ACTA UNIVERSITATIS AGRICULTURAE SUECIAE

SILVESTRIA 171

Distribution and Seasonal Variation of Macro-nutrients, Starch and Radio-nuclides in Short Rotation *Salix* Plantations

Yuehua von Fircks

SWEDISH UNIVERSITY OF AGRICULTURAL SCIENCES

Distribution and seasonal variation of macro-nutrients, starch and radio-nuclides in short rotation *Salix* plantations

Yuehua von Fircks

Akademisk avhandling som för vinnande av skoglig doktorsexamen kommer att offentligen försvaras i sal L, SLU, Ultuna, tisdagen den 6 februari 2001, kl. 9.30.

Abstract

The present work consists of two main parts. The first part includes studies of distribution and seasonal variation of macro-nutrients and starch in *Salix* plants. The second part deals with the uptake and distribution of radio-nuclides ^{137}Cs and ^{90}Sr in *Salix* plants grown in contaminated soil.

In the first part, the experiments were carried out in growth chambers and under outdoor conditions, using cutting-propagated *Salix viminalis* L. and *Salix dasyclados* Wimm. plants. Nutrients were supplied using steady-state nutrient techniques with two nutrient levels. The studies showed that plants cultured under high availability of nutrients had: i) higher concentrations of all macro-nutrients, ii) a delay of leaf senescence and dormancy, iii) an earlier growth start, and iv) contained less starch compared with plants grown under low nutrient availability plants. Between 40-50% of N and about 60% of P was withdrawn from the leaves prior to abscission and stored mainly in the aboveground perennial organs. Starch proved to be an abundant nutrient, particularly in roots, which had larger amounts of starch than aboveground plant parts during most of the seasons. The root starch in coppiced plants decreased more rapidly than in intact plants, indicating that starch reserves are important for early phases of growth and that coppicing creates a strong sink for internal carbohydrate reserves.

In the second part, an experiment was carried out in lysimeters contaminated artificially with ^{137}Cs and ^{90}Sr, and a field trial was established on agricultural soil in an area contaminated with radio-caesium from the Chernobyl accident. These studies showed that the ^{137}Cs concentration in leaves decreased from summer to autumn while the ^{90}Sr concentration in leaves increased during the same time. The fine roots had the highest ^{137}Cs concentration, whereas the ^{90}Sr concentration was highest in leaves. The low transfer rate of ^{137}Cs from the soil to the plants resulted in low levels of ^{137}Cs in the wood ashes. It was therefore concluded that fast-growing *Salix* coppicing systems exhibit promising features for a possible economic utilisation of contaminated agricultural soils.

Keywords: accumulation, ash recycling, Chernobyl accident, contamination, coppice systems, nutrient cycling.

Distribution:
Swedish University of Agricultural Sciences
Department of Short Rotation Forestry
Box 7016, SE-750 07 Uppsala, Sweden

Uppsala 2000
ISSN 1401-6230
ISBN 91-576-6055-7

Distribution and Seasonal Variation of Macro-nutrients, Starch and Radio-nuclides in Short Rotation *Salix* Plantations

Yuehua von Fircks
Department of Short Rotation Forestry
Uppsala

Doctoral thesis
Swedish University of Agricultural Sciences
Uppsala 2000

Acta Universitatis Agriculturae Sueciae
Silvestria 171

ISSN 1401-6230
ISBN 91-576-6055-7

Tryck: SLU Service/Repro, Uppsala 2000

Abstract

von Fircks, Y. 2000. *Distribution and seasonal variation of macro-nutrients, starch and radio-nuclides in short rotation* Salix *plantations*
Doctor's dissertation.
ISSN 1401-6230, ISBN 91-576-6055-7.

The present work consists of two main parts. The first part includes studies of distribution and seasonal variation of macro-nutrients and starch in *Salix* plants. The second part deals with the uptake and distribution of radio-nuclides ^{137}Cs and ^{90}Sr in *Salix* plants grown in contaminated soil.

In the first part, the experiments were carried out in growth chambers and under outdoor conditions, using cutting-propagated *Salix viminalis* L. and *Salix dasyclados* Wimm. plants. Nutrients were supplied using steady-state nutrient techniques with two nutrient levels. The studies showed that plants cultured under high availability of nutrients had: i) higher concentrations of all macro-nutrients, ii) a delay of leaf senescence and dormancy, iii) an earlier growth start, and iv) contained less starch compared with plants grown under low nutrient availability plants. Between 40-50% of N and about 60% of P was withdrawn from the leaves prior to abscission and stored mainly in the aboveground perennial organs. Starch proved to be an abundant nutrient, particularly in roots, which had larger amounts of starch than aboveground plant parts during most of the seasons. The root starch in coppiced plants decreased more rapidly than in intact plants, indicating that starch reserves are important for early phases of growth and that coppicing creates a strong sink for internal carbohydrate reserves.

In the second part, an experiment was carried out in lysimeters contaminated artificially with ^{137}Cs and ^{90}Sr, and a field trial was established on agricultural soil in an area contaminated with radio-caesium from the Chernobyl accident. These studies showed that the ^{137}Cs concentration in leaves decreased from summer to autumn while the ^{90}Sr concentration in leaves increased during the same time. The fine roots had the highest ^{137}Cs concentration, whereas the ^{90}Sr concentration was highest in leaves. The low transfer rate of ^{137}Cs from the soil to the plants resulted in low levels of ^{137}Cs in the wood ashes. It was therefore concluded that fast-growing *Salix* coppicing systems exhibit promising features for a possible economic utilisation of contaminated agricultural soils.

Keywords: accumulation, ash recycling, Chernobyl accident, contamination, coppice systems, nutrient cycling.

Author's address: Yuehua von Fircks, Swedish University of Agricultural Sciences, Department of Short Rotation Forestry, Box 7016, SE-750 07 Uppsala, Sweden
Yuehua.von.Fircks@lto.slu.se

Contents

Appendix

Papers I-IV

The present thesis is based on the following papers, which will be referred to by their Roman numerals.

I. von Fircks, Y. & Ericsson, T. Seasonal variation of macro-nutrients in *Salix dasyclados* Wimm. grown at two nutrient levels. (Submitted).

II. von Fircks, Y. & Sennerby-Forsse, L. 1998. Seasonal fluctuation of starch in root and stem tissues of coppiced *Salix viminalis* L. plants grown at two nitrogen regimes. Tree Physiology 18, 243-249.

III. von Fircks, Y., Rosén, K. & Sennerby-Forsse, L. Uptake and distribution of ^{137}Cs and ^{90}Sr in *Salix viminalis* L. plants. (Submitted)

IV. von Fircks, Y. & Rosén, K. Uptake and accumulation of ^{137}Cs in *Salix viminalis* L. grown on radio-contaminated agricultural soils. (Manuscript).

The published paper is reproduced with permission from Tree Physiology.

