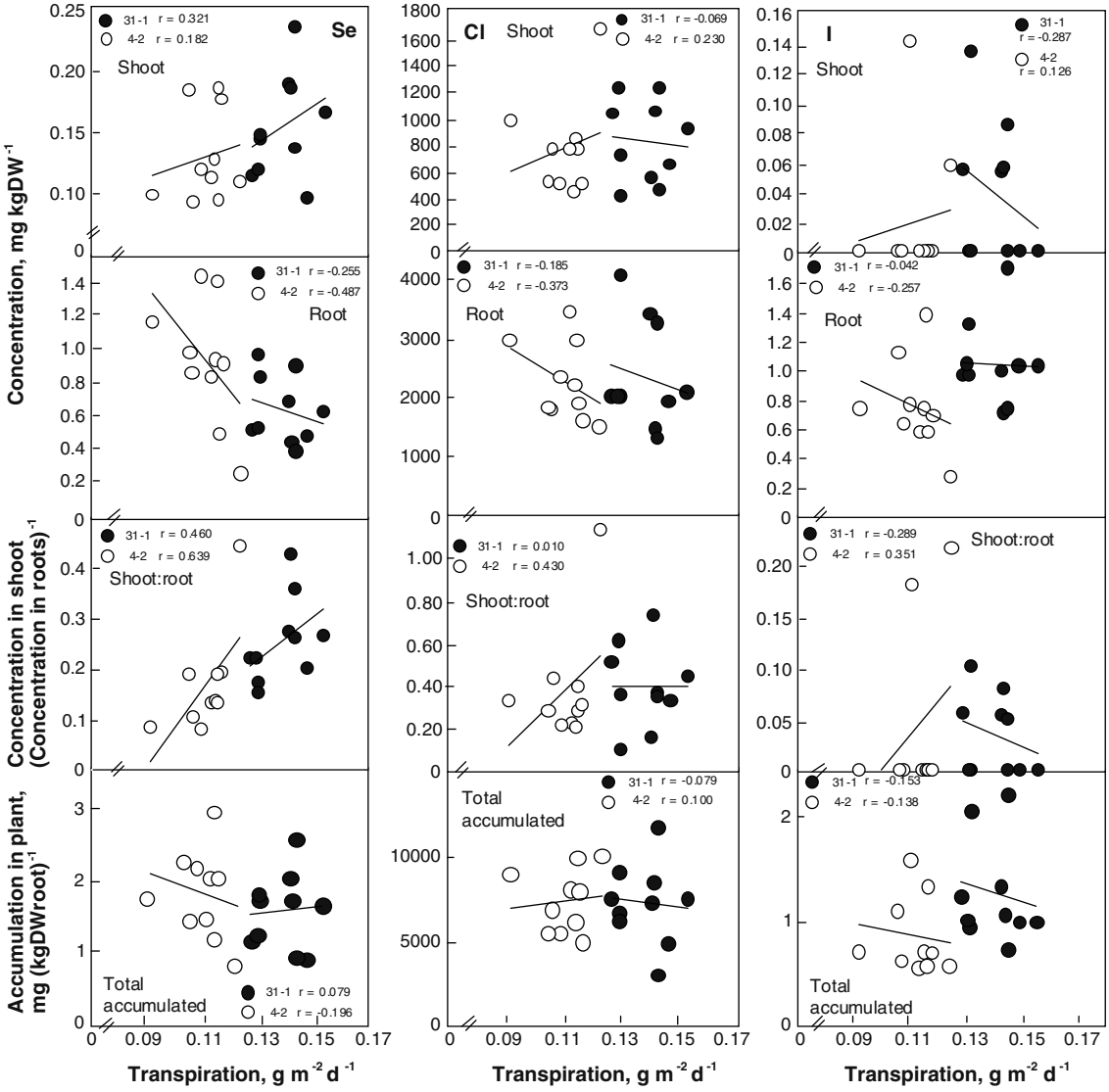

Figure 3-13. *Influence of transpiration rate on total accumulation, concentration in root and shoot and distribution to shoot of Se, Cl, and I in two Salix clones over 3 days.*

3.4 Influence of growth on element uptake

The low and high growth rates (i.e. biomass production) were approximately 0.5 and 1.75% per day, respectively, and the low and high plant weights similarly differed by a factor of approximately 3 (Figure 3-14a, b). The DW:FW ratio increased 1.5 times with increased biomass production, due to higher production of dry matter at the higher light intensity giving higher biomass production (Figure 3-14c). The shoot:root dry weight ratio, however, did not differ (Figure 3-14d). In none of the mentioned cases were differences detected between the clone types (Figure 3-14).

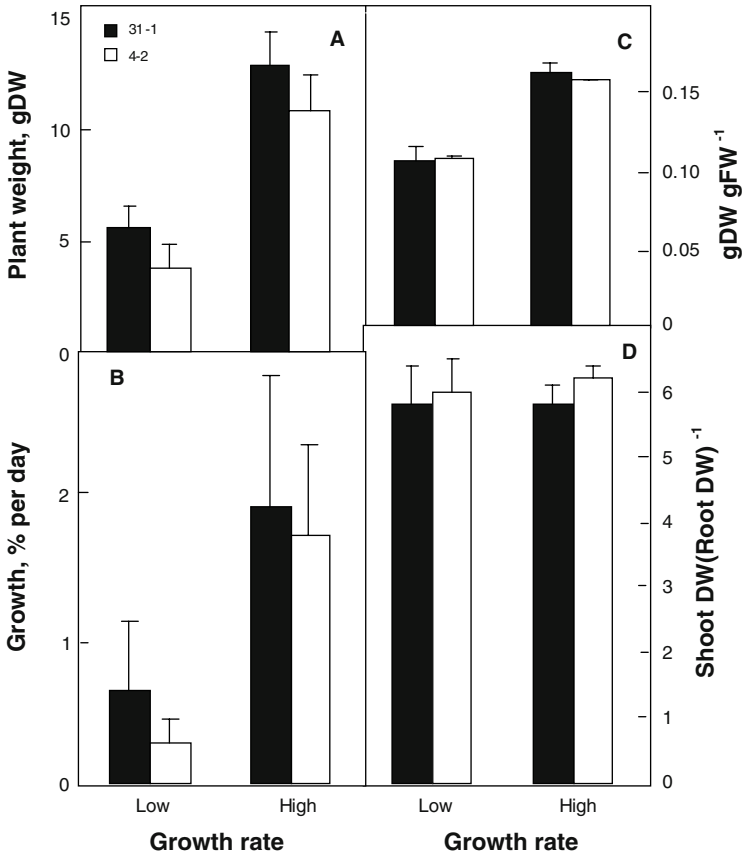

Figure 3-14. *Influence of growth rate on plant weight, growth rate, DW:FW ratio and shoot:root ratio in two Salix clones over 3 days.*

The accumulation of elements decreased with increased biomass production, significantly for Ni, Sr, Mo, and Cl, and insignificantly for Se, I (clone 31-1), La, and Th (Figures 3-15 to 3-17). In the case of Cs and I (clone 4-2) there was a tendency to increase; however, the low growth rate prevented the uptake of I in clone 4-2. The concentration of the elements in the roots showed nearly the same trend, i.e. a significant decrease of Ni, Sr, Mo, Th (clone 31-1), and Cl, and an insignificant decrease for La, Th (clone 4-2), and I (clone 31-1) with increased biomass production. A tendency to increase with increasing biomass was found for Cs, Se (clone 4-2), and I (clone 4-2). The concentration of Ni (clone 4-2), Sr, Mo, Cs (clone 31-1), I (clone 4-2), and Se in shoots significantly decreased with increasing rate of biomass production, while only insignificantly decreasing for La, Cl, and Th (clone 4-2). The concentration of Th (clone 31-1) insignificantly increased with increasing biomass production rate. Finally, the shoot:root concentration ratio significantly decreased for Mo, Sr, Cs, and Se, a similar trend being found for La. The ratio significantly increased in clone 31-1 for Ni and Th, and in both clones for I, while insignificantly increasing for Cl (clone 31-1).

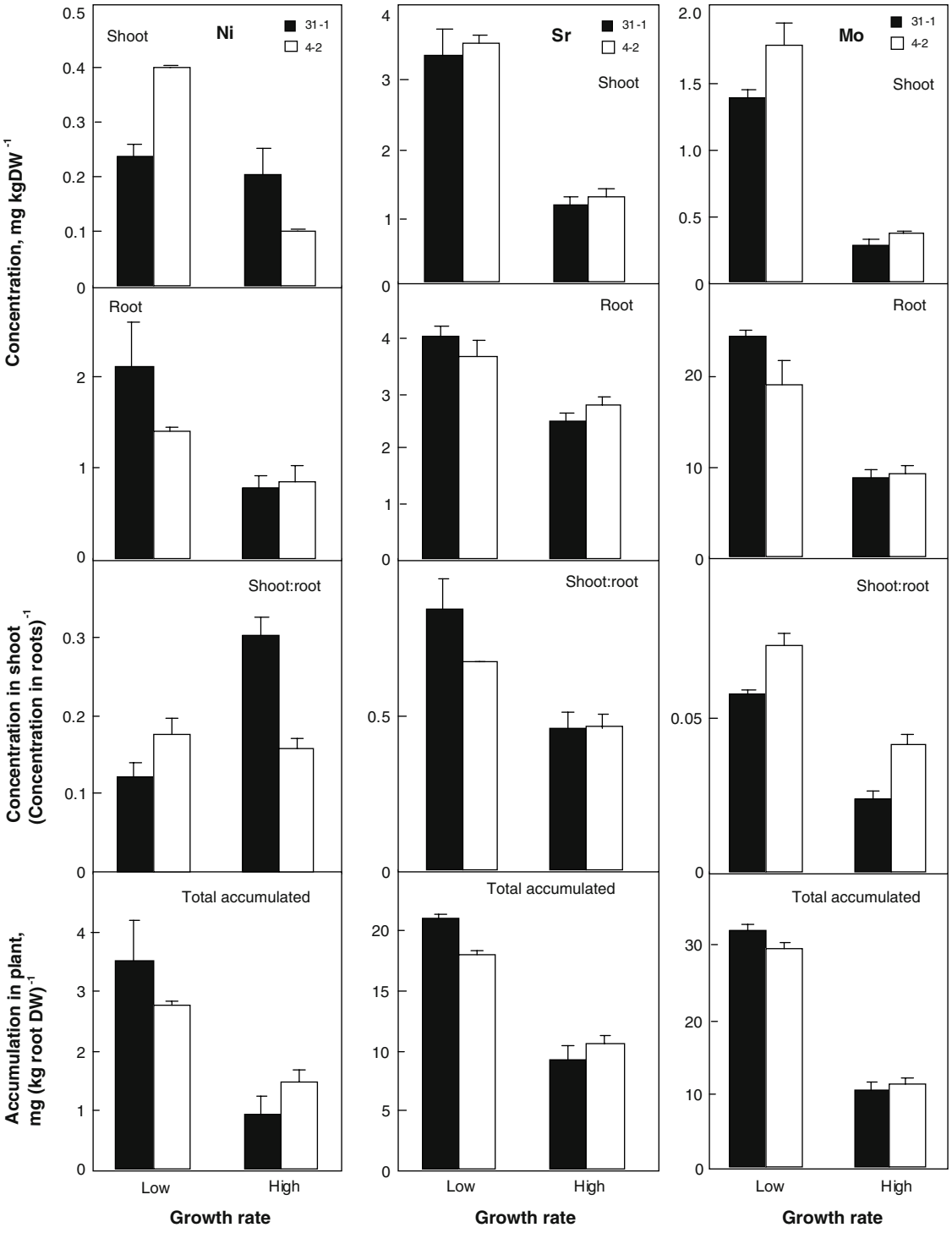

Figure 3-15. *Influence of growth rate on total accumulation, concentration in roots and shoots and distribution to shoot of Ni, Sr, and Mo in two Salix clones over 3 days.*

