

Some effects of nitrogen nutrition on caesium uptake and translocation by species in the Poaceae, Asteraceae and Caryophyllidae

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Abstract

There is current interest in managing and manipulating ¹³⁷Cs transfer from soil to plants. We hypothesized that N source might affect Cs uptake by plants and report experiments that confirm this. Uptake experiments using hydroponics with a variety of species in the Poaceae, Asteraceae and Caryophyllid clade grown in a variety of N regimes with excess N and then acutely exposed to Cs showed that N nutrition could affect Cs uptake rates, total amounts of Cs taken up and root:shoot ratios of Cs. In general, the Caryophyllids tested produced significantly less shoot and root biomass but had higher Cs uptake rates when grown on NH₄⁺ rather than NO₃⁻, whilst species from the Poaceae and Asteraceae almost always produced similar shoot and root biomass and had similar Cs uptake on NH₄⁺, NO₃⁻ or glycine as N sources. This is the first time that plants grown on an organic-N source have been demonstrated to take up Cs. Physiological experiments using N-starvation and the N-metabolism inhibitor methionine sulfoxamine (MSX) demonstrated that Cs transport into the root was inversely related to NH₄⁺ transport, i.e. NH₄⁺-grown plants had higher Cs uptake rates if there is no NH₄⁺ present during uptake but lower Cs uptake rates if NH₄⁺ is present. It is suggested that taking account of N ecophysiology might help refine predictions of soil-to-plant transfer of ¹³⁷Cs and, in some instances, be useful for managing or manipulating it. It is noted that there is much recent research into N nutrition in plants that might be useful in achieving this.

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1. Introduction

Research into ¹³⁷Cs transfer from soils to plants has recently begun to expand from making predictions of plant ¹³⁷Cs concentrations to managing and manipulating them. For example, in most soils contaminated with ¹³⁷Cs it is now clear that it will persist in the rooting zone for many years (Smith et al., 2000), necessitating amelioration strategies based on managing ¹³⁷Cs transfer from soils to plants (White et al., 2003). Further, because there are currently no economically viable methods to clean up all ¹³⁷Cs-contaminated soils, and enhanced plant uptake of other contaminants from soils is showing potential as a decontamination method (e.g. Huang et al., 1998; Ma et al., 2001), ‘phytoextraction’ has

been investigated for soils contaminated with ¹³⁷Cs (Lasat et al., 1997; Dushenkov et al., 1999; Fuhrmann et al., 2003; Willey et al., 2001). These trials have shown that manipulations to enhance soil-to-plant transfer are needed if phytoextraction is to be useful for ¹³⁷Cs.

Minotti et al. (1965) and Jackson et al. (1968) reported that NH₄⁺-grown wheat seedlings had significantly higher Cs uptake than NO₃⁻-grown ones, and the experiments of Shaw and Bell (1991) showed that NH₄⁺ and Cs could compete during uptake by wheat. Given that NH₄⁺ concentrations in soils can vary by several orders of magnitude (Glass et al., 2002), such results indicate that soil NH₄⁺ concentrations might affect Cs transfer from soil to plants. Evans and Dekker (1969) provided the first field test of this phenomenon and showed that additions of NH₄⁺ to soil significantly increased ¹³⁷Cs uptake by oat plants. Similar results have recently been reported with ¹³⁷Cs uptake by rye grass (Paasikillio

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and Sormunen-Cristian, 2002). Significant NH_4^+ -induced increases in Cs uptake have, therefore, all been reported in plants in the family Poaceae (Wheat, Oats and Rye). Experiments at Brookhaven National Laboratory (Lasat et al., 1997; Lasat et al., 1998; Fuhrmann et al., 2002; Fuhrmann et al., 2003) and near Chernobyl (Dushenkov et al., 1999) have shown that NH_4^+ additions can increase ^{137}Cs desorption from soils by an order of magnitude in the laboratory but that additions of NH_4^+ to soil in the field did not increase ^{137}Cs transfer to plants, almost all of which were in the families Chenopodiaceae or Amaranthaceae on the Caryophyllid clade.