Introduction

Background

In Sweden, short rotation forestry systems with fast-growing *Salix* species are used for production of biomass for energy (Christersson et al. 1993). The plantations are established as an alternative crop on surplus agricultural land, *i.e.* areas not used for food or fodder production. The potential annual production in energy forestry exceeds 10 t/ha per year over a lifetime of 20-25 years (Sennerby-Forsse et al. 1992, Christersson et al. 1993). With the 16,000 ha presently cropped with *Salix*, annual energy production can be estimated at 0.8 TWh (assuming 5 MWh t^{-1} d.w.), which corresponds to approximately 1% of the Swedish biofuel production (Bollmark 2000). Production of woody biomass will also add to the sequestering of carbon dioxide in order to keep the net accumulation of atmospheric greenhouse gases down. The net carbon uptake in a *Salix* plantation producing 10 tonnes of dry matter per ha and year is approximately 250 kg, which equals 917 kg CO_2 per hectare per year (Perttu & Aronsson 1999). In Sweden, the main *Salix* species used for short rotation forestry are *Salix viminalis* L. and *Salix dasyclados* Wimm. Selected and improved plant materials, which are hardy and resistant, are grown in coppice plantation systems in southern and middle parts of Sweden (Elowson 1999). A short rotation *Salix* plantation is established with 20-cm long, dormant stem cuttings. The cuttings are planted in the spring (May-early June) at a depth of about 18 cm. During the first year of establishment 2-3 shoots will emerge from the cutting and the root system develops from preformed root primordials in the cutting (Fjell 1985, Sennerby-Forsse & Johansson 1989). After 3-5 years the stems are harvested in wintertime, and during the next spring, new shoots will grow from auxillary buds at the remaining stool or stump. The ability to produce new shoots after removal of the shoot system exists in many deciduous and some coniferous trees, and is particularly expressed in *Salix viminalis* and *Salix dasyclados* (Sennerby-Forsse et al. 1992, Sennerby-Forsse & Zsuffa 1995). The woody biomass is harvested for production of wood chips and is used in district heating systems as a replacement for oil and coal.

Commercially grown *Salix* plantations in Sweden are mainly established south of 60° N, i.e. in areas where the growing season is, on average, 180 days or longer (Alriksson 1997). Cumulative global radiation in the area of interest for *Salix* production range from 3400 to 3700 MJ m^{-2} y^{-1} (Josefsson 1995). Cumulative precipitation in Sweden during the growing season declines from the southwest to the northeast, ranging from 350 to 550 mm (Eriksson 1992). As with other crops, production in short-rotation *Salix* plantations depends largely on the soil characteristics. In sandy soils, the availability of nutrients and water is critical for production of willow biomass. Loam, clay loam and heavy clay are fertile soils with high water retention capacity and are therefore often more suitable for short-rotation *Salix* plantations (Danfors et al. 1998). Consequently, the choice of site and appropriate fertilisation regime are of great importance in order to achieve high yields (Christersson 1986, Alriksson 1997).

In the central-eastern part of Sweden there are areas of agricultural land suitable for energy forestry. However, in May 1986, parts of these areas were contaminated with radio-caesium (Cs) and radio-strontium (Sr) from the accident at the nuclear power plant at Chernobyl in the Ukraine. The released ^{137}Cs and ^{90}Sr from the Chernobyl accident were deposited over large areas of Europe. The total release of ^{137}Cs amounted to 100 PBq and of ^{90}Sr to 10 PBq (Devell et al. 1996). In Sweden, the total fallout of ^{137}Cs was estimated to be 4.25 PBq or about 5% of the amount released from Chernobyl. The deposition of ^{137}Cs, mainly in central and northern parts of Sweden, ranged from 10 to >80 kBq/m^2, with a maximum of more than 200 kBq/m^2 (Edvardsson 1991, Mattsson & Moberg 1991) (Figure 1). The deposition levels of Chernobyl-derived ^{90}Sr in Sweden have not been established, but are estimated to about one percent of the ^{137}Cs-fallout (Forsberg 2000). These nuclides are chemically related to, and behave similarly to, some of the bio-essential cations. For example, whereas Cs can be compared with K, Sr is similar to Ca, and a common trait for all four is that they easily enter the food chain (Shaw & Bell 1994).

The Swedish radiological protection limit of ^{137}Cs for the consumption of food was set at 300 Bq/kg, but with a special limit of 1500 Bq/kg for reindeer, wild game, freshwater fish, berries and mushrooms (Åhman & Åhman 1994). Although the deposition levels of ^{137}Cs in most Swedish agriculture soils permit food production, there are other areas in Europe with heavily contaminated soils, which are not suitable for production of food or fodder. The search for alternative use of radio-contaminated areas has resulted in a growing interest in energy plantations with fast-growing *Salix* species.

However, knowledge regarding the effects of radio-nuclides on growth processes and production in *Salix* is very limited and new studies in this field were therefore initiated. Some years after the Chernobyl accident, a pilot study using contaminated soils in a pot experiment showed that young *Salix* plants accumulated caesium preferably in the root system (Sennerby-Forsse et al. 1993). The results from this pilot study led to a more comprehensive project including a field study with the main aim to achieve some understanding of the cycling of radio-nuclides in *Salix* plants. Since biomass plantations are cultivated mainly for the production of wood chips for combustion it was also considered important to assess the content of radio-nuclides in the ashes after combustion of the wood chips.

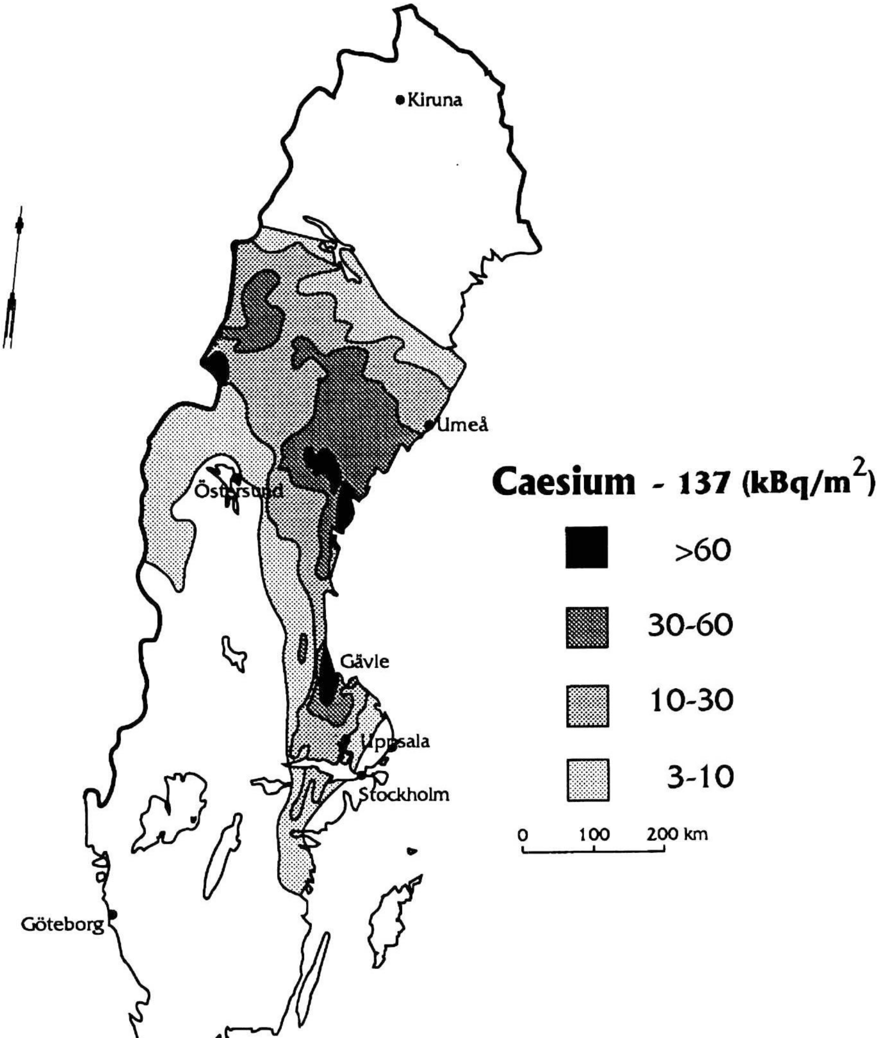

Figure 1. The deposition of ^{137}Cs in Sweden from the Chernobyl accident, May to October 1986 (SGAB 1986).