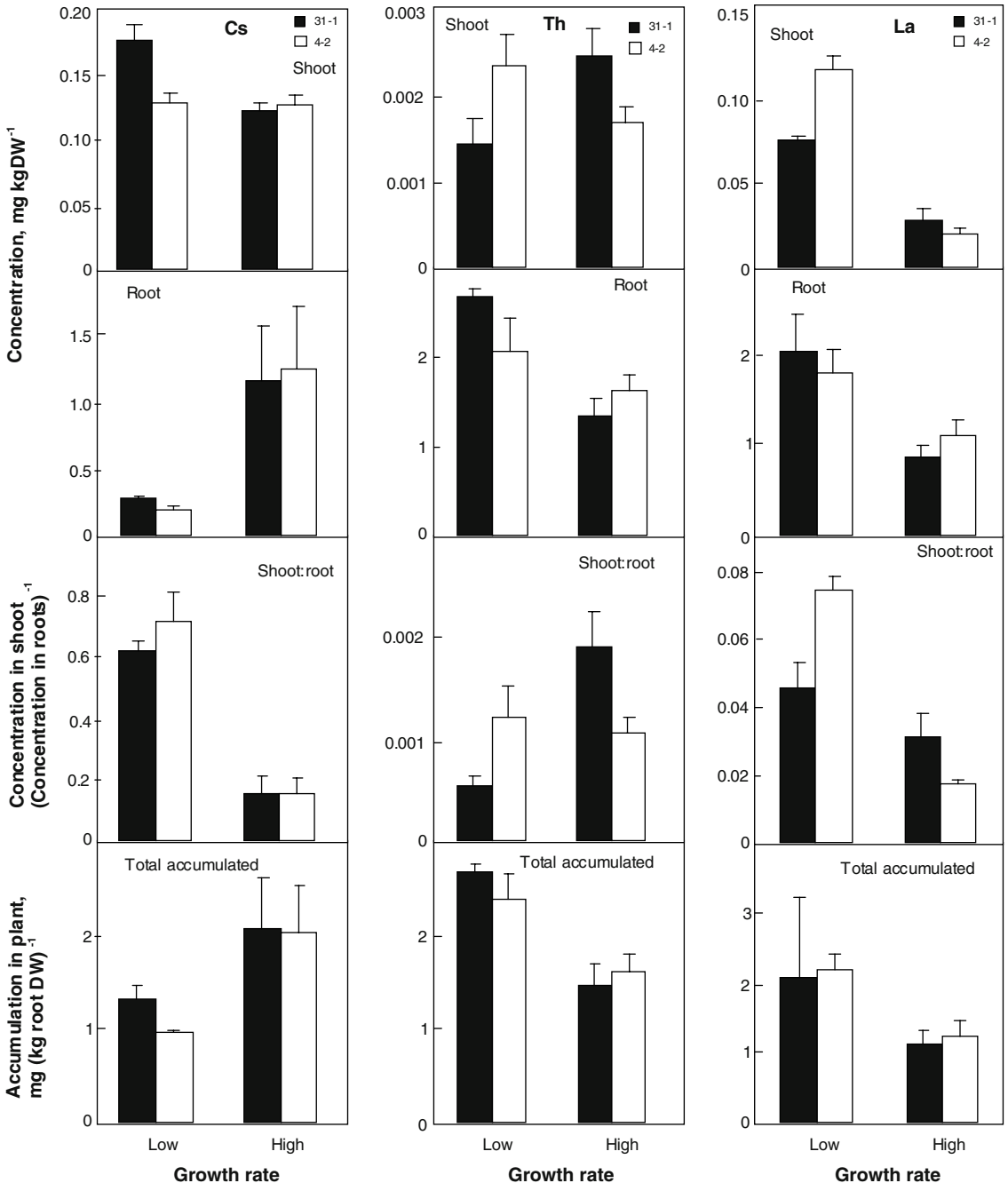

Figure 3-16. *Influence of growth rate on total accumulation, concentration in roots and shoots and distribution to shoot of Cs, Th, and La in two Salix clones over 3 days.*

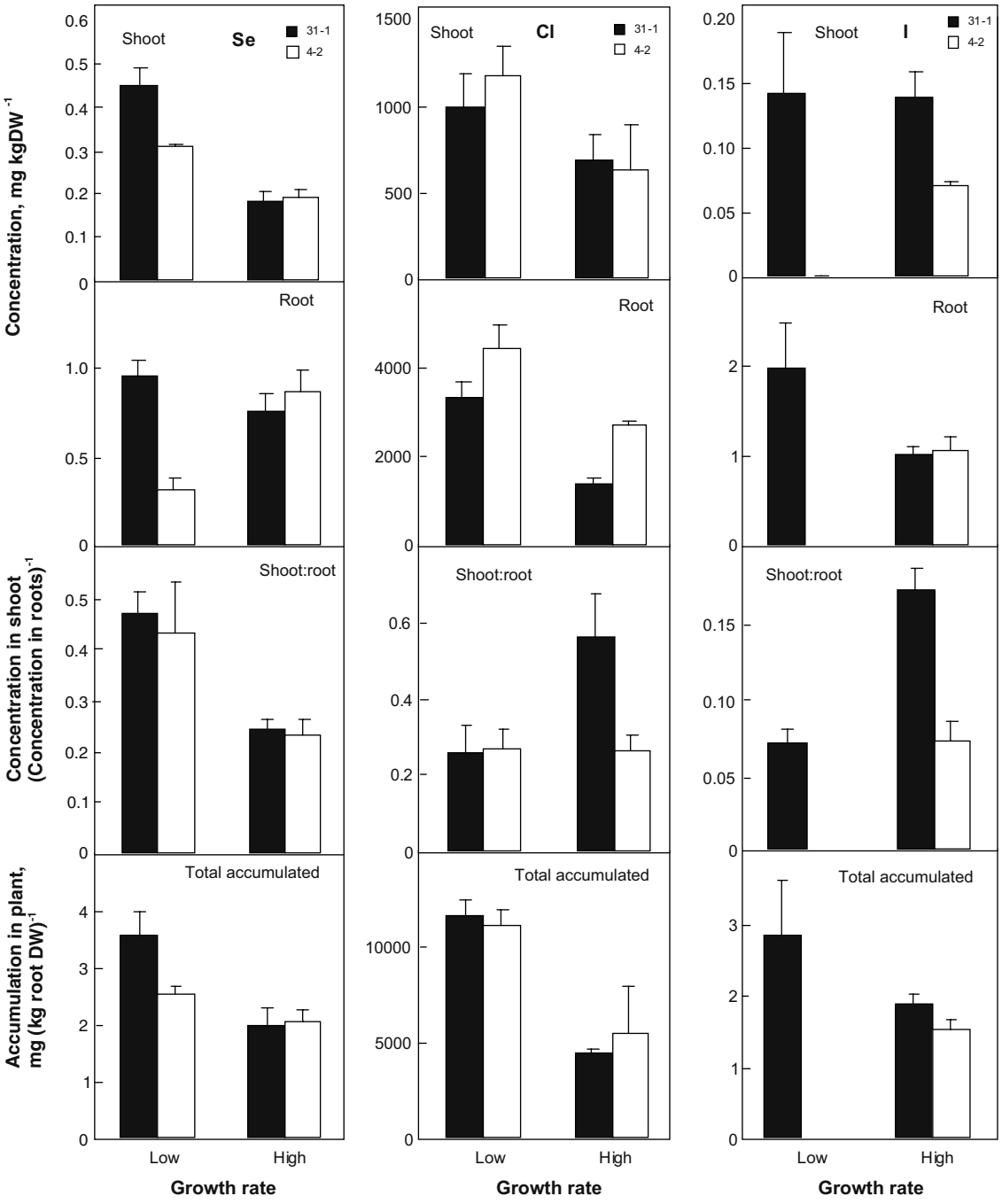

Figure 3-17. *Influence of growth rate on total accumulation, concentration in roots and shoots and distribution to shoot of Se, Cl, and I in two Salix clones over 3 days.*

3.5 Influence of growth and water relations on element net uptake

The uptake of elements during the 3 days experiment, i.e. net uptake and effective uptake and the translocation to the shoot of what has been taken up during the 3 days was calculated. The elements behaved differently. The growth rate had no influence on the effective uptake and µg taken up per plant of Ni, Th and La, increased that of Cs, Se, and I and decreased that of Sr, Mo, and Cl (Table 3-3). When calculated the uptake based on

root mass, i.e. net uptake during 3 days this decreased for all elements except Cs, which increased with increased growth rate. The translocation of I to the shoot increased while that of Th and La decreased with increased growth rate.

Table 3-3. Net uptake and translocation to the shoot of elements during 3 days experiment. Translocation is calculated as amount transported to the shoot of what has been taken up during 3 days given in %, and net uptake is calculated as amount taken up during 3 days in relation to root dry weight given as µg(gDWroot)$^{-1}$. Amount of the element that has been taken up during 3 days per plant (µg plant^{-1}), and effective uptake, which is calculated as µg element in plant per µg element added as well as the amount of element added to the plant, is also indicated. Data are means of 3–4 values.

Clone/Treatm		Ni	Sr	Mo	Cs	La	Th	Se	Cl	I
Growth-rate influence study										
Translocation										
31-1	low	34	83	28	78	27	0	73	27	30
	high	44	69	69	41	9	0	57	85	47
4-2	low	60	82	46	80	33	1	76	10	12
	high	40	27	18	45	2	1	58	79	35
Net uptake										
31-1	low	2.64	15.88	23.40	1.30	3.07	2.67	3.54	4,407	2.67
	high	1.14	1.91	1.93	2.06	1.01	1.46	1.92	1,017	1.68
4-2	low	3.18	17.87	18.69	0.94	2.80	2.06	2.14	3,229	1.43
	high	0.69	2.41	0.39	2.02	1.13	1.61	2.03	422	1.32
µg plant^{-1}$_{(net\ uptake)}$										
31-1	low	1.97	9.73	11.21	1.07	2.17	2.24	2.80	3,454	1.95
	high	1.93	3.16	3.63	3.87	1.83	2.66	3.47	1,628	3.11
4-2	low	1.39	6.39	3.23	0.54	1.32	1.28	1.20	2,099	0.75
	high	0.99	3.62	0.42	3.08	1.65	2.38	3.02	634	1.96
Effective uptake										
31-1	low	0.67	2.22	1.86	0.16	0.31	0.19	0.71	5.33	0.30
	high	0.66	0.88	0.64	0.58	0.26	0.23	0.88	1.25	0.48
4-2	low	0.47	1.46	0.53	0.08	0.19	0.11	0.30	3.15	0.12
	high	0.33	0.83	0.26	0.46	0.23	0.21	0.76	0.94	0.30
Water-uptake influence study										
Translocation										
31-1	0	64.1	34.6	56.4	45.9	8.2	0.5	57.8	50.0	46.1
	8	55.1	56.1	26.3	68.0	8.0	1.6	54.8	31.3	54.1
	16	0.1	5.3	29.1	47.4	0.0	0.9	38.2	38.6	12.1
4-2	0	40.3	26.6	–	38.4	2.6	0.7	57.5	–	34.6
	8	17.1	8.1	–	67.9	0.5	1.8	51.1	0.2	0.0
	16	0.0	12.3	–	55.8	1.6	1.4	49.3	25.0	0.0
Net uptake										
31-1	0	1.15	2.82	2.39	2.68	1.09	1.46	2.81	725	2.36
	8	1.44	5.51	4.95	1.04	1.26	0.77	2.81	3,999	0.99
	16	0.83	1.31	3.12	0.52	0.69	0.24	1.91	3,737	0.33
4-2	0	0.69	2.92	1.13	2.08	1.15	1.62	2.61	430	1.53
	8	0.77	1.48	1.16	0.69	0.94	0.78	2.28	1,439	0.15
	16	0.69	1.34	1.20	0.48	0.72	0.33	1.62	754	0.09

Clone/Treatm		Ni	Sr	Mo	Cs	La	Th	Se	Cl	I
µg plant^{-1}$_{(net\ uptake)}$										
31-1	0	1.93	3.87	3.89	3.87	1.83	2.66	3.47	295	3.11
	8	1.51	5.45	4.63	0.90	1.63	0.85	3.08	2,929	0.87
	16	2.08	2.95	5.68	0.76	1.76	0.59	3.11	5,444	0.64
4-2	0	0.99	2.52	1.56	2.76	1.66	2.38	3.02	610	1.96
	8	1.16	2.11	1.84	0.78	1.36	1.21	2.71	1,668	0.17
	16	0.93	2.33	2.13	0.62	1.40	0.63	2.17	1,021	0.18
Effective uptake										
31-1	0	0.66	0.88	0.64	0.58	0.26	0.23	0.88	0.46	0.48
	8	0.51	1.24	0.77	0.14	0.23	0.07	0.78	4.53	0.14
	16	0.71	0.67	0.94	0.11	0.25	0.05	0.79	8.41	0.10
4-2	0	0.34	0.57	0.26	0.42	0.24	0.21	0.77	0.94	0.30
	8	0.39	0.48	0.30	0.12	0.20	0.10	0.69	2.58	0.03
	16	0.32	0.53	0.35	0.09	0.20	0.05	0.55	1.58	0.03
Transpiration-influence study										
Translocation										
31-1		35	24	14	37	2.5	0.14	58	71	33
4-2		22	–	–	62	4.0	0.57	50	51	68
Net uptake										
31-1		0.30	1.33	2.27	1.65	0.92	1.66	1.54	2,052	1.12
4-2		0.22	1.14	1.08	0.79	0.95	2.75	1.81	693	0.67
µg plant^{-1}$_{(net\ uptake)}$										
31-1		0.61	3.01	5.69	3.76	2.14	3.81	3.31	3,392	2.53
4-2		0.36	2.22	1.93	1.53	1.84	5.35	3.11	792	1.30
Effective uptake										
31-1		0.21	0.69	0.94	0.57	0.31	0.33	0.84	5.24	0.40
4-2		0.11	0.52	0.32	0.23	0.27	0.46	0.79	1.22	0.20
Added, µg		2.94	4.38	6.04	6.65	6.95	11.60	3.95	647	6.45

The water uptake decrease diminished the net uptake of Sr, Cs, La, Th, Se, and I, while not that of Ni, Mo or Cl. The accumulation calculated as µg per plant increased for Mo, and decreased for Cs, Th and I. The translocation to the shoot of the elements was also affected by the water uptake since a diminished water uptake decreased the transpiration rate (Figure 3-2). Diminished water uptake decreased the translocation of Ni, Sr, La and I to the shoot. The effective uptake for Cs, Th and I decreased while that of Cl increased with increased water uptake.