Molecular biological investigations have transformed the understanding of plant N-nutrition (Glass et al., 2002). It is now thought that up to seven transport proteins in the AMT1 family are responsible for NH_4^+ uptake and transport in plants (Glass et al., 2002), although with the exception of AMT1.1, their Cs transport capacity is unknown. Their expression is dependent on N source, plant N status, plant species and plant organ. AMT1.1 has some Cs transport activity (Ninneman et al., 1994), and given that NH_4^+ and Cs^+ have a very similar hydrated size, which causes them to interact during adsorption to soil, interactions between NH_4^+ and Cs transport seem possible. The uptake of NO_3^- by plants is primarily regulated by NRT2 proteins (Glass et al., 2002), which seem unlikely to be able to transport Cs, but the presence of NO_3^- up-regulates expression of NO_3^- transporters and down-regulates expression of NH_4^+ transporters, probably via feedback based on cytosolic glutamine concentrations (Crawford and Glass, 1998). Interestingly, it has also become clear in the last decade that many plants can use organic forms of soil nitrogen, such as glycine, in significant quantities (Lipson and Nasholm, 2001), including both plant species that grow in ^{137}Cs contaminated agricultural (Nasholm et al., 2000) and natural ecosystems (Persson and Nasholm, 2001). Uptake of organic N also affects NH_4^+ uptake via feedback through cytosolic glutamine concentrations (Glass et al., 2002). The genes and proteins that control numerous aspects of N uptake and metabolism in the model plant *Arabidopsis thaliana* are rapidly being identified (Crawford and Forde, 2002). Overall, such studies are emphasising the central role of N uptake and metabolism in whole-plant physiology and ion uptake (Crawford et al., 2000). Given that such research is opening up the possibility of genetically engineering plant N uptake, with consequent effects on ion uptake, it seems an appropriate moment to reinvestigate the effects of N nutrition on Cs uptake by plants.

It is now known that plants in the Poaceae, such as the wheat used by Minotti et al. (1965), Jackson et al. (1968), and Shaw and Bell (1991) have, on average, much lower Cs uptake than those on the Caryophyllid clade in such families as the Chenopodiaceae, Amaranthaceae and Polygonaceae (Broadley and Willey, 1997; Broadley et al., 1999a,b; Tang et al., 2003). Species in the Asteraceae have also been noted to have high uptake of Cs (Tang and Willey, 2003; Willey et al., 2005). Such inter-taxa differences suggest that efforts

to minimise soil-to-plant transfer of Cs might best focus on species in the Poaceae, whilst efforts to maximise transfer might focus on members of the Caryophyllid clade and the Asteraceae. Significantly, it also appears that there might be some phylogenetic constraints on the sources of nitrogen that plants can utilise, with the Poaceae often reported as preferring a mixed $\text{NO}_3^-/\text{NH}_4^+$ source, although a wide phylogenetic perspective on plant N preferences has not yet been reported (Glass et al., 2002). Here, using hydroponic systems in which soil interactions have been eliminated, we report five separate experiments that used plants in the Poaceae, Asteraceae and Caryophyllidae to investigate different aspects of plant N-nutrition affects on Cs uptake. One objective was to clarify the apparently contradictory effect of NH_4^+ nutrition on Cs uptake in plants in the Poaceae and Caryophyllidae but our overall aim was to investigate the effects of the N-nutrition of plants on Cs uptake.

2. Methods

In experiments in Sections 2.1–2.3 plants were grown hydroponically in large volumes of different Cs-free N-sources that provided excess readily available nutrients and then given an acute exposure to Cs by immersing their roots in small volumes of solutions containing just radiolabeled Cs and physiological saline (CaSO_4). This eliminated the effects of soil factors and nutrient deficiencies on Cs uptake, prevented interactions (either long-term or short-term) between Cs uptake and nutrient uptake, and gave approximately instant insights into the effects on Cs uptake by minimising the effects of homeostatic mechanisms and other feedback effects during radiolabeling. Protocols of this type were chosen in an attempt to dissect physiological effects of N-source rather than to simulate field conditions. In experiments in Sections 2.1–2.3 there was no significant depletion of radio-caesium during radiolabeling and, because a stable Cs carrier was used, no detectable radio-caesium adsorbed to flasks or tubs.

2.1. Nitrogen source and ^{137}Cs activities in plant shoots

The objective of this experiment was to test the effects of the full range of N-sources that plants are now known to utilise on Cs uptake to shoots using plant species known to have contrasting Cs uptake behaviours. Seeds of *Hordeum vulgare*, *Amaranthus cruentus*, *Chenopodium album*, *Carthamus tinctorius* and *Zinnia elegans* were surface sterilised by soaking in 1% NaOCl for 10 min then 5% H_2O_2 for 1 min, rinsed in deionised water, and germinated in heat-treated, inert vermiculite in 36 gauze-bottomed tubs of each species for hydroponic culture. Nine replicates of each species were cultured in four Hoagland's solutions modified to contain four different N sources: zero N, $\text{Ca}(\text{NO}_3)_2$, glycine and NH_4Cl . The three N solutions each contained 0.715 mM N. Each growth solution had a volume of 40 L, had pH adjusted

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