The distribution and seasonal variation of mineral nutrients and starch in plants

Macro-nutrients

Stored mineral nutrients such as K, P, Ca, Mg and S in perennial tissues are of vital importance for early season leaf development (Melillo 1981). The nutrient reserves will help plants to overcome periods of low soil temperature and hence low root activity. The availability of these nutrients in plant tissues is also important during later stages of growth since each of them in different ways affect the growth process through carbon fixation, carbon allocation and the build-up of carbohydrate stores in leaves and perennial organs (Ericsson 1995). The amount of stored minerals in perennial organs is the result of late season root uptake and/or retranslocation of easily mobile elements from senescing leaves. In order to establish highly productive and sustainable *Salix* plantations, it is essential to pay attention to the seasonal dynamics in nutrient reserves, and the factors affecting their build-up and utilisation. Fertilisation and harvesting practices, stresses in the form of frost, insects/diseases, drought, and soil compaction are factors affecting the nutrient stores and hence the productivity of intensively managed *Salix* plantations (Christersson 1999).

According to the literature, most of the studies so far in the area of nutrient cycling in plants have been directed at nitrogen, while information about the other macro-nutrients is less abundant. Titus & Kang (1982), Tromp (1983), Kato (1986) and Millard (1993, 1996) studied seasonal dynamics of N in trees and showed that leaves constitute the dominant N sink during summer. It has been shown that leaves on small trees may contain up to 50% of the total N in plants (Dickson 1991). Up to 80% of the leaf N can be retranslocated into perennial tissues before leaf abscission (Chapin & Kedrowski 1983, Bernier 1984, Ericsson 1994). In perennial plant parts, N is stored both as soluble amino compounds and as proteins. In apple trees, about 90% of the N are stored as protein during winter, mostly in stem bark and also to some extent in the root (Titus & Kang 1982). Stored N is remobilised the following spring and used for growth of new shoots (Bollmark 2000). The seasonal allocation pattern of N varies between species and cultural conditions (Chapin & Kedrowski 1983, Millard 1996). Regarding P, K, Ca and Mg, Chapin et al. (1990) concluded that the first three nutrients are recycled in plants while Ca is not. Chapin & Kedrowski (1983) reported P storage in evergreen trees to be primarily in foliage, whereas in deciduous trees, P is stored in stems. According to Kramer & Kozlowski (1979) and Ericsson (1994), the status of mineral nutrients in plants is an important factor that affects synthesis and translocation of reserve nutrients.

The following short overview of the mineral elements included in this study is focused on their main role in plant growth, carbon allocation and reserve accumulation in leaves and perennial tissues.

Nitrogen

Nitrogen is found in every living cell, in the chlorophyll and in proteins/enzymes. Abundance of N leads to green succulent growth while N deficiency often causes loss of colour, reduction in protein production and gradual yellowing and stunted growth (Kramer & Kozlowski 1979, Mehra & Farago 1994). Root growth is favoured over shoot growth under N-limiting growth conditions (Ericsson 1995).

It has also been shown that N-shortage results in a build-up of non-structural carbohydrates (starch) in the leaves (McDonald et al. 1986, Thorsteinsson et al. 1990, Rytter & Ericsson 1993, Bollmark et al. 1999).

Phosphorus

Phosphorus is an essential element for all living organisms since it is part of the DNA molecule. P is also found in the membrane and participates in metabolic processes of the cells (Marschner 1995). In the case of P limitation, starch accumulation occurs as a consequence of a reduced sugar export from the chloroplasts to the cytosol (Champigny 1985, Sharkey 1985, Sivak & Walker 1986). Carbon allocation to roots is favoured in plants limited by P (Ericsson & Ingestad 1988).

Potassium

Potassium is essential in all cell metabolic processes. K has a major role in plant nutrition as an enzyme activator for a number of processes including respiration, protein synthesis and photosynthesis (Marschner 1995). K-limitation has been found to cause a decrease in the rate of photosynthesis (Linder & Rook 1984) and a concomitant decrease in the concentration of soluble carbohydrates, and particularly starch, in the leaves (Ericsson & Kähr 1993). Carbon allocation to roots, and hence root growth, is restricted in plants limited by K (Ericsson & Kähr 1993, Ericsson 1995).

Calcium

Calcium occurs in considerable quantities in cell walls as calcium pectate and apparently influences cell wall elasticity. It is also involved in N metabolism (Kramer & Kozlowski 1979). Ca is relatively immobile, and a deficiency of this element has been shown to result in serious injury to meristematic regions (Kramer & Kozlowski 1979). It has long been known that the nature and extent of the expression of environmental stresses, particularly ion stresses, in plants depends on Ca. Shortage of Ca interferes mainly with the activity of apical shoot meristems, and in this way favours root growth over shoot growth (Ericsson 1995).

Magnesium

Magnesium is essential for chlorophyll formation and activation of a large number of enzymes, particularly those required for carbon fixation (Clarkson & Hanson 1980). Shortage of Mg will have a negative impact on the formation of carbohydrate stores (Ericsson & Kähr 1995). As in the case of K-shortage, plants limited by Mg allocate less carbon resources to roots compared with optimal Mg conditions (Ericsson & Kähr 1995).

Sulphur

Sulphur is a constituent of the amino acids cysteine and methionine, and hence of proteins (Marschner 1995). It is also very important for the action of some enzymes and coenzymes. Accordingly, protein synthesis is inhibited under conditions of S-deficiency. S-limited plants show increased carbohydrate stores and favour root growth over the shoot (Ericsson 1995).

Starch/carbohydrates

After shoot harvest in *Salix* coppice systems the new shoot generation initially relies on internal nutrient reserves in roots and stumps (Dickmann & Pregitzer 1992, Sennerby-Forsse et al. 1992). These reserves are mainly composed of carbohydrates (starches and different types of sugars), lipids and proteins (N) (Sauter et al. 1988, Wetzel et al. 1989). Starch is the most common storage form of carbohydrates in trees (Tromp 1983, Dickson 1991, Kozlowski 1992) and is often used as an indicator of tree carbohydrate status (Ford & Deans 1977, Adams et al. 1986). Starch/sugars are direct products of photosynthesis and the primary energy storage compounds. They are also the basic organic substances from which most other organic compounds found in plants are synthesised. Carbohydrate reserves in roots and stumps are believed to play an important role in the resprouting of coppice (Dickmann & Pregitzer 1992, Kozlowski 1992).

Carbohydrates and especially starch have been examined in many tree species (Kramer & Kozlowski 1979, Nelson & Dickson 1981, Essiamah & Eschrich 1985, Bonical et al. 1987, Kozlowski 1992). Concentrations and locations of these nutrient reserves in trees vary during the growing season. In branches and stems of deciduous trees, starch concentration often has two maxima, one in autumn and one in spring (Essiamah & Eschrich 1985). Starch is accumulated in the trees in late summer and autumn, as the growth-demand decreases. Associated with cooler temperatures in winter, the stored starch is hydrolysed to soluble sugar (*e.g.* sucrose, raffinose, stachyose), which is believed to increase cold-hardiness (Levitt 1980). Starch is re-synthesized in early spring before bud-break and depleted again during the spring growth flush (Essiamah & Eschrich 1985). According to literature, the pattern of starch accumulation and storage in roots differs between species and site conditions (Dickson 1991). Although much is known about starch in trees, few studies relate to coppice regeneration and the role of starch in resprouting (Sennerby-Forsse & von Fircks 1987, Bollmark et al. 1999). A better understanding of the role of nutrient reserves in coppice plants would help elucidate the mechanisms underlying coppice yields and provide a more reliable set of criteria for selecting and improving coppice plants.