Transfer factors are not possible to use when dealing with water culture but instead one can use the effective uptake, which in principle is the same thing but calculated on the amount basis instead of concentration basis. It should, however, be noted that the effective uptake of Cl is over 1, which cannot be possible and cannot be explained.

There was no influence by transpiration on the translocation from root to shoot of the part of the element taken up during the three days, not either on net uptake. Therefore, only the mean values based on the 10 different transpiration rates are shown in Table 3-3.

In Table 3-4 is given data on the total amount of the element per plant as well as the total amount per plant taken up during 3 days related to the total amount of the element in the plant. In that table one can see that µg plant$^{-1}_{(net\ uptake)}$/µg plant$^{-1}_{(total)}$ is very high for the elements that earlier was not present in the nutrient medium and therefore was not of high concentration in the plant tissue prior to the uptake experiment.

Table 3-4. Total amount of elements per plant (µg plant$^{-1}_{(Total)}$), and its relation to the amount of the element that has been taken up per plant during the 3 days experiment (µg plant$^{-1}_{(net\ uptake)}$). Data are means of 3–4 values.

		Ni	Sr	Mo	Cs	La	Th	Se	Cl	I
Growth-rate influence study										
µg plant$^{-1}_{(total)}$										
31-1	low	2.66	18.72	26.79	1.08	2.27	2.25	2.80	8,103	2.08
	high	3.52	16.94	20.11	3.88	2.04	2.68	3.47	9,944	3.41
4-2	low	1.80	11.83	17.12	0.54	1.37	1.28	1.20	6,387	0.85
	high	2.13	15.82	16.79	3.08	1.80	2.39	3.02	9,253	2.22
µg plant$^{-1}_{(net\ uptake)}$/µg plant$^{-1}_{(total)}$						..				
31-1	low	74	68	73	100	96	100	100	43	94
	high	55	23	19	100	89	99	100	8	91
4-2	low	77	64	65	100	96	100	100	34	88
	high	46	23	9	100	92	100	100	7	88
Water-uptake influence study										
µg plant$^{-1}_{tot}$										
31-1	0	3.52	16.94	20.11	3.88	2.04	2.68	3.47	9,944	3.41
	8	2.47	18.64	23.57	1.23	2.02	1.33	3.40	14,867	1.59
	16	3.71	15.20	28.37	0.76	1.90	0.62	3.11	15,713	1.04
4-2	0	2.13	15.82	16.79	3.08	1.80	2.39	3.02	9,253	2.22
	8	2.18	12.49	15.92	0.79	1.47	1.22	2.71	12,779	0.52
	16	2.58	14.12	21.41	0.62	1.50	0.65	2.17	13,006	0.54
µg plant$^{-1}_{(net\ uptake)}$/µg plant$^{-1}_{(total)}$										
31-1	0	55	23	19	100	89	99	100	3	91
	8	61	29	20	73	81	64	91	20	55
	16	56	19	20	99	93	96	100	35	62
4-2	0	46	16	9	90	92	100	100	7	88
	8	53	17	12	100	93	99	100	13	32
	16	36	17	10	99	93	98	100	8	33
Transpiration-influence study										
µg plant$^{-1}_{tot}$										
31-1		3.8	22.7	37.3	8.1	4.5	8.2	4.9	21,449	5.5
4-2		1.7	15.5	18.2	1.5	2.0	5.4	3.5	14,882	1.7
µg plant$^{-1}_{(net\ uptake)}$/µg plant$^{-1}_{(total)}$ (%)										
31-1		16	13	15	47	47	47	68	16	46
4-2		21	14	11	100	93	100	89	5	79

4 Discussion

4.1 Uptake and translocation

4.1.1 Clone differences

All elements were taken up and translocated in both clones, except for I in clone 4-2 at the low growth rate (Figure 3-17). This element, I, was not translocated to the shoot in clone 4-2 under conditions of low water flow caused by either low water uptake (Figure 3-6) or insufficient transpiration rate (Figure 3-13). The latter is likely the reason for the difference between the two clones, since clone 31-1 had a higher transpiration rate due to the large total leaf area (Figure 3-9) and I was much more strongly influenced by the water flow than were the other elements. This seems to be the only obvious clone difference found in this investigation. Despite the fact that the two clone types were chosen because they differed in terms of the accumulation of several metals (i.e. one was a high and the other a low accumulator), the accumulation of the elements tested in this investigation did not differ between the clones. Since it has been shown that a clone difference in the uptake of one metal does not necessarily imply a difference for another metal /Greger et al. 2001/, it is possible that other *Salix* clone types may show a difference. On the other hand, it is possible that *Salix* clone types may vary greatly in uptake *only* for Cd, Cu, and Zn; in the case of, for example, Hg there is no clone difference in uptake /Wang and Greger 2004/.

4.1.2 Differences in the uptake and distribution of various elements in *Salix*

One assumption was that the relationship between the elements in the solution (ng L^{-1}; Table 3-2) should be mirrored in both the uptake and the shoot concentration, making it possible to use plants in mapping the presence of specific waters originating from nuclear waste sites, in soil water originating from deep water. When dealing with the total uptake, the expected relationship was maintained by Ni, Cs, Th, La, Se, and I, comprising one group, while Sr, Cl, and Mo maintained their own relationship (Table 3-2). This means that the uptake differed between these two groups of elements. However, we should not forget that there are other environmental conditions than just water relations and light (causing different growth rates) that can differentially influence element uptake in nature /Greger 2004/.

Regarding translocation to the shoots, other groupings appear. One group consists of Ni, Sr, Mo, Cs, Se, Cl, and I, which were translocated in nearly the same proportions as occurred in the solution. Thorium and La differed from the members of this group by factors of 100 and 10, respectively. Therefore, if using *Salix* shoots in mapping a specific combination of elements in soil water, based on the uptake group and shoot concentration group, Ni, Cs, and Se could be included in such a scheme; however, even though I appears in the group it is questionable whether it should be used in any such mapping, due to the differences in I translocation detected between the clones (Figures 3-6, 3-13, and 3-17).

4.2 Influence of water relations and growth on element uptake and translocation

One question was whether element uptake was related to water uptake. If so, a 4-fold decrease in water uptake should translate into a 4-fold decrease in element uptake if there were a 1 to 1 relationship. This research shows that a 4-fold decrease in water uptake reduced the uptake of Ni and Sr by 1.33 times, La by 1.5 times, Se by 2 times, Cs by 4 times, I by 4.5 times, and Th by 5 times; Mo and Cl were unaffected, and the uptake of no element increased (Figures 4-1 to 4-17). This means that the uptake rates of Cs, I, and Th are more or less totally dependent on the water uptake rate, while those of Ni, Sr, La, and Se are only somewhat dependent.

Another question was whether element translocation (distribution) to the shoot depended on the transpiration stream rate. Increasing the transpiration rate 1.33 fold increased distribution to the shoots of Ni, Mo, Cs (one clone), and Se by 2 times and La by 3 times (insignificant for Ni and Mo). Only in one case was the opposite found: increased transpiration decreased Cs translocation by a factor of 2 in one of the clones. This means that translocation to the shoots of Ni, Mo, Se, and La is more or less dependent on the transpiration stream; however, in the case of La some other factor is likely operative, since there was a 2 to 1 relationship. If consider the calculations and mass balance figures (Figures 4-1 to 4-18) it is found that a decrease in water uptake also decreased the translocation of elements to the shoot. This is due to closure of stomata, decreasing the transpiration as well as too small quantities of water to move to the top and therefore creates a stop in the xylem sap flow, which of course decreases the movement of elements upwards. However, this does not mean that the element translocation is depending on the transpiration rate as such, since if increasing the transpiration rate via open stomata does not influence the element translocation (Tables 4-1, 4-2).

The third question was how an increase in plant growth could influence element uptake, and whether a dilution effect, arising from this growth, was also exerted on these elements. It was found that a 3-fold growth increase insignificantly increased the uptake of Cs by 2 times, and also that I uptake increased in one case (Figures 4-7 and 4-17). For all the other elements, increased plant growth decreased their relative uptake rate: significantly for Cl (2.4 times), Sr (2 times), Ni and Mo (both by 3 times), and insignificantly for Th (1.8 times), Se (1.4 times), and La (2 times) (Figures 4-1, 4-3, 4-5 and 4-9, 4-11, 4-13, 4-15, 4-17). This means that for some, but not all, of the studied elements, a dilution effect was found, and that for Ni and Mo a 1 to 1 relationship was found. One reason for the dilution effect could have been that the element concentration in the solution became diluted over time; this was, however, not the case, since the element concentration in the solution *increased* with time, approximately 1.5-fold after 3 days (Figure 3-1).

4.3 Elements having similar effects

This research shows that the uptake and translocation of the 9 elements are differently affected, and to various extents, by growth rate, water uptake, and transpiration (Figures 4-1 to 4-9). No inter-element similarities were found that were traceable to shared properties such as their being anions (MoO_4^{2-}, Cl^-, I^-, and SeO_4^{2-}) or cations (Ni^{2+}, Cs^+, Sr^{2+}, La^{3+}, and Th^{4+}), similar charge (Cl^-, I^-), (MoO_4^{2-} and SeO_4^{2-}), (Ni^{2+} and Sr^{2+}), their being non metals (Cl^-, I^-, and SeO_4^{2-}), metals (Ni^{2+}, Cs^+, Sr^{2+}, La^{3+}, Th^{4+}, and MoO_4^{2-}), or heavy metals (Ni^{2+}, La^{3+}, Th^{4+}, and MoO_4^{2-}), or their being nutrient elements (Ni^{2+}, MoO_4^{2-}, and Cl^-). There was one exception, however, in that transpiration had absolutely no influence on Cl^- and I^- (Figures 4-8 and 4-9). In terms of transpiration effects, MoO_4^{2-} and Sr^{2+}

showed similar responses in that uptake and accumulation in roots and shoot decreased (Figures 4-2 and 4-3). In terms of plant growth effects, MoO_4^{2-}, Sr^{2+}, and La^{3+}, responded similarly in that uptake, accumulation in roots and shoots, and distribution to the shoots all decreased with increasing growth (Figures 4-2, 3-3, and 4-6). Furthermore, reduced water uptake decreased both uptake and accumulation in roots and shoots for SeO_4^{2-} and La^{3+} (Figures 4-6 and 4-7), whereas Cl^- and MoO_4^{2-} were not influenced at all by water uptake (Figures 4-3 and 4-8). The similar responses of some elements could thus not be explained by chemical or other similarities between them.

4.4 Response of each element

4.4.1 Nickel

Nickel is taken up as Ni^{2+} by the plant and seems to follow the water flow into the plant, at least to some extent, since Ni accumulation decreases with decreasing water uptake rate (Figure 4-1). It also appears that when the water uptake decreases, the distribution of Ni to the shoots also decreases, while the accumulation in root increases (Figure 4-1). Thus, the influence of water uptake on Ni uptake seems not to be as strong as it is on the translocation of Ni to the shoots. In plants, nickel distribution to the shoots increases with a faster transpiration rate; thereby both the shoot:root concentration ratio and Ni concentration in the shoots increase (Figure 4-1). Thus, Ni is influenced by the water flow in the plant, and to the greatest extent by transpiration.

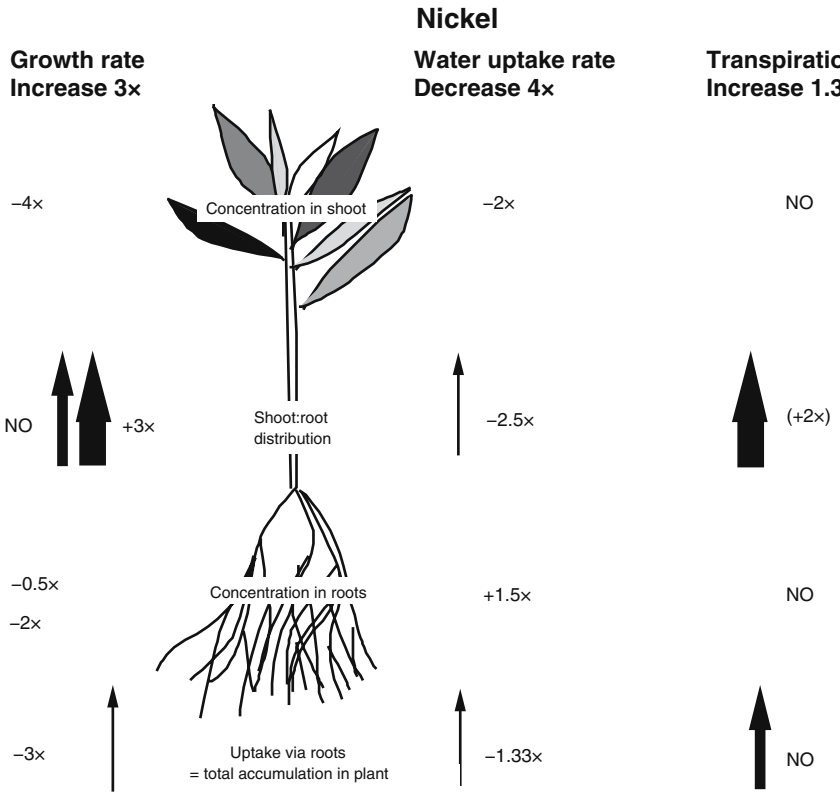

Figure 4-1. *Summary of influence on total uptake normalized to root biomass, concentration in roots and shoots, and distribution to the shoots of Ni; shown as increase (thick arrows and +), decrease (thin arrows and –) or no change (medium arrows and NO) in relation to growth rate increase, water uptake rate decrease and transpiration rate increase, respectively (in parentheses = not significant). Differences between clones are indicated in two different values.*

Plant growth was found to decrease Ni uptake (Figure 4-1). In clone 31-1, an approximately 3-fold growth increase (Figure 4-1) decreased both Ni uptake and Ni accumulation in roots by 3 and 2 times, respectively (Figure 3-15), implying nearly a 1 to 1 relationship. This of course had an indirect influence on the distribution of Ni to the shoots, which increased with increased growth rate due to the decreased Ni accumulation in the roots (Figure 4-1) and not due to increased shoot growth in relation to root growth (Figure 3-14d). In the other clone type, the relationships between plant growth and element uptake and root accumulation were 1 and 0.17, respectively, since a 3-fold growth increase decreased uptake by 3 times and root accumulation by 0.5 times. In this case, the distribution of Ni to the shoots did not change, since the concentration of Ni in the shoots decreased by a factor of 3, i.e. a nearly 1 to 1 relationship with growth rate.