Uptake and distribution of radio-nuclides from soil to plant

The main long-term pathway of radio-nuclides to humans after fallout is through intake of contaminated food products, either plant- or animal products. For this reason, many studies of the uptake of radio-nuclides in food- or fodder plants have been carried out (Coughtrey & Thorne 1983, Lembrechts 1993). The most extensively studied radio-nuclides with respect to biological incorporation and the contamination of food chains are ^{137}Cs and ^{90}Sr.

Caesium, ^{137}Cs

This alkaline metal, a man-made isotope with a physical half-life of 30.2 years, emits both gamma- and beta radiation during decay and shows rapid incorporation into biological systems. Cs has been reported to be chemically related to K and enters plants and the food chain in a similar manner to K. ^{137}Cs is distributed rather homogeneously throughout the body, resulting in a uniform whole-body irradiation with a resulting risk of cancer in various organs. It has been spread in relatively large quantities through nuclear weapon tests and accidental releases from nuclear power plants.

Strontium, ^{90}Sr

^{90}Sr is an alkaline earth metal and has a physical half-life of 28.1 years. Sr has been considered to be chemically related to Ca and also enters easily into the food chain. It has been spread in relatively large quantities through nuclear weapon tests and accidental releases from nuclear power plants. ^{90}Sr is a pure beta-emitter and is specifically transferred to the bone tissue, thereby increasing the risk of skeletal cancer (Forsberg 2000).

It is well known that Cs and Sr can easily be transferred into plants and that the soil - plant - relationship is rather complex. There is considerable evidence to suggest that variation exist between plants species in the uptake ability of radio-nuclides from the soil. Other factors affecting uptake and distribution of radio-nuclides in plants are soil type (soil texture, soil moisture content, soils mineral content and soil nutrient status), chemical forms of radio-nuclides in soil, climate, mycorrhizas and agricultural practices (Carini 2001).

K-fertilisation has been reported to affect and decrease the transfer of Cs from contaminated soils to the plants (De Preter et al. 1991, Rosén 1991, Smolders et al. 1996). It has been shown that K can replace Cs in exchangeable sites in the soil matrix due to their chemical similarity (Lembrechts 1993). Other studies have demonstrated that the behaviour of Cs deviated from K to a certain degree, since the former element was taken up more slowly than the latter (Marschner 1986). It has also been reported that Ca-fertilisation reduces the transfer of Sr from contaminated soils to the plants (Nisbet 1993).

Studies concerning the uptake of radio-nuclides from soil to plants started in the 1950s following the tests of nuclear weapons. After the Chernobyl accident, the number of studies increased dramatically all over the world. Different climate zones as well as different eco-systems and plant types (woody trees, shrubs and herbaceous plants) have been the subject of investigations (Coughtrey & Thorne 1983, Lembrechts 1993, Carini 2001). Results concerning uptake of Cs and Sr vary between different species according to, among other factors, different soil characteristics (Carini 2001). Carini (2001) showed that the Cs uptake was higher in trees while the uptake of Sr was higher in shrubs. Both trees and shrubs had a higher uptake rate of Cs and Sr than annual crops (Carini 2001, Coughtrey et al.

2001). Many species are known to accumulate comparatively high concentrations of Cs under natural and semi-natural conditions, often much higher than those associated with agricultural ecosystems (Howard et al. 1996, Rosén 1996). Studies in Sweden after the Chernobyl accident have dealt with the flow of ^{137}Cs and ^{90}Sr between soil and plants both in boreal forest ecosystems (Johanson et al.1991, Melin et al. 1994, Nylén 1996, McGee et al. 2000) and in an agricultural environment with annual crops (Rosén 1996, Forsberg 2000). In general, results have shown that uptake of ^{137}Cs in forest plants is higher than in agricultural plants. The concentrations of ^{137}Cs in a number of plant species in boreal forest ecosystems was ranked highest in heather (*Calluna vulgaris*) followed by bilberry (*Vaccinium myrtillus*) >Scots pine (*Pinus syvestris*) >birch (*Betula pendula*) >fireweed (*Epilobium angustifolium*), which is supposed to be a general trend in the boreal forests (Nylén 1996). Among coniferous species, the tissue concentration of Cs decreased in the following order: twigs >needles >bark >wood, while the corresponding concentrations in birch (*Betula* spp) were similar in twigs, leaves and bark and lower in wood (McGee et al. 2000).

Objectives

The focus of this thesis is on a number of different elements and their accumulation and distribution in fast-growing *Salix* clones. The common characteristics of these elements are that they are - or could be - used as nutrients by the plants. A conspicuous characteristic of *Salix* spp. is their ability to utilise the sources available for growth. Although this capacity is well-known and has contributed to the high production rate of these species, information concerning the internal nutrient dynamics involved in coppice-plantations of *Salix* is still fragmented. Since *Salix* plantations are potential crops for radio-nuclide-contaminated agricultural land there is a need for more knowledge concerning the cycling of radio-nuclides in *Salix* plantations.

The main aims of this thesis were to study:

i) the seasonal variation and distribution of N, P, K, Ca, Mg and S in relation to nutrient availability in a whole-plant perspective,

ii) the tissue localisation and seasonal fluctuation of starch in roots and stems of coppiced plants, and

iii) the uptake and distribution of ^{137}Cs and ^{90}Sr in *Salix* plants and the level of ^{137}Cs in the ashes after combustion of stem wood.

Material and methods

Plant material, growth conditions and treatments

Pot experiment under greenhouse/outdoor conditions (Paper I):

Woody cuttings of *Salix dasyclados* Wimm., clone 77056, were cultivated in a greenhouse at Ultuna, Uppsala. Washed sand was used as substrate. The plants received a daily amount of a complete nutrient solution (Ericsson 1981), which corresponded to a relative addition rate of 0.08 (Low-Nutr) and 0.12 $g\ g^{-1}\ day^{-1}$ (High-Nutr) (Ingestad & Lund 1986). After establishment, plants were transferred from the greenhouse to outdoor conditions in order to expose them to a natural climate from autumn to next spring. Harvests were carried out nine times during the whole experiment. At each harvest, five plants from each treatment were randomly selected and separated in roots, cuttings, stems and leaves. Leaf area, dry weight and macro-nutrient concentrations in roots, cuttings, stems and leaves were determined.

Pot experiment in climate chamber (Paper II):

Woody cuttings of *Salix viminalis* L., clone 78183, were used in this experiment. The cuttings were planted in quartz sand in a climate chamber. Artificial seasons were created by prolonging the night from 6 to 16 hours per day and decreasing the day/night temperatures from 25/15 to 4/4. Starch concentration in stems and roots was studied during five growth phases (active growth, pre-dormancy, dormancy, post-dormancy and active growth) of the artificial seasonal cycle. Treatments included two levels of nitrogen supply (High-Nutr and Low-Nutr) and coppicing. A complete nutrient solution (Ericsson 1981) was added daily during phases 1 and 2. The nutrient amounts added followed an accumulated S-shaped curve with small additions at the beginning and end of the fertilisation period, and with a maximum after 3 weeks (Jonsson et al. 1997). The average relative addition rate of N was 0.059 (Low-Nutr) and 0.079 $g\ g^{-1}\ day^{-1}$ (High-Nutr). The shoots on half of the plant material were removed during plant dormancy, leaving about 2 cm of the cut stem. Five harvests were carried out during the experiment. At each harvest, 10 plants from each treatment were randomly selected and separated into roots, cuttings, stems and leaves. Root- and stem samples for anatomical examination with light microscopy and image analysis were taken and the remaining plant parts were dried for chemical analysis of starch.

Lysimeter experiment under field conditions (Paper III):

Woody cuttings of *Salix viminalis* L., clone 78183, were grown in micro-plots under field conditions at the research station of the Department of Radioecology, near Uppsala. The plough layer, 0-23 cm, of the soil consisted of loam or clay loam and the subsoil was loamy sand. The topsoil layers were homogeneously contaminated with ^{137}Cs and ^{90}Sr (Fredriksson et al. 1969). The experiment was carried out during three years. The plots were fertilised with 60 kg N/ha and three levels of K, consisting of 0 kg, 80 kg and 240 kg K per ha, respectively, during the two first years. Before onset and at termination of the experiment, soil samples were taken in order to determine the soil characteristics. Samples for ^{137}Cs and ^{90}Sr activity measurements in different plant parts were taken during the different seasons and different years. At the end of the experiment, all shoots and roots were harvested for activity measurements. Above-ground growth was measured during the autumn as shoot height and shoot diameter at 55 cm height. At the same time, the number of living shoots per plant was counted.

Field experiment (Paper IV):

Woody cuttings of *Salix viminalis* L., clone 78112, were planted on Chernobyl-contaminated sandy soil near the town of Gävle in east central Sweden. The experiment was carried out for four years. Experimental plots were fertilised annually with 60 kg N/ha, 0 or 48 kg K/ha, respectively, during the second and third years and other essential mineral nutrients were given in the proportions to N found optimal for *Salix* (Ericsson 1981). Samples of different plant parts were collected every year during different seasons for ^{137}Cs activity measurements. Growth was measured during the autumn as shoot height and shoot diameter at 55 cm height. At the same time, the number of living shoots per plant was counted. After combustion of harvested stems, the bottom- and fly ash, respectively, were collected for activity measurements.

Chemical analysis

Plants

All macro-nutrients except N were analysed with a plasma emission photospectrometer (Jobin Yvon JY–70 plus, Longjumeau, France). Nitrogen was determined by an elemental analyzer (Elemental Analyzer NA 1500, Rodano, Italy). Starch concentrations were determined using the method decribed by Steen & Larson (1986), slightly modified for the Hitachi U1100 spectrophotometer and Hitachi AS 3000 auto-sampler (Hitachi, Tokyo, Japan). For detailed information, see papers I and II.

Soil

The particle-size distributions were analysed by sedimentation, using the hydrometer method according to Day (1965). The total content of N was analysed in duplicate on an elemental analyser (Leco), and pH was measured in de-ionised water using the soil-solution ratio 1:2.5. P and K were extracted with ammonium lactate solution and 2M HCl in order to obtain the easily soluble and slightly bound fractions (Egner et al. 1960).

Light-microscopy studies and image analysis of starch

On each sampling occasion, samples from stems and roots were taken for light-microscopy studies and image analysis of the localisation and accumulation of starch. Image analysis was used as a complement to light microscopy in order to quantify the amount of starch on a cellular level. Detailed descriptions of procedures for handling samples used for light-microscopy and image analysis are given in paper II.

Radiometric analyses and calculation of transfer factors

Activity concentrations of ^{137}Cs in plant samples were determined by means of high-purity germanium detector systems housed in a low-background laboratory. Activity concentrations of ^{90}Sr were measured via its decay product ^{90}Y (yttrium) after separation by means of liquid-liquid extraction. ^{90}Y separation was carried out according to the method described by Suomela et al. (1993). All activity data were measured and corrected back for decay to the date of the experimental start.

Transfer factors, TFg, were calculated with the following formula and used to describe the transfer of ^{137}Cs and ^{90}Sr from the soil to the plants (IAEA 1987).

$$\mathrm{TFg} = \frac{\text{Plant activity concentration (Bq/kg d.w.)}}{\text{Ground deposition (Bq/m}^2\text{)}}$$

Unit: *[m^2 /kg d.w.]*

Combustion

The combustion of stem samples was carried out in a pilot scale (5kW) bubbling fluidised bed (BFB). The aim was to create a combustion situation similar to the combustion procedure in full-scale power plants. The temperature in the bed was maintained at around 830 ± 20 °C during the combustion process (Öhman & Nordin 1998). Both bottom ash and fly ash were collected for ^{137}Cs determination.

Statistical analyses

Statistical analysis was performed by Systat for Windows Version 5.0, 8.0 and 9.0. Pair-wise comparisons were made using the Least Significant Difference (LSD)-method. The confidence level was 95%.

Results and discussion

Uptake, distribution and seasonal variation of macro-nutrients and starch storage in *Salix* (I, II)

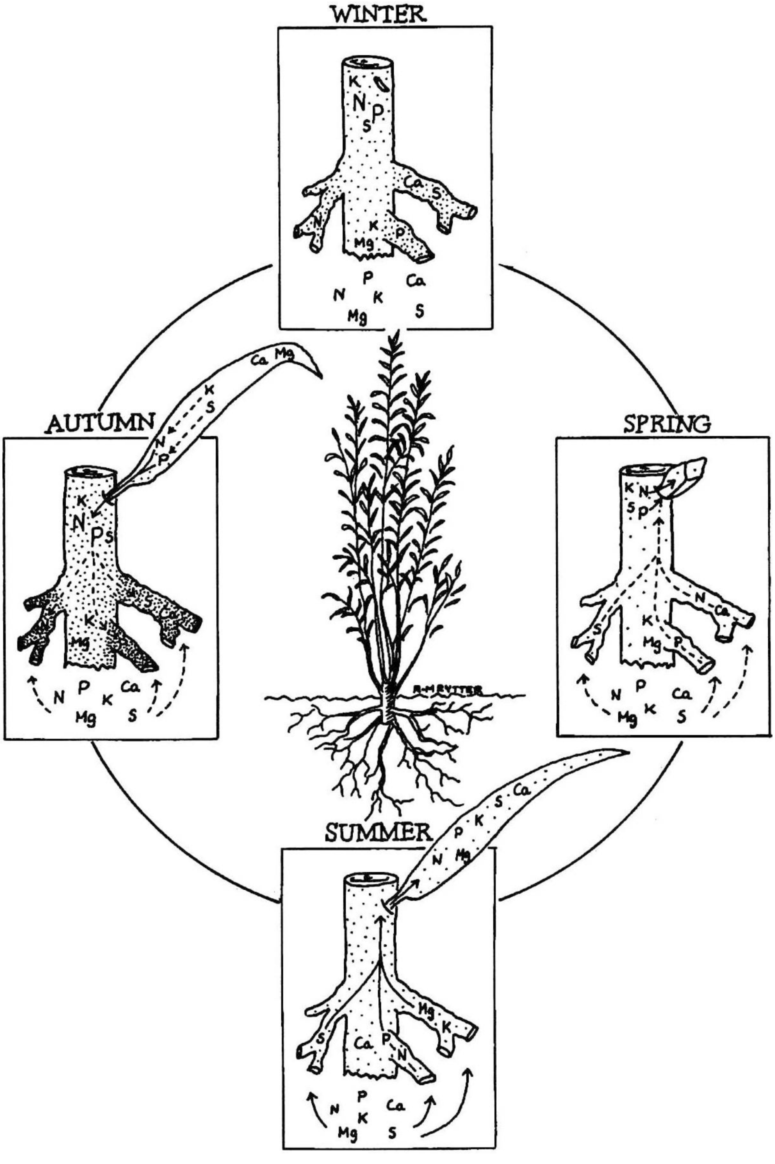

Figure 2. Seasonal variation and internal cycling of macro nutrients (N, P, K, Ca, Mg and S) and starch in roots, stems and leaves of fast-growing *Salix* spp. Large and small fluxes of mineral nutrients are represented by solid and broken arrows. The frequency of dots indicates the amount of starch in the tissues.