The distribution of Ni in the plant-solution system after three-days uptake and its effect by growth rate and water relations is shown in Figure 4-2.

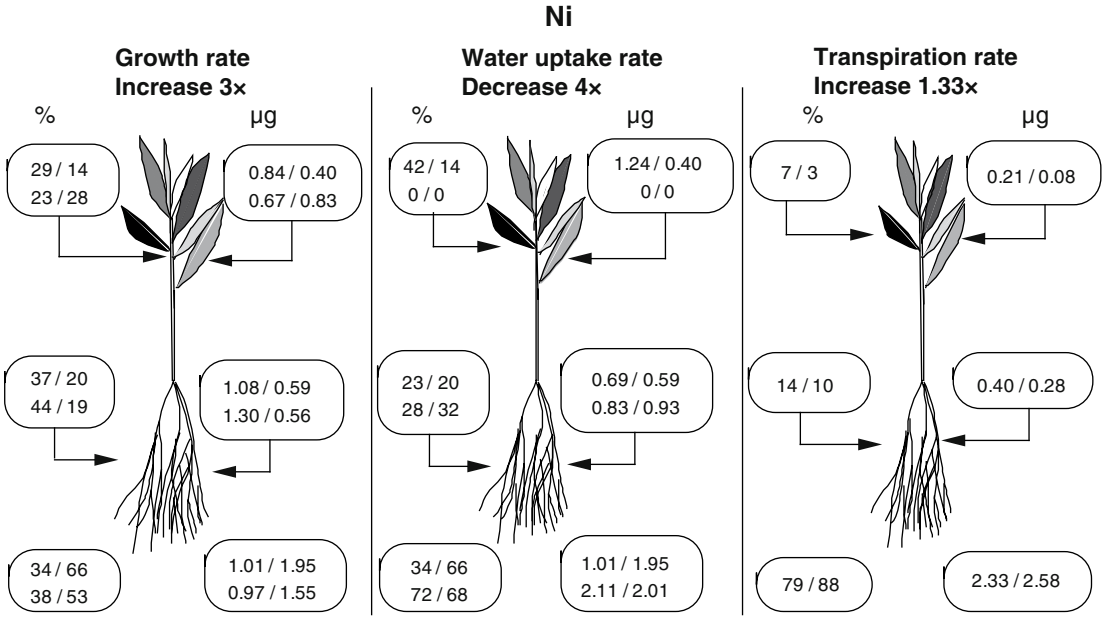

Figure 4-2. *Summary of net uptake and distribution between root and shoot of Ni, which had been taken up during 3 days. The distribution between solution, roots and shoot is given as percentage as well as in amount (µg) per compartment. Data to the left and to the right are from clone 31-1 and 4-2, respectively. The lower data is from low rate (of growth or water uptake) and the upper from high rate, meaning effects by increase in growth rate upwards and effects by decreasing in water uptake downwards. Data from the transpiration experiment are given as mean values due to absence of influence by transpiration. Data are based solely on what has been taken up during the 3 days experiment and the solution contained 2.94 µg Ni at start.*

4.4.2 Strontium

The total uptake of Sr decreased slightly with decreasing water uptake (Figure 4-2), which is also mirrored in an insignificant decrease in Sr concentration in both shoots and roots (Figure 3-4). An increased transpiration rate tended to decrease both the total uptake and the concentration of Sr in both roots and shoots, but there was no influence on the Sr distribution between roots and shoots. Thus, it seems that Sr uptake is little influenced by either water uptake or transpiration rate. Strontium is likely taken up as Sr^{2+}; due to its similarity to Ca it often imitates the behaviour of Ca. In the transpiration stream Ca binds to the negative charges of the vessel walls, and is thus not directly translocated to the shoots via the xylem sap /Bell and Biddulph 1963, Van de Geijn and Petit 1979/. This is one possible explanation of the behaviour.

Strontium is obviously influenced by growth rate, as Sr uptake decreases by 2 times when the growth rate increases by 3 times (Figure 4-2). At the same time as Sr concentration in the shoots decreases by 3 times (twice the decrease in concentration in the roots), distribution to the shoots also decreases. Thus, growth increase dilutes Sr in the plant tissue in a 0.7 to 1 relationship.

The distribution of Sr in the plant-solution system after three-days uptake and its effect by growth rate and water relations is shown in Figure 4-4.

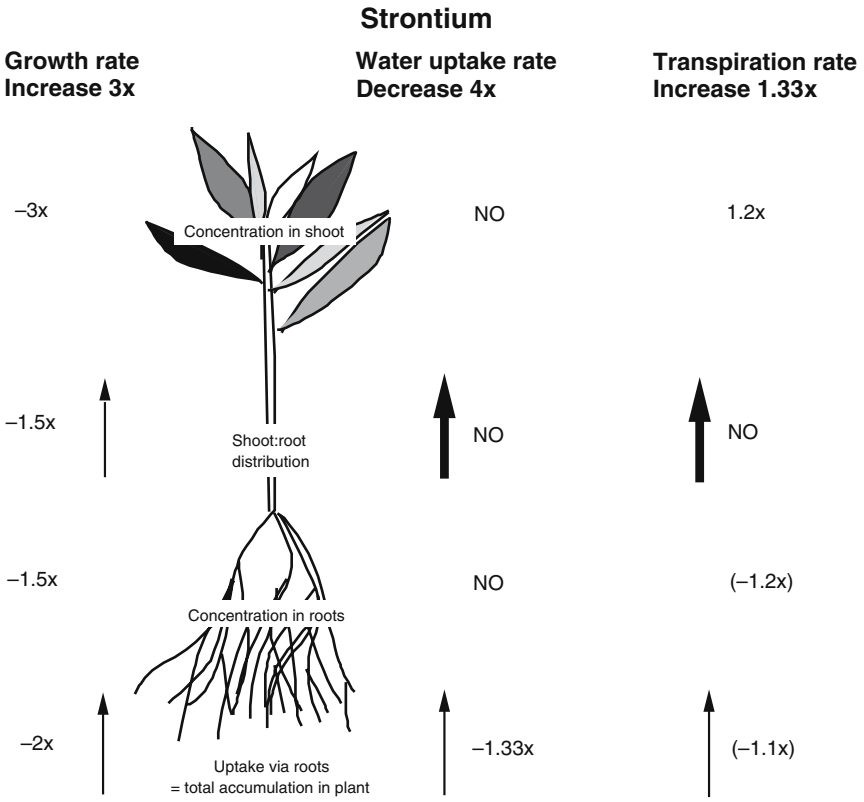

Figure 4-3. *Summary of influence on total uptake normalized to root biomass, concentration in roots and shoots, and distribution to the shoots of Sr; shown as increase (thick arrows and +), decrease (thin arrows and –) or no change (medium arrows and NO) in relation to growth rate increase, water uptake rate decrease and transpiration rate increase, respectively (in parentheses = not significant). Differences between clones are indicated in two different values.*

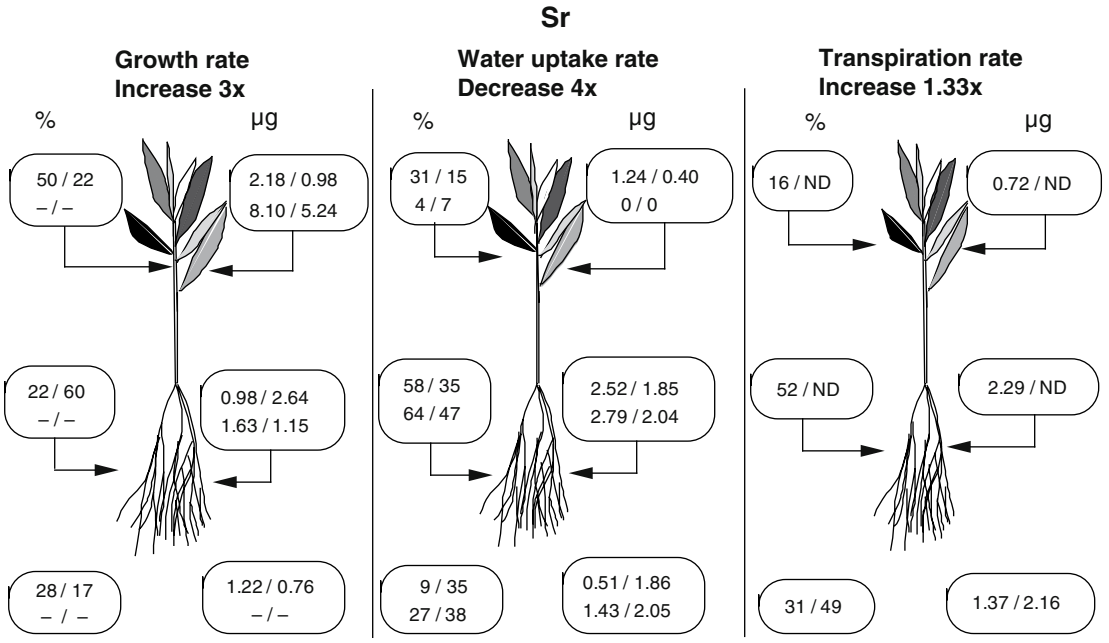

Figure 4-4. *Summary of net uptake and distribution between root and shoot of Sr, which had been taken up during 3 days. The distribution between solution, roots and shoot is given as percentage as well as in amount (µg) per compartment. Data to the left and to the right are from clone 31-1 and 4-2, respectively. The lower data is from low rate (of growth or water uptake) and the upper from high rate, meaning effects by increase in growth rate upwards and effects by decreasing in water uptake downwards. Data from the transpiration experiment are given as mean values due to absence of influence by transpiration. Data are based solely on what has been taken up during the 3 days experiment and the solution contained 4.38 µg Sr at start.*

4.4.3 Molybdenum

Molybdenum is taken up as the anion MoO_4^{2-} /Mengel and Kirkby 1982/. This element seems not to be influenced by the water uptake rate (Figure 4-3). However, transpiration decreased both Mo uptake and Mo concentration in roots and shoots, while the distribution to the shoots increased (Figure 3-9). The latter effect occurred because Mo concentration decreases more in the roots than in the shoots. The change in water flow in the plant to the shoots may therefore be the crucial factor that affects the Mo uptake, and not the water uptake as such.

Molybdenum is obviously influenced by the growth rate in a more or less similar manner as Sr is (Figure 4-3). Molybdenum uptake decreases by 3 times when the growth rate increases by 3 times. Concurrently, the Mo concentration in the shoots decreases further, even more than the root concentration does, thus distribution to the shoots decreases. The growth rate thus causes a dilution effect in the whole plant, and especially in the shoot.

The distribution of Mo in the plant-solution system after three-days uptake and its effect by growth rate and water relations is shown in Figure 4-6.