Macro-nutrients and starch in plant tissues

The seasonal dynamics in plant growth, and the uptake and storage of nutrient reserves are largely controlled by external factors like temperature (spring) and photoperiod (autumn). Data in the literature and results from the present studies allow us to discern the following patterns with regard to growth, macro-nutrient uptake and distribution, as well as starch storage in coppiced *Salix* plantations (Figure 2). The picture is far from complete, but may help to structure our present state of knowledge and to indicate areas where more information is required.

Summer

The concentration of N, P and K in roots, stem and leaves decreased throughout the summer at the same time as the contents of these elements in the tissues increased. The decrease in tissue concentration was an effect of an increased xylem to phloem ratio in perennial organs and a consequence of growth exceeding the rate of nutrient supply (I). The decline in tissue N, P and K concentrations was observed both under low- and high nutrient conditions. A decline in the tissue N concentration of the same magnitude as in the present study has been found in the laboratory as well as in field-grown *Salix viminalis* plants (Nilsson & Ericsson 1986, Bollmark et al. 1999). The concentration of Ca, Mg and S in all plant parts remained fairly constant during the period of active growth, except in roots, where a significant decrease in S concentration was observed. An increase in the leaf Ca- and Mg concentration is generally observed in *Salix* under field conditions (Rytter & Ericsson 1993). These elements are passively transported in the xylem, and accumulate in leaves as a consequence of transpiration (Marschner 1995). This transportation mechanism explains why the concentration and content of Ca and Mg in leaves generally mirror the soil conditions of the same elements (Ericsson 1994). During the phase of rapid biomass increment, low levels of starch were found in perennial organs and particularly in stems. A negative correlation between starch concentrations in all organs and plant N status was observed (II). The build-up of carbohydrate stores under N-limiting growth conditions is a normal feature in plants (McDonald et al. 1986, Wetzel et al. 1995, Bollmark et al. 1999). It has been shown for *Salix viminalis* that leaves constitute the major storage organ for carbohydrates during the summer (Bollmark et al. 1999).

Autumn

The phase of active growth comes to an end once the critical night length has been reached and the signals for growth cessation and frost hardiness development have been perceived. Thereafter, plants enter into a new phase of development, the autumn phase. This shift in developmental stage occurs during the first half of September in *Salix dasyclados* (clone 77056). As days got shorter and air temperatures fall, the cambium activity slows down and ceases completely towards the end of autumn (Sennerby-Forsse & von Fircks 1987). As a consequence, shoot growth decreases and stops completely at the time of leaf fall. In our study, the High-Nutr plants stopped growing about two weeks later than Low-Nutr plants (I). A similar effect from N-fertilisation has also been observed for other tree species (Cannell 1989). The roots continued to grow throughout the entire autumn, although progressively at a slower rate (I). A pronounced root activity during the autumn phase has been demonstrated in lysimeter grown *Salix viminalis* (Rytter 1997). Inorganic N taken up during this season is, according to Dickson (1991), converted to organic N and generally stored in the roots.

The N-concentration in leaves continued to decrease during autumn in parallel with the fraction of the plant-N associated with the leaf (I). The opposite pattern was observed in the perennial organs. Between 40 - 50% of the leaf-N was withdrawn prior to leaf abscission in this investigation (I). A retranslocation efficiency of N from leaves of the same magnitude as in our study has been observed in other broad-leaf tree species (*e.g.* review by Ericsson 1994). The major part of the withdrawn N is often stored in stem bark as protein (Titus & Kang 1982, Chapin & Kedrowski 1983). In a transmission electron microscopy study performed with *Salix dasyclados*, Sennerby-Forsse & von Fircks (1987) showed large numbers of protein bodies in stem phloem parenchyma cells. A similar observation with regard to N-storage has been reported for poplars by Stepien et al. (1991).

About 60% of the leaf-P was withdrawn prior to leaf abscission in our study. Values as high as 67% of the leaf-P pool have been reported for poplars (Bernier 1984). Phosphorus is generally stored in woody plant parts as organic-P, *e.g.* lipids (Chapin & Kedrowski 1983). Withdrawal of K and S from leaves during the autumn was very limited in this investigation and occurred only under low-nutrient condition (I). Depending on tree species and cultural conditions, between 10 to 70% of the leaf-K in deciduous trees is withdrawn from foliage during the autumn (*e.g.* review by Ericsson 1994). In our study, the levels of Mg and Ca in leaves were rather stable during the period of leaf abscission (I). Mg retranslocation from senescing leaves is otherwise a normal feature under conditions when the soil supply of this element is low (Bernier 1984). Withdrawal of Ca rarely takes place prior to leaf abscission, but has been reported for poplars (Bernier 1984). This element is considered immobile in the phloem (Marschner 1995). Mobility in the phloem is a necessary characteristic of mineral elements in order to be withdrawn from senescing leaves and transported to storage tissues in the perennial organs. To my knowledge, there is no previous information available showing in which part of the perennial organs Mg is stored during the dormant season.

Carbohydrates exported from the leaves to perennial organs during the later stages of the growing season are mainly stored as starch (Dickson 1991, Kozlowski 1992). In *Salix viminalis* the starch concentration in roots and stems increased significantly during the phase of growth retardation and reached its maximum in the late autumn (II, Bollmark et al. 1999). A similar starch accumulation pattern under field conditions has also been found for other species (Kramer & Kozlowski 1979, Essiamah & Eschraich 1985). Roots of *Salix* contained more starch than the stems. In both organs, phloem and cortex contained more starch than the xylem (II). Sennerby-Forsse & von Fircks (1987) showed an accumulation of large starch grains in plastids of *Salix* stems. In the present study, roots under Low-Nutr conditions contained significantly more starch than roots of High-Nutr plants. According to von Fircks (1994), *Salix* plants are vulnerable to frost damage in early autumn as the stem tissues have not yet developed sufficient freezing tolerance to enable them to survive stresses associated with freeze-/ or drought induced dehydration of cells. Accumulation of carbohydrates, lipids and protein bodies, the main storage form of nitrogen in plants, has been suggested to be one of the essential factors associated with the initial stages of cold acclimation (Yelenosky 1978).

Winter

The concentration of nitrogen and other mineral nutrients remained stable in all perennial organs during the phase of dormancy. The main storage form of N during this period is protein (Titus & Kang 1982, Wetzel et al. 1989). It has been shown that during late autumn – early winter starch in roots and stems is converted into sugars (Sauter 1988, Bollmark et al. 1999). This decrease in starch content probably reflects the temperature dependency of starch when being converted into sugar. The dissolution of starch to sugar is believed to be important for binding water, maintaining membrane properties, and increasing freezing tolerance (Levitt 1980). By using light microscopy and image analysis it was shown that the decrease in starch occurred in phloem and cortex tissues (II). A reduction in the pool of soluble carbohydrates during the winter has been demonstrated in laboratory-grown *Salix viminalis* and probably reflects metabolic activity in both stems and roots during this period (Bollmark et al. 1999). Rytter (1997) has shown that roots of *Salix viminalis* are active during frost-free periods and during mild winters roots of this species can grow throughout the whole year. During winter, cambial cells in *Salix* are characterised by having small vacuoles, often with granular and a markedly lower number of starch grains (Sennerby-Forsse & von Fircks 1987).

Spring phase

Three developmental phases can be identified during the spring: (i) initiation of mitotic activity, (ii) bud swelling, and (iii) bud break and the appearance of new leaves. Plants grown under High-Nutr conditions started to grow about one week earlier than plants cultured under Low-Nutr availability (I). According to Titus and Kang (1982), the levels of storage proteins in perennial tissues decrease at the time of bud swelling. A peak in N concentration in xylem sap during bud burst and early leaf development has been observed in deciduous species (Glavac & Jocheim 1993). In the present study, the nitrogen concentration in roots, cuttings and stems decreased in parallel with the development of the new shoots. Temperature is the most important factor influencing mobilisation and dissolution of starch during this period (Sauter 1988). In the early spring phase, sugars are usually re-converted to starch (Essiamah & Eschrich 1985). However, in the present study this phenomenon was not observed. On the contrary, the starch concentration in root phloem and cortex decreased progressively throughout the spring period. The necessity of large carbohydrate- as well as nitrogen stores in roots and stems for rapid early season shoot development has been demonstrated in *Salix viminalis* by Bollmark et al. (1999). In our study the decrease in starch concentration during early spring was more pronounced in High-Nutr plants, and the growth rate of these plants was considerably higher compared with Low-Nutr plants (I). In coppiced plants, the depletion of starch in roots was more pronounced than in intact plants. The proximity of the new shoot to the carbohydrate source in the roots may offer an explanation of this observation. It should be noted however, that a significant part of the carbohydrate stores in dormant *Salix* plants is also located in the stems and the access to this carbohydrate source will be lost at harvest.

Factors influencing uptake and distribution of macro-nutrients

Nitrogen is the mineral nutrient element required in the largest amount by plants (Marschner 1995). Besides water, nitrogen shortage is one reason why the growth potential of *Salix* is rarely reached in commercial plantations (Christersson 1999). It has been shown that there is a strong positive relationship between the N status of *Salix* plants (*e.g.* the nitrogen concentration in the leaves), and growth rate (Ericsson 1981). From this, it follows that uptake of all essential nutrient elements in a *Salix* plantation is strongly influenced by the N availability in the soil and, thus, by the N-status of the crop.

The availability of an element in the soil may significantly affect the uptake of another nutrient besides the fact that uptake of mineral nutrients is strongly controlled by the plant nitrogen status. The binding strength of the highly hydrated Mg^{2+} to cell walls and plasma membranes is rather low. Other cations such as K and Ca therefore compete quite effectively with Mg^{2+} and strongly depress the uptake rate of this element. This strong antagonism between elements is in agreement with observations of Mg-deficiency induced in crop plants by extensive application of K and Ca fertilisers (Mehra & Farago 1994). This phenomenon was not observed in the present study, probably because a balanced nutrient solution and a substrate low in Ca were used. At low soil pH, however, Ca may stimulate uptake of K (Marscher 1995). The negative effect of a high proton concentration on the integrity of plasma membranes is relieved by this cation (Marschner 1995). The pH of the soil has also a strong impact on the solubility and thereby the availability of the different plant nutrients (Moore et al. 1995). Root development, and hence uptake of all nutrient elements, in fast-growing *Salix* species is strongly influenced by pH as such and values below 5 in *Salix* plantations should be avoided (Ericsson 1981, Ericsson & Lindsjö 1981). The physical properties of the soil, such as the bulk density, are also of vital importance for root development, and thereby uptake of water and nutrients. The most spectacular yields in *Salix* plantations have been obtained on sandy soils when the crop received daily additions of both water and nutrients (Christersson 1986).

Impact of the chosen growth techniques on nutrient dynamics

Nutrient availability is commonly measured in terms of nutrient concentration in the root medium (Epstein 1972). This is a universal practice, manifested all the way from field analysis of soil to basic research, where fundamental theories on ion uptake are based on nutrient concentration in solution. However, the use of nutrient concentration in the soil solution as a treatment variable in plant growth experiments has little to do with the continuous, natural processes that take place in the soil and determine the soil fertility. These processes vary from day to day within a given season because of climatic influences such as humidity and temperature. The practice of applying large doses of nutrient elements at relatively long time intervals (days - weeks - years) in field- or laboratory studies often causes the plant nutrient status to change over time. The interpretation of data collected from such experiments is very difficult since the nutrient status of plants affects most physiological processes. This problem can be avoided by adding the mineral nutrients in frequent, small and exponentially increasing doses throughout the experimental period (Ingestad & Lund 1986). Stability in growth rate and internal tissue mineral concentrations can be achieved in this way. This was the technique employed when studying uptake, accumulation and distribution of the macro- nutrients N, P, K, Ca, Mg and S (I). However, about two-thirds of the biomass increment took place after the final fertiliser addition. As a consequence, nutrient uptake and growth went out of phase and the commonly observed decrease, particularly in leaf N concentration, started already during the phase of active growth. This imbalance between nutrient supply and growth caused a decrease in the plant nutrient status towards the end of the growing season. This incident may have affected the intensity of nutrient withdrawal from senescing leaves. However, neither the nutrient retranslocation process as such nor the location of nutrient storage in the perennial tissues during winter, are likely to have been affected.

The technique for steady state mineral nutrition was originally designed to control growth of young seedlings during their early stages of development. Once the test plants left the exponential growth phase, the precise control of the plant nutrient status was difficult to maintain. Jonsson et al. (1997), however, modified this technique in such a way that plants can be cultured at any nutrient regime for one or several growth periods. This was achieved by growing the plants in a growth chamber, where a full growth cycle was induced by varying photoperiod and temperature. The nutrient additions followed a sigmoid-shaped curve, *i.e.* small doses of nutrients were given in the beginning and towards the end of the growing season with a maximum at growth peak. This approach was used in paper II when studying seasonal fluctuations of starch in root- and stem tissues of intact and coppiced *Salix viminalis* plants under two nitrogen regimes. The expected decline in leaf nitrogen concentration due to retranslocation took place after growth cessation and mirrored the pattern generally observed under field conditions (Nilsson & Ericsson 1986, Rytter & Ericsson 1993).

Uptake, distribution and seasonal variation of radio-caesium and radio-strontium in *Salix* (III, IV)

Plant roots are believed to take up Cs and Sr in a manner similar to K and Ca, although K is usually preferred to Cs (Coughtrey & Thorne 1983, Marschner 1986). The transfer of radio-nuclides from contaminated soil to plants is the result of a series of closely co-ordinated steps from root uptake, transport within the root and further between the roots and the aerial parts of the plant.

Radio-caesium and radio-strontium in plants

The distribution of radio-nuclides in plants varies considerably between species (Coughtrey & Thorne 1983). The biomass distribution of a tree changes with the age of the tree and so does the internal distribution of Cs and Sr.