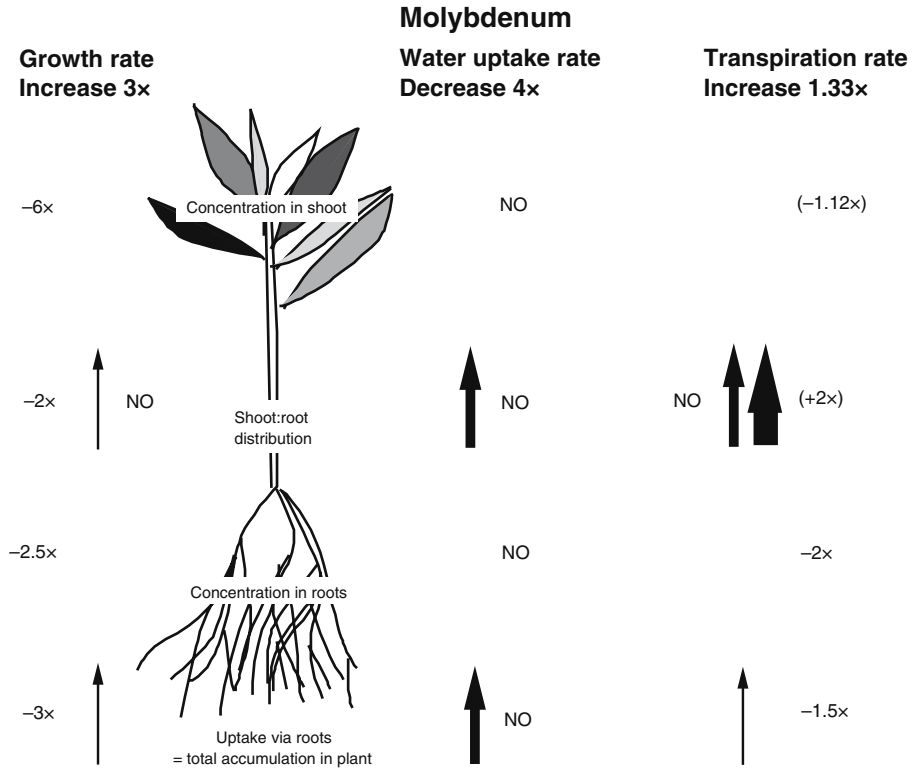

Figure 4-5. *Summary of influence on uptake normalized to root biomass, concentration in roots and shoots, and distribution to the shoots of Mo; shown as increase (thick arrows and +), decrease (thin arrows and –) or no change (medium arrows and NO) in relation to growth rate increase, water uptake rate decrease and transpiration rate increase, respectively (in parentheses = not significant). Differences between clones are indicated in two different values.*

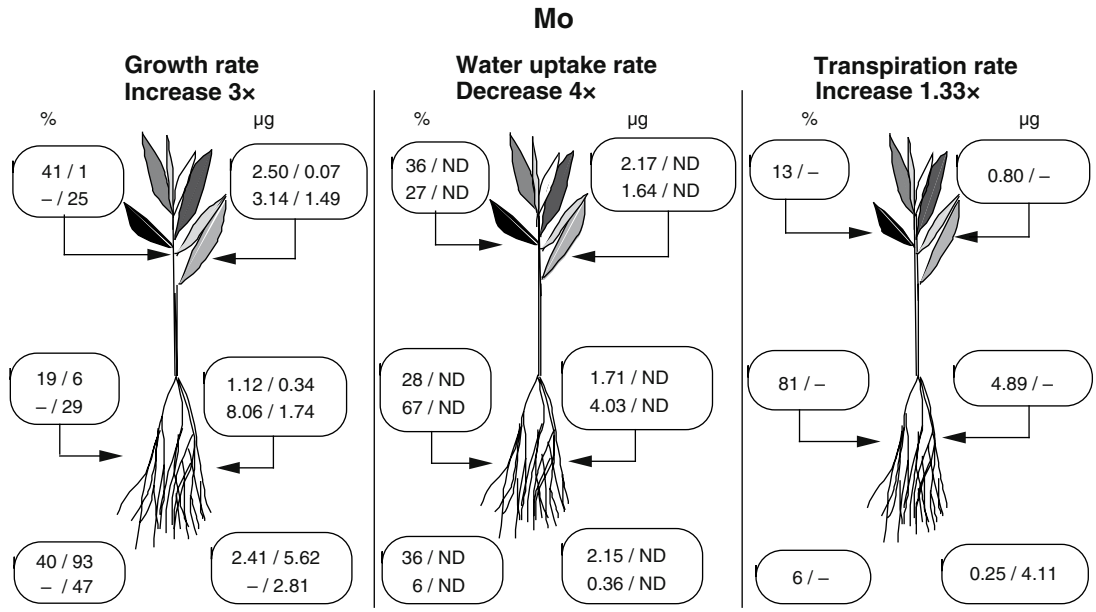

Figure 4-6. *Summary of net uptake and distribution between root and shoot of Mo, which had been taken up during 3 days. The distribution between solution, roots and shoot is given as percentage as well as in amount (µg) per compartment. Data to the left and to the right are from clone 31-1 and 4-2, respectively. The lower data is from low rate (of growth or water uptake) and the upper from high rate, meaning effects by increase in growth rate upwards and effects by decreasing in water uptake downwards. Data from the transpiration experiment are given as mean values due to absence of influence by transpiration. Data are based solely on what has been taken up during the 3 days experiment and the solution contained 6.04 µg Mo at start.*

4.4.4 Caesium

In the case of Cs, which is taken up as Cs^+, the uptake is decreased by 4 times with a 4-fold decrease in water uptake rate (Figure 4-4). The increased distribution of Cs to the shoots depends on the shoot concentration decreasing by only 4 times while the root concentration decreases by a greater margin. Transpiration seems to affect the two clones differently, likely due to the differing transpiration rates between them (Figure 3-12). The higher transpiration rate increased the Cs uptake and thereby the concentration in roots; however, the distribution to the shoots of Cs increased at a lower transpiration rate, i.e. in the other clone. These differences may also depend on specific clone properties. In all circumstances the water relations seem to be important for the uptake and translocation of Cs in plants.

The growth rate increase also tended to increase the Cs uptake (Figure 4-4). This was also the case with root Cs concentration, but the Cs concentration in shoots either decreased or was unaffected; therefore the distribution of Cs to the shoots was depressed by the growth rate. The absence of dilution with increasing growth rate was only found for Cs and seems to be specific to this element.

The distribution of Cs in the plant-solution system after three-days uptake and its effect by growth rate and water relations is shown in Figure 4-8.

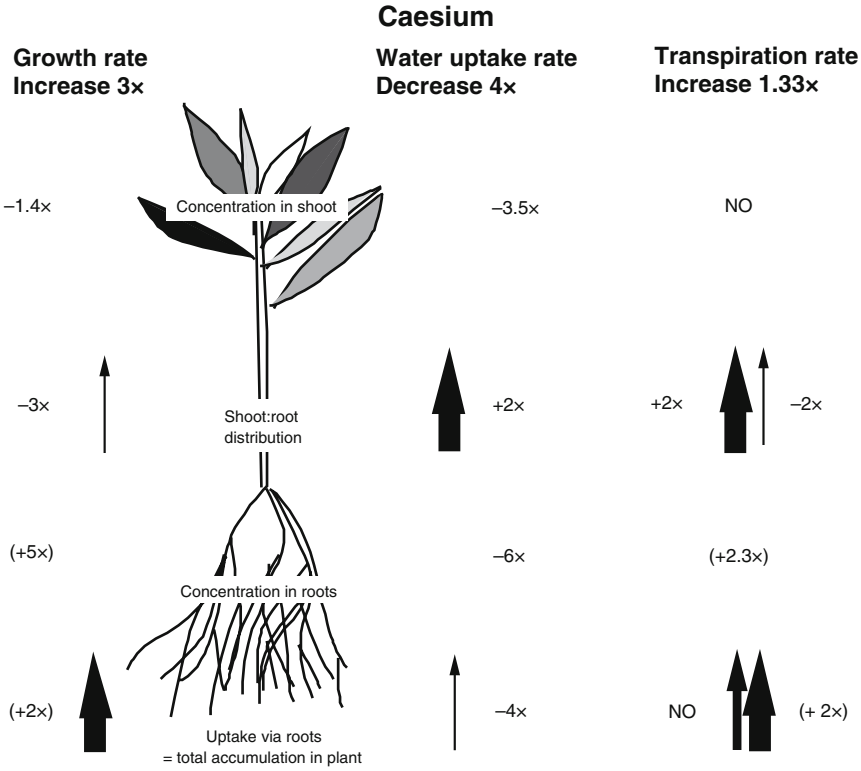

Figure 4-7. *Summary of influence on uptake normalized to root biomass, concentration in roots and shoots, and distribution to the shoots of Cs; shown as increase (thick arrows and +), decrease (thin arrows and –) or no change (medium arrows and NO) in relation to growth rate increase, water uptake rate decrease and transpiration rate increase, respectively (in parentheses = not significant). Differences between clones are indicated in two different values.*

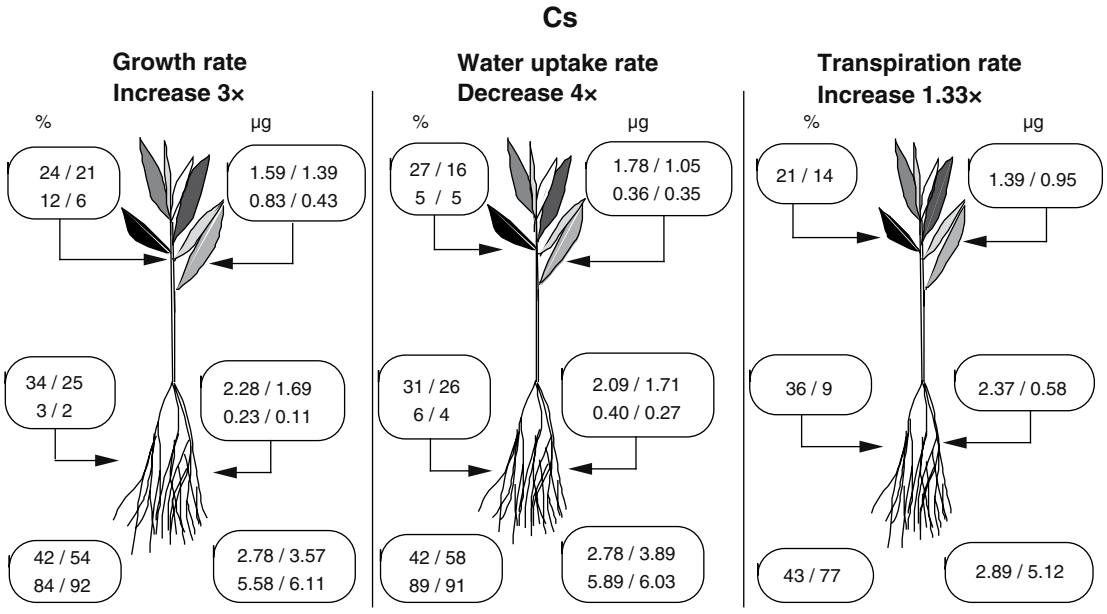

Figure 4-8. *Summary of net uptake and distribution between root and shoot of Cs, which had been taken up during 3 days. The distribution between solution, roots and shoot is given as percentage as well as in amount (µg) per compartment. Data to the left and to the right are from clone 31-1 and 4-2, respectively. The lower data is from low rate (of growth or water uptake) and the upper from high rate, meaning effects by increase in growth rate upwards and effects by decreasing in water uptake downwards. Data from the transpiration experiment are given as mean values due to absence of influence by transpiration. Data are based solely on what has been taken up during the 3 days experiment and the solution contained 6.65 µg Cs at start.*

4.4.5 Thorium

Thorium, present as the Th^{4+} cation, seems to be influenced by water relations (Figure 4-5). Both Th uptake and Th concentration in roots was depressed by decreased water uptake. However, since the Th concentration in shoots was not affected, the distribution of Th to the shoots increased with decreased water uptake, meaning no increased translocation of Th to the shoots. There was a tendency for both Th uptake and root concentration of Th to decrease in both clone types as transpiration increased. However, no clear trend was found for Th distribution to the shoots. Thus, Th uptake and Th concentration in roots (but not in shoots) are both influenced by water relations.

Th uptake and concentration in roots decreased with increasing growth rate, whereas the distribution to shoots arising from the stable shoot concentration increased in clone 31-1 with increased growth rate (Figure 3-16). Clone 4-2 was not affected.

One obvious finding regarding Th is the stable Th accumulation in shoots, which remained unchanged despite changes in water relations and growth. One explanation could be the very low shoot:root concentration distribution of Th – the lowest of all tested elements (Table 3-2).

The distribution of Th in the plant-solution system after three-days uptake and its effect by growth rate and water relations is shown in Figure 4-10.

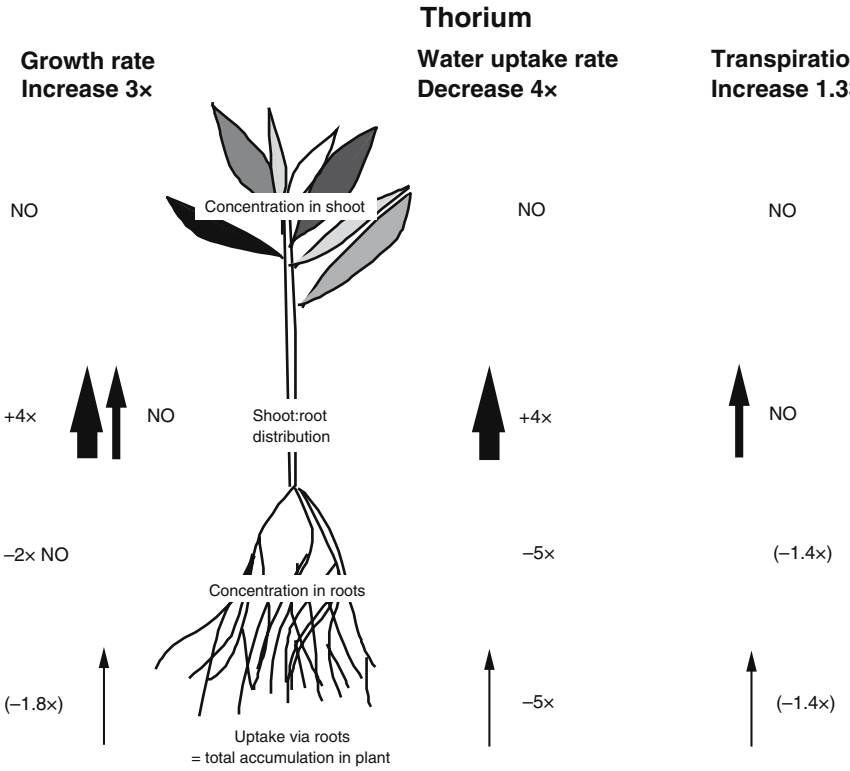

Figure 4-9. *Summary of influence on uptake normalized to root biomass, concentration in roots and shoots, and distribution to the shoots of Th; shown as increase (thick arrows and +), decrease (thin arrows and –) or no change (medium arrows and NO) in relation to growth rate increase, water uptake rate decrease and transpiration rate increase, respectively (in parentheses = not significant). Differences between clones are indicated in two different values.*

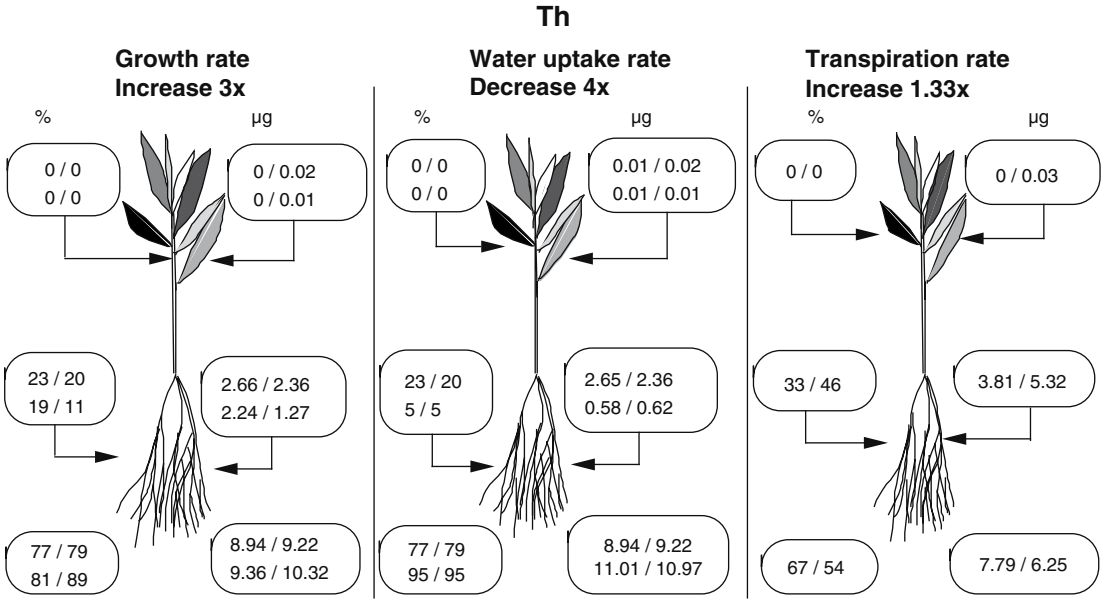

Figure 4-10. *Summary of net uptake and distribution between root and shoot of Th, which had been taken up during 3 days. The distribution between solution, roots and shoot is given as percentage as well as in amount (µg) per compartment. Data to the left and to the right are from clone 31-1 and 4-2, respectively. The lower data is from low rate (of growth or water uptake) and the upper from high rate, meaning effects by increase in growth rate upwards and effects by decreasing in water uptake downwards. Data from the transpiration experiment are given as mean values due to absence of influence by transpiration. Data are based solely on what has been taken up during the 3 days experiment and the solution contained 11.60 µg Th at start.*

4.4.6 Lanthanum

Lanthanum was present as La^{3+}. The uptake of this element as well as the root and shoot concentration of La is slightly decreased by the water uptake decrease (Figure 3-5). This means that the water uptake has little influence on La in plants. The transpiration rate increase also decreased the shoot:root concentration ratio; however, this was due to the lowered La uptake and root La concentration of the plant (Figure 3-9). Thus, decreased water flow decreases both La uptake and root and shoot concentration.

Lanthanum is influenced by the growth rate, i.e. a 3-fold increased growth rate decreased both the uptake and root and shoot concentration of La (Figure 3-16). The distribution of La to the shoots behaved in similar fashion. However, since the uptake and root accumulation effects are not significant, and since the decrease is greater for shoot concentration and distribution, growth thus influences the distribution of La to the shoots rather than dilutes La in the whole plant tissue.

The distribution of La in the plant-solution system after three-days uptake and its effect by growth rate and water relations is shown in Figure 4-12.

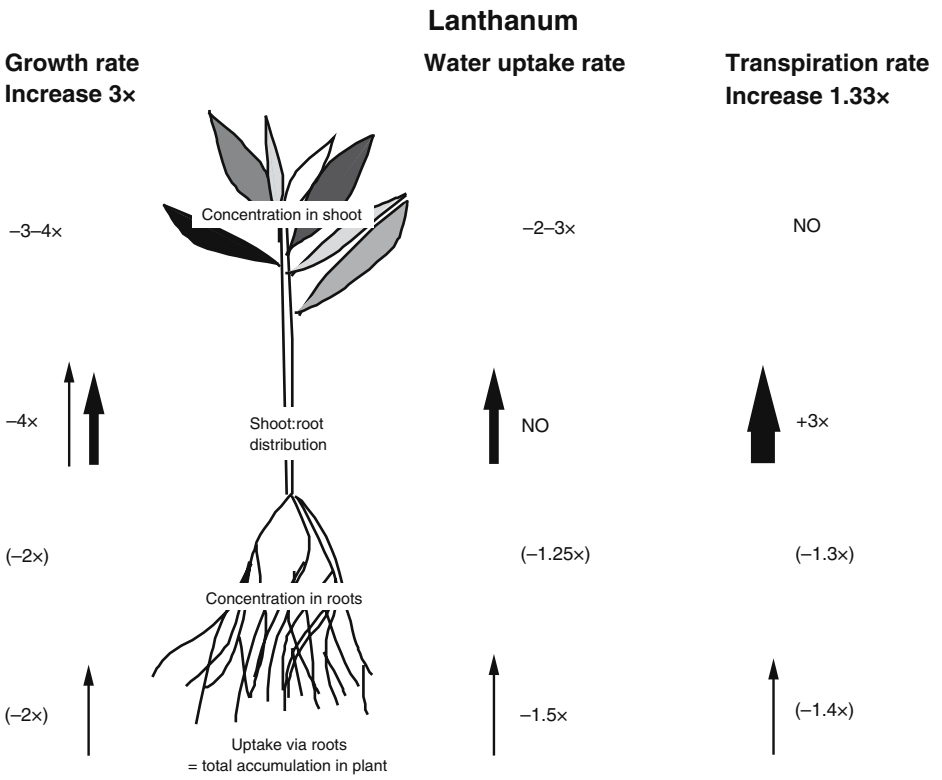

Figure 4-11. *Summary of influence on uptake normalized to root biomass, concentration in roots and shoots, and distribution to the shoots of La; shown as increase (thick arrows and +), decrease (thin arrows and –) or no change (medium arrows and NO) in relation to growth rate increase, water uptake rate decrease and transpiration rate increase, respectively (in parentheses = not significant). Differences between clones are indicated in two different values.*

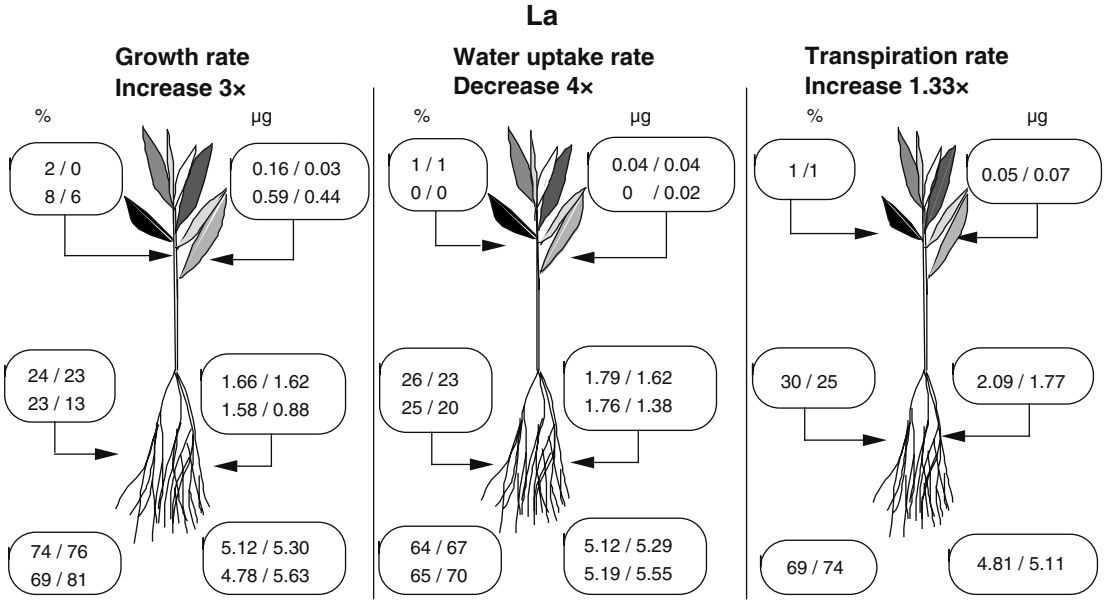

Figure 4-12. *Summary of net uptake and distribution between root and shoot of La, which had been taken up during 3 days. The distribution between solution, roots and shoot is given as percentage as well as in amount (µg) per compartment. Data to the left and to the right are from clone 31-1 and 4-2, respectively. The lower data is from low rate (of growth or water uptake) and the upper from high rate, meaning effects by increase in growth rate upwards and effects by decreasing in water uptake downwards. Data from the transpiration experiment are given as mean values due to absence of influence by transpiration. Data are based solely on what has been taken up during the 3 days experiment and the solution contained 6.95 µg La at start.*

4.4.7 Selenium

Selenium is taken up as SeO_4^{2-}, and only at the lowest water uptake level was there any effect: a decreased uptake and root and shoot concentration of Se (Figure 4-7). Since the transpiration rate did not influence the uptake, the decreased root and increased shoot concentration was due to an increased distribution of Se to the shoots with increased transpiration rate. Thus transpiration influences Se translocation to the shoots.

Increased growth rate tended to decrease the uptake, shoot:root concentration ratio, and the shoot concentration of Se; the root concentration of Se was either unaffected or increased (Figure 3-17). Thus, the real effect is that increased growth decreases the distribution of Se to the shoots, therefore decreasing the shoot concentration while increasing that of the roots, since the uptake was not significantly decreased. The effect of growth rate is thus expressed in Se distribution rather than in dilution in the whole plant.

The distribution of Se in the plant-solution system after three-days uptake and its effect by growth rate and water relations is shown in Figure 4-14.

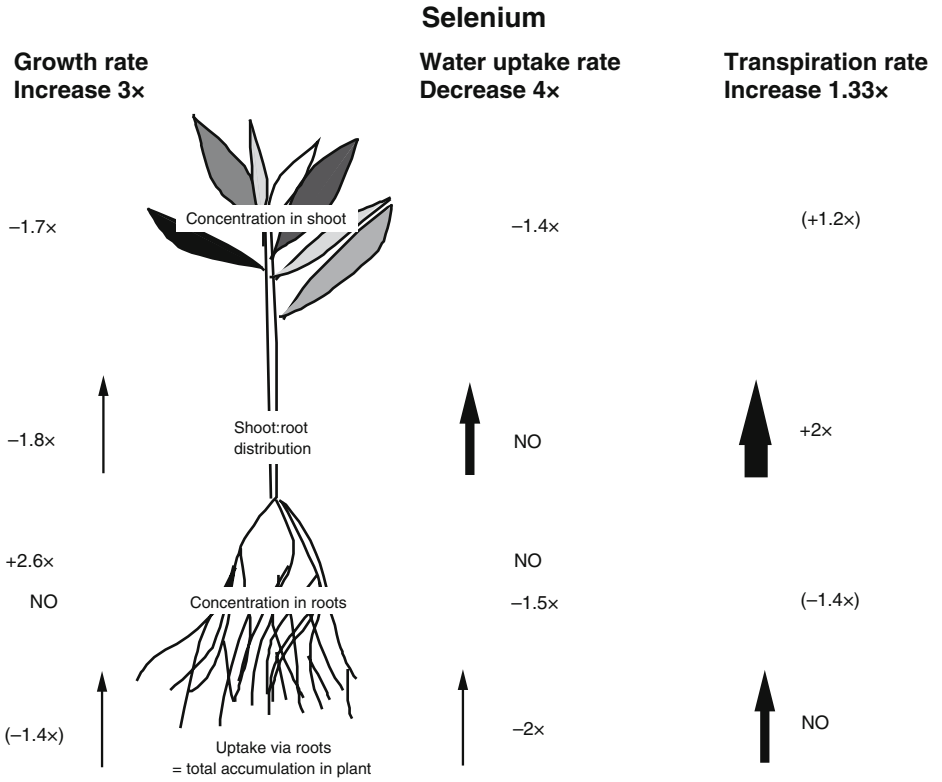

Figure 4-13. *Summary of influence on uptake normalized to root biomass, concentration in roots and shoots, and distribution to the shoots of Se; shown as increase (thick arrows and +), decrease (thin arrows and –) or no change (medium arrows and NO) in relation to growth rate increase, water uptake rate decrease and transpiration rate increase, respectively (in parentheses = not significant). Differences between clones are indicated in two different values.*