In the present study (III), the concentration of ^{137}Cs in the different plant parts varied. The highest concentration was found in roots followed by leaves, stems, and cuttings. About 50% of the ^{137}Cs were found in roots (Figure 3). This is in agreement with the findings of Sennerby-Forsse et al. (1993), where 90% of the Cs was found in very young *Salix* roots. Among the roots, the fine roots (0-1 mm) had the highest ^{137}Cs concentration in our study (III, IV). Within the root system 45-55% of ^{137}Cs was found in fine roots (0-1 mm), 10% in roots sized 1-2 mm in diameter, and 35-45% was found in the coarse roots (>2 mm) (III). There are several reasons for the high concentration of ^{137}Cs in the roots. One possible explanation is that a selective barrier in the xylem vessel prevents the transport of Cs further into the shoots (Erdei & Trivedi 1991). Buysse et al. (1995) suggested a limited capacity to withhold Cs in the shoots due to a limited uptake of Cs in the vacuoles. In our study, about 10% of the ^{137}Cs amount were found in the stems (Figure 3) and one-year-old stems had a higher ^{137}Cs concentration than two-year-old stems (III). This is in agreement with Skarlou et al. (1999) who found that the transfer of Cs to new branches in olive trees was higher than that to old branches. The same trend was found in studies of forest trees and bushes where transfer values of Cs, seven years after the Chernobyl deposition, were significantly higher in younger shoots than in older shoots, both in dwarf shrubs (*Vaccinium myrtillus*) and in conifers (*Picea abies*) (Strebl et al. 1995). Other studies have shown ^{137}Cs to be easily transported in parenchyma rays of the xylem to the bark and be accumulated as an increasing gradient from the base of the tree and upwards (Momoshima & Bondietti 1994, Karavaeva et al. 1994). In fruits and vegetables, about 50% of root-absorbed Cs is found in above-ground parts (Coughtrey & Thorne 1983).

The Sr content of leaves is generally 2-6 times higher than that of shoots or roots (Coughtrey & Thorne 1983). Based on previous data it was assumed that the distribution of Sr within cereal crops would be about 10% in roots, 45% in straw, 30% in leaves, 13% in inflorescence and 2% in grain (Coughtrey & Thorne 1983). Data on Sr distribution in woody plants are very limited. The results from our study showed that 15% of ^{90}Sr was found in roots, 35% in stems and cuttings and 50% in leaves (Figure 3).

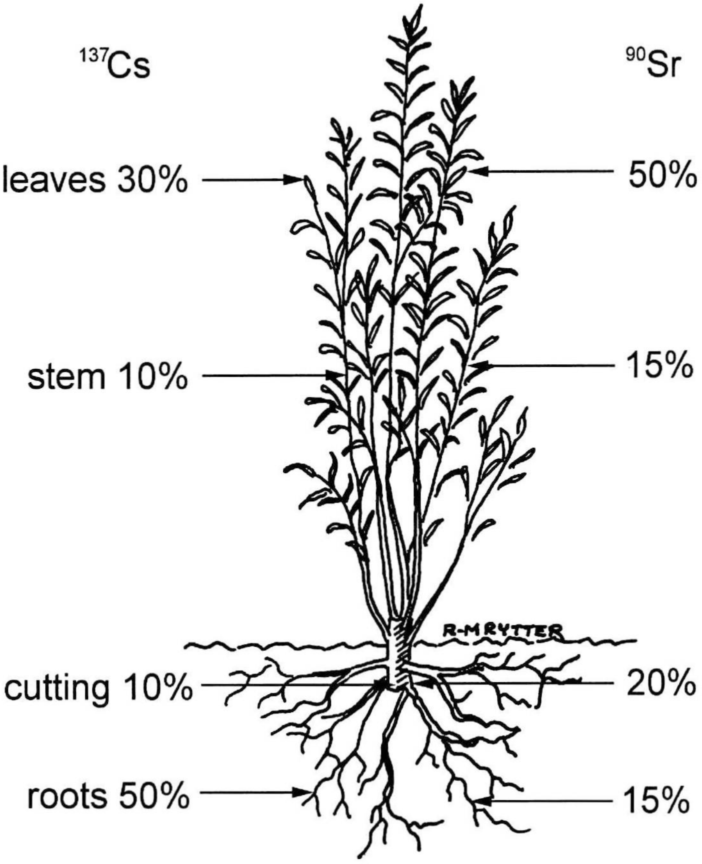

Figure 3. The distribution of ^{137}Cs and ^{90}Sr (per cent of total amount) in a *Salix* plant after the first growing season. Values are shown for two-year-old roots and one-year-old shoots.

Seasonal variation of K- and Ca-ions in soil solutions may influence Cs and Sr uptake and this may to some extent explain the variability in the soil-to-plant transfer factors for these nuclides reported in papers III and IV. Carini (2001) collected data from fruit trees during the years following the Chernobyl accident. It was shown that the Cs was retranslocated from leaves into perennial organs such as stems and roots. During the following spring, this radionuclide was translocated to the new leaves. Carini (2001) also pointed out that the total annual loss of Cs through removal of leaves and fruits was a very small fraction of the total content in plants. In our study, the ^{137}Cs concentration of leaves decreased from summer to autumn, as has also been found in Scots pine (Nylén 1996). The withdrawal of ^{137}Cs from senescing leaves is analogous to the behaviour of K (Ericsson 1994). On the other hand, the ^{90}Sr concentration in leaves increased from summer to autumn, as is often the case with Ca. Accumulation of Ca in leaves throughout the growing season is a normal feature (Bernier 1984, Ericsson 1994).

Differences in uptake and distribution of radio-caesium and radio-strontium

Many studies have shown that the behaviour of Cs and Sr are fundamentally different in the soil (Shaw & Bell 1994). Cs has a high degree of attachment and 'fixation' to soil minerals, particularly within the clay fraction (Cremer et al. 1988), whereas Sr remains relatively mobile and hence available for uptake by plant roots. In the case of Cs the relative proportion of clayey material within a contaminated soil, and particularly its minerals, will strongly determine the degree of soil-to-plant transfer of this nuclide (Bell et al. 1988). It has been shown that considerably more than 90% of Sr exists in exchangeable forms in the soil (Francis 1978). Forsberg (2000) studied the behaviour of ^{137}Cs and ^{90}Sr in agricultural soils in Sweden and showed that the chemical availability of ^{137}Cs in soil was already very low three to four years after contamination. Conversely, ^{90}Sr remained easily extractable even after nearly 40 years. It was also shown that migration of ^{137}Cs was very slow in most soil types, and slower than that of ^{90}Sr under almost all conditions. In our study the transfer of ^{90}Sr from soil to plant was considerably higher than for ^{137}Cs. The distribution patterns of ^{137}Cs and ^{90}Sr were also quite different in our study (Figure 3).

Factors influencing uptake and distribution of radio-caesium and radio-strontium

Important factors influencing the uptake of radio-nuclides are the chemical-physical characteristics of the soil. Characteristics such as soil texture, soil moisture content, soil mineral- and organic content, soil pH, the concentration of chemical elements in the soil solution, soil cation exchange capacity (CEC) and the chemical form of radio-nuclides in soil, are important. The effect of soil texture is related to its mineral content. In mineral soil, Sr is more easily taken up than Cs, which was shown in our study (III) as well as in the study by Nisbet & Shaw (1994). In organic soils, on the other hand, plant uptake of Cs is higher than uptake of Sr (Nisbet & Shaw 1994, Paasikallio et al. 1994). The reason for the higher uptake of Cs is due to the fact that the organic matter loosens the fixation of Cs to clay minerals. (Van Bergeijk et al. 1992, Dumat & Staunton 1999). It has also been reported that while Sr uptake was higher in sandy soils, the uptake was clearly lower in peat soils, which was explained by