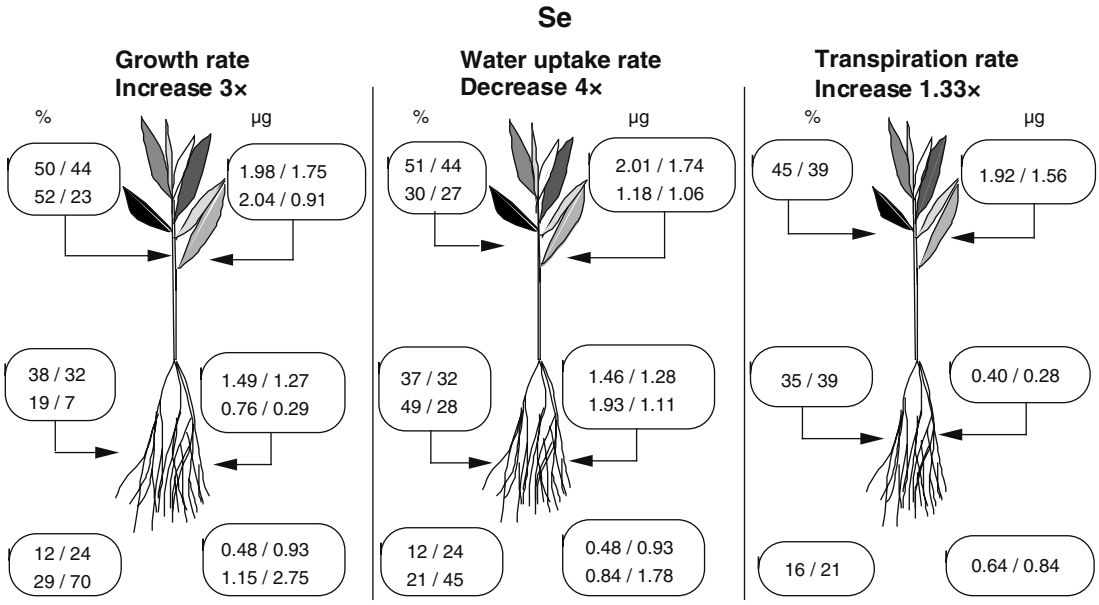

Figure 4-14. *Summary of net uptake and distribution between root and shoot of Se, which had been taken up during 3 days. The distribution between solution, roots and shoot is given as percentage as well as in amount (µg) per compartment. Data to the left and to the right are from clone 31-1 and 4-2, respectively. The lower data is from low rate (of growth or water uptake) and the upper from high rate, meaning effects by increase in growth rate upwards and effects by decreasing in water uptake downwards. Data from the transpiration experiment are given as mean values due to absence of influence by transpiration. Data are based solely on what has been taken up during the 3 days experiment and the solution contained 3.95 µg Se at start.*

4.4.8 Chlorine

The Cl^- uptake was not clearly affected by either the water uptake rate or transpiration rates (Figure 4-8). This means that the water relations of the plant do not influence Cl uptake, and that it is not directly driven by the water flow. This is likely because Cl enters the plant cells to a great extent, staying there to be used for non-metabolic activities such as regulating the chemo-electropotential difference across membranes for the cellular transport of other elements and substances /Marschner 1995/.

Increased growth rate decreased both Cl uptake and root concentration; the decreased Cl concentration in shoots was insufficiently depressed, and therefore the distribution of Cl to the shoots increased in clone 31-1 (Figure 4-8). Growth thus dilutes Cl in a nearly 1 to 1 relationship.

The distribution of Cl in the plant-solution system after three-days uptake and its effect by growth rate and water relations is shown in Figure 4-16.

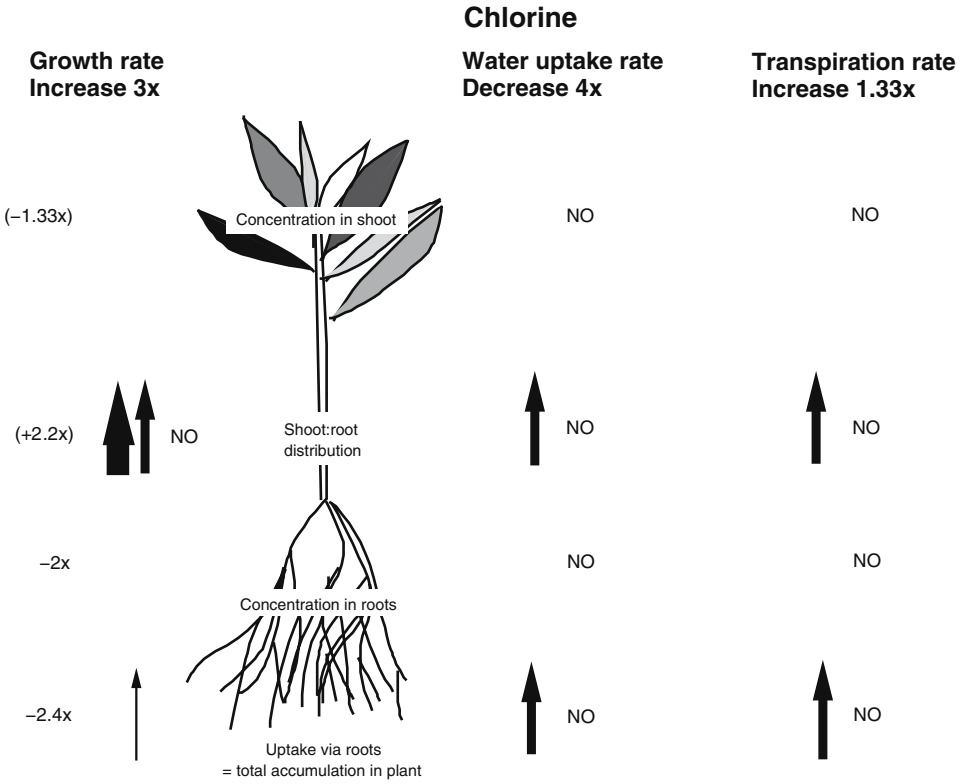

Figure 4-15. *Summary of influence on uptake normalized to root biomass, concentration in roots and shoots and distribution to the shoots, of Cl; shown as increase (thick arrows and +), decrease (thin arrows and –) or no change (medium arrows and NO) in relation to growth rate increase, water uptake rate decrease and transpiration rate increase, respectively (in parentheses = not significant). Differences between clones are indicated in two different values.*

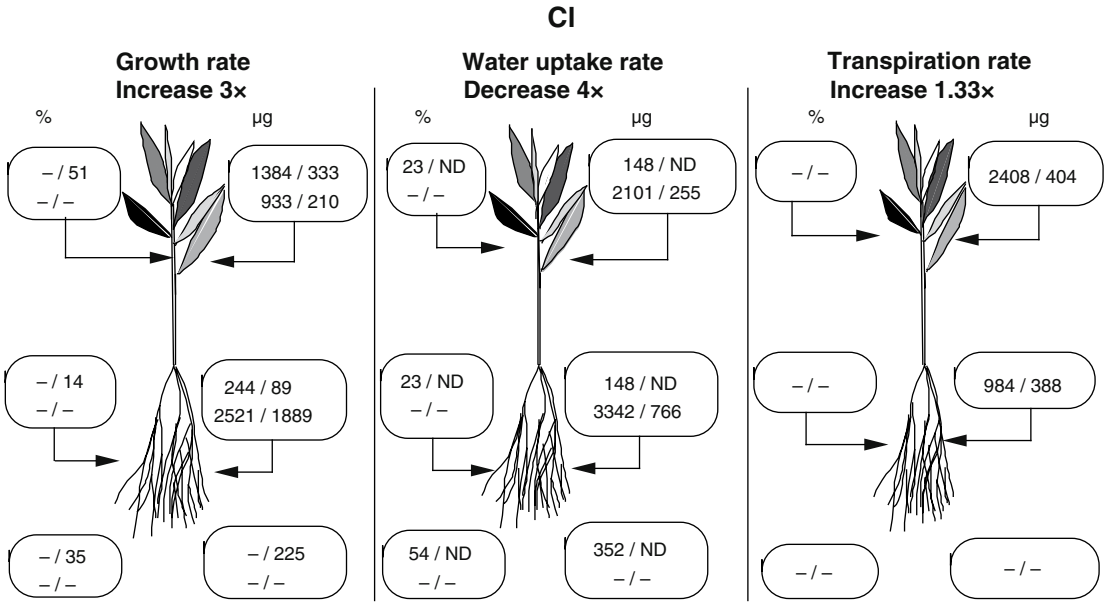

Figure 4-16. *Summary of net uptake and distribution between root and shoot of Cl, which had been taken up during 3 days. The distribution between solution, roots and shoot is given as percentage as well as in amount (µg) per compartment. Data to the left and to the right are from clone 31-1 and 4-2, respectively. The lower data is from low rate (of growth or water uptake) and the upper from high rate, meaning effects by increase in growth rate upwards and effects by decreasing in water uptake downwards. Data from the transpiration experiment are given as mean values due to absence of influence by transpiration. Data are based solely on what has been taken up during the 3 days experiment and the solution contained 647 µg Cl at start.*

4.4.9 Iodine

Iodine was present as I^-, and I uptake decreased with decreased water uptake in a nearly 1 to 1 relationship (Figure 4-9). The concentration in roots and shoots also decreased, though not to the same extent; this was likely due to decreased growth and to a reduced shoot:root growth (Figure 3-2) that increased tissue concentration of I, especially in the shoots. Transpiration effects were not evident. One may conclude that water uptake, though not transpiration, influences I uptake and translocation, as was the case for clone 31-1. Clone 4-2 did not take up or translocate I at low water flow, and none of the taken-up I was translocated to the shoots at the two lower water-uptake rates. It is possible that the higher transpiration rate of clone 31-1 than of clone 4-2 (Figure 3-13) accounts for the clone difference in I uptake and distribution.

The I uptake in the two clones was also differently influenced by the growth rate. Clone 4-2 displayed no uptake of I at the lowest growth rate (Figure 3-17), I uptake and distribution to the shoots only appearing at the higher growth rate. In the other clone growth rate had no effect on I uptake; however, distribution of I to the shoots increased due to decreased root concentration of I with increased growth rate. Iodine thus will not be diluted by increased growth rate. The distribution of I in the plant-solution system after three-days uptake and its effect by growth rate and water relations is shown in Figure 4-18.

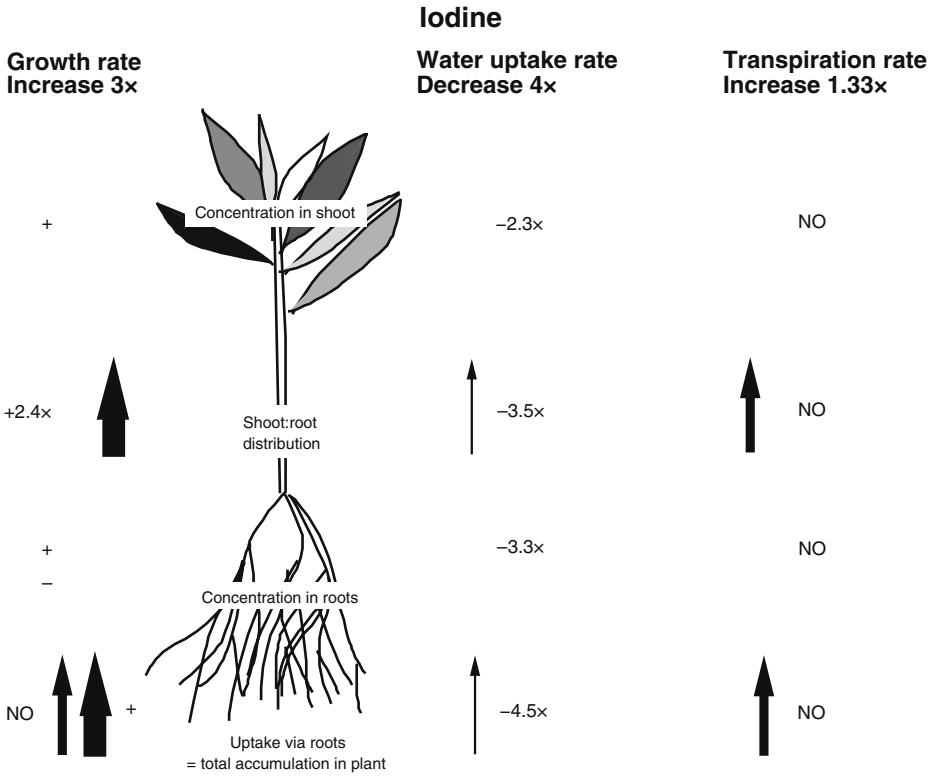

Figure 4-17. *Summary of influence on uptake normalized to root biomass, concentration in roots and shoots, and distribution to the shoots of I; shown as increase (thick arrows and +), decrease (thin arrows and –) or no change (medium arrows and NO) in relation to growth rate increase, water uptake rate decrease and transpiration rate increase, respectively (in parentheses = not significant). Differences between clones are indicated in two different values.*

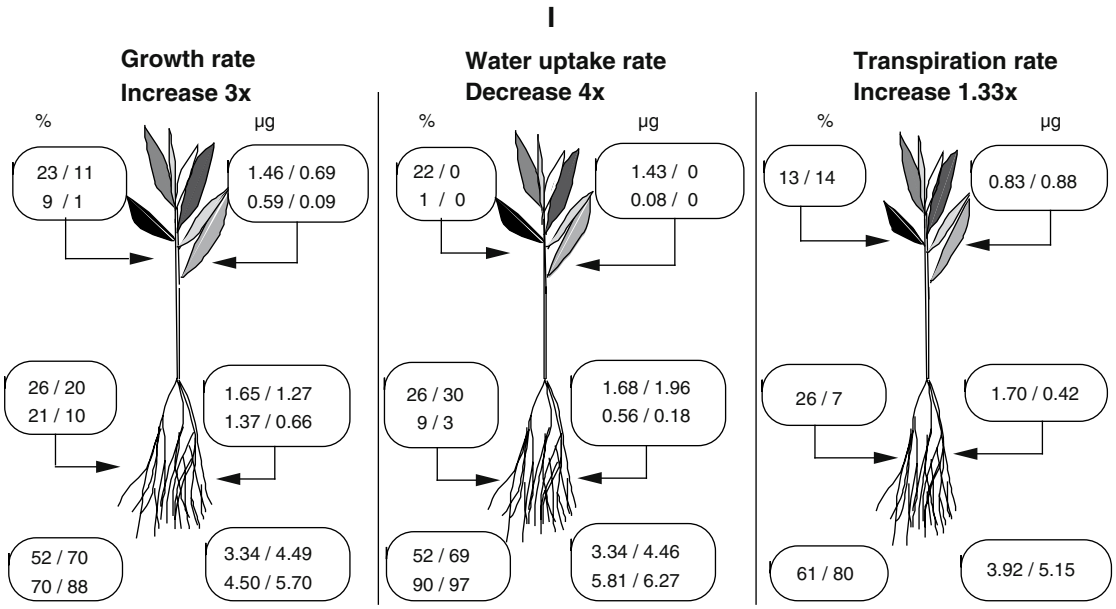

Figure 4-18. *Summary of net uptake and distribution between root and shoot of I, which had been taken up during 3 days. The distribution between solution, roots and shoot is given as percentage as well as in amount (µg) per compartment. Data to the left and to the right are from clone 31-1 and 4-2, respectively. The lower data is from low rate (of growth or water uptake) and the upper from high rate, meaning effects by increase in growth rate upwards and effects by decreasing in water uptake downwards. Data from the transpiration experiment are given as mean values due to absence of influence by transpiration. Data are based solely on what has been taken up during the 3 days experiment and the solution contained 6.45 µg I at start.*

4.5 Conclusion

This work shows that the uptake and distribution of various elements are differently influenced by water flow and growth rate; moreover, it is not possible to judge from their chemical properties how these elements will react. However, in most cases increased growth rate diluted the concentration of the element in the tissue, reduced uptake of water reduced the element uptake, while transpiration had no effect on the translocation of elements to the shoot (Table 4-1). The reason to the higher influence values in Table 4-2 compared with Table 4-1 is due to that data in Table 4-1 are based on total concentration values while in Table 4-2 data are based only on amount taken up during the experiment period.

Table 4-1. Summary of influence of water uptake on element total uptake normalized to root biomass, of transpiration on element distribution to the shoots, and of growth rate on element total uptake. Decrease (–), increase (+), and no change (0) is shown. Data in parentheses indicate tendencies, i.e. not significant.

	Ni	Sr	Mo	Cs	La	Th	Se	Cl	I
Water uptake decrease 4× influence on total uptake	–1.3×	–1.3×	0	–4×	–1.5×	–5×	–2×	0	–4.5×
Transpiration increase 1.3× influence the distribution to the shoot	(+2×)	0	0	0	+3×	0	+2×	0	0
Growth rate increase 3× influence total uptake	–3×	–2×	–3×	(+2×)	(–2×)	(–1.8×)	(–1.4×)	–2.4×	+/–

Table 4-2. Summary of influence of water uptake on element net uptake, of transpiration on element translocation to the shoots, and of growth rate on element net uptake. Decrease (–), increase (+), and no change (0) is shown. Data in parentheses indicate tendencies, i.e. not significant.

	Ni	Sr	Mo	Cs	La	Th	Se	Cl	I
Water uptake decrease 4× influence on net uptake	(–1.2×)	–2.2×	0	–5×	–1.6×	–5.5×	–1.5×	+3×	–12×
Transpiration increase 1.3× influence the translocation to the shoot	0	0	0	0	0	0	0	0	0
Growth rate increase 3× influence net uptake	–3.5×	–7.5×	–28×	+2×	–3×	–1.5×	(–1.4×)	–6×	(–1.3×)

4.6 Acknowledgement

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5 References

Abrams M M, Shennan C, Zasoski J, Burau R G, 1990. Selenomethionine uptake by wheat seedlings. Agron. J. 82: 1,127–1,130.

Asher C J, Butler G W Peterson P J, 1977. Selenium transport in root systems of tomato. J. Exp. Bot. 28: 279–291.

Bell C W, Biddulph O, 1963. Translocation of calcium. Exchange versus mass flow. Plant Physiol. 38: 610–614.

Bunzl K, Albers B P, Schimmack W, Belli M, Ciuffo L, Menegon S, 2000. Examination of a relationship between ^{137}Cs concentrations in soils and plants from alpine pastures. J. Environ. Radioact. 48: 145–158.

Buysse J, Van den Brande K, Merckx R, 1995. The distribution of radiocesium and potassium in spinach plants grown at different shoot temperatures. J. Plant Physiol. 146: 263–267.

Cataldo D A, Mc Fadden, K M, Garland T R Wildung R E, 1988. Organic constituents and complexation of nickel (II), iron (III), cadmium (II), and plutonium (IV) in soybean xylem exudates. Plant Physiol. 86: 734–739.

Cline J F, Hungate F P, 1960. Accumulation of potassium, caesium and rubidium in bean plants grown in nutrient solutions. Plant Physiol. 35: 826–829.

Coughtrey P J, Thorne M C, 1983. Radioelement distribution and transport in terrestrial and aquatic ecosystems. A critical review of data. Vol. 1. A. A. Balkema, Rotterdam, the Netherlands. ISBN 90 6191 278 4.

Ekvall L, Greger M, 2003. Effects of biomass-producing factors on Cd uptake in two Swedish ecotypes of *Pinus sylvestris*. Environ. Pollut. 121, 401–411.

Erdei L, Trivedi S, 1991. Caesium/potassium selectivity in wheat and lettuce of different K^+ status. J. Plant Physiol. 138: 696–699.

Garrels R M, Christ C L, 1965. Solutions, minerals and equilibria. Harper & Row, New York.

Göthberg A, Greger M, Holm K, Bengtsson B-E, 2004. Uptake and effects of cadmium, mercury and lead in the tropical macrophyte *Ipomea aquatica* in relation to nutrient levels. J. Environ. Qual. 33: 1,247–1,255.

Greger M, Ögren E, 1991. Direct and indirect effects of Cd^{2+} on the photosynthesis and CO_2-assimilation in sugar beets *(Beta vulgaris).* Physiol. Plant. 83: 129–135.

Greger M, 1999. Metal availability and bioconcentration in plants. In. Heavy metal stress in plants from molecules to ecosystems. (Eds M. N. V. Prasad and J. Hagemeyer). pp 1–28, Springer Verlag. ISBN 3-540-65469-0.

Greger M, Landberg T, 1999. Use of willow in phytoextraction. Int. J. Phytorem. 1:115–123.

Greger M, Landberg T, Berg B, 2001. Salix clones with different properties to accumulate heavy metals for production of biomass. Report to STEM. 51 pp, Akademitryck AB, Edsbruk, Sweden. ISBN 91-631-1493-3.

Greger M, 2004. Uptake of elements by plants. SKB TR-04-14, Svensk Kärnbränslehantering AB.

Ingestad T, 1982. Relative addition rate and external concentration; driving variables used in plant nutrition research. Plant, Cell Environ. 5: 443–453.

Kannan S, Ramani S, 1978. Studies on molybdenum absorption and transport in bean and rice. Plant Physiol. 62: 179–181.

Krämer U, Cotter-Howells J D, Charnock J M, Baker A J M, Smith J A C, 1996. Free histidine as a metal chelator in plants that accumulate nickel. Nature 379: 635–639.

Landberg T, Greger M, 1994. Can heavy metal tolerant clones of Salix be used as vegetation filters on heavy contaminated land?. *In* Willow vegetation filters for municipal wastewaters and sludges. A biological purification system. Proc. of a study tour, conference and work shop in Sweden, 5–10 June 1994. Ultuna, Uppsala. (Eds. P Aronsson & K Perttu), pp 133–144, Rapport 50, Avd. f. Skoglig intensivodling, SLU. ISBN 91-576-4916-2.

Landberg T, Greger M, 1996. Differences in uptake and tolerance to heavy metals in *Salix* from unpolluted and polluted areas. Appl. Geochem. 11: 175–180.

Landberg T, Greger M, **2002.** Interclonal variation of heavy metal interactions in *Salix viminalis*. Environ. Tox. Chem. 21: 2,669–2,674.

Larsson M, 1992. Translocation of nitrogen in osmotically stressed wheat seedlings. Plant Cell Environ. 15: 447–453.

Lindroth A, Cienciala E, 1996. Water use efficiency of short-rotation *Salix viminalis* at leaf, tree and stand scales. Tree Physiol. 16: 257–262

Markert B, 1992. Multielements analysis in plant materials – analytical tools and biological questions. In. Biogeochemistry of trace metals (Ed Adriano D C), pp 401–428, Lewis Publ., Boca Raton ISBN08-7371-523-3.

Markert B, 1994. Plants as biomonitors – Potential advances and problems. In Biogeochemistry of trace elements. (Eds Adriano D C, Chen Z S and Yang S S), pp 601–613, Science and Technology Letters, Northwood, NY.

Marschner H, 1995. Mineral nutrition of higher plants. Academic Press, Camebridge. ISBN 0-12-473542-8.

Mengel K, Kirkby E A, 1982. Principles of plant nutrition. 3rd ed. International Potash Institute, Bern.

Menzel R G, 1965. Soil–plant relationships of radioactive elements. Health Phys. 11: 1,325–1,332.

Momoshima N, Bondietti E A, 1990. Cation binding in wood: applications to understanding historical changes in divalent cation availability to red spruce. Can. J. Forest Res. 20: 1,840–1,849.

Mortensen J L, Marcusiu E C, 1963. The loss of radioactive isotopes from the leaves of plants in dry conditions. Radiat. Bot. 3: 163–167.

Myttenaere C, Masset M, 1965. Distribution of strontium and calcium in *Pisum sativum* in connection with the strontium-calcium ratio of nutrient solution. Ann. Physiol. Veg. 7: 97–104.

Perttu K, Eriksson J, Greger M, Göransson A, Blombäck K, Klang-Westin E, Landberg T, 2003. Förråd och flöden av kadmium i systemet mark-Salix. Content and fluces of cadmium in the soil–willow system. STEM-report, ER 19: 2003.

Shalhevet J, 1973. Effect of mineral type and soil moisture content on plant uptake of Cs-137. Radiat. Bot 13: 165–171.

Tiffin L O, 1972. Translocation of micronutrients in plants. In. Micronutrients in agriculture. (Eds. Mortwedt, J. J., Giordano, P. M. and Lindsay, W. L.), pp 199–229, Soil Science Society of America, Madison, WI.

Tiffin L O, 1977. The form and distribution of metals in plants: an overview. In Proc. Hanford life Sciences Symp., pp 315–334 U. S. Dept. of Energy, Symposium Series, Washington DC.

Van der Borght O, Kirchmann R, Van Puymbroek S, Fagniart E, 1967. ^{45}Ca, ^{85}Sr and ^{134}Cs absorption and translocation in isolated root systems of tomato plants. In Radioecological concentration processes. (Eds Åberg, B. and Hungate, F. P.), pp 415–420, Proc. International Symposium, Stockholm 1966, Pergamon Press. Oxford.

Van de Geijn S C, Petit C M, 1979. Transport of divalent cations. Cation exchange capacity of intact xylem vessels. Plant Physiol. 64: 954–958.

Vanek T, Soudek, P, Tykva R, 2001. Basic requirements for radiophytoremediation and radiophytomonitoring. In. Wastewater treatment and plants as a green liver: the European approach, experience and trends. pp 25, Abstract of COST Action 837 WG4 meeting at Larnaca 18–19 May 2001.

Wang Y, Greger M 2004 . Clonal differences in Hg tolerance, uptake and distribution in willow. J. Environ. Qual. 33: 1,779–1,785.

Whicker F W, Hinton T G, Orlandini K A, Clark S B, 1999. Uptake of natural and anthropogenic actinides in vegetable crops grown on a contaminated lake bed. J. Environ. Radioact. 45: 1–12.

White M C, Baker F D, Chaney R L, Decker A M, 1981. Metal complexation in xylem fluid. II. Theoretical equilibrium model and computational computer program. Plant Physiol. 67: 301–310.

Wolterbeek H Th, 1987. Cation exchange in isolated xylem cell walls of tomato. I. Cd^{2+} and Rb^{2+} exchange in adsorption experiments. Plant, Cell Environ. 10: 30–44.

Zhang S Z, Shan X-Q, 2001. Speciation of rare earth elements in soil and accumulation by wheat with rare earth fertilizer application. Environ. Pollut. 112: 395–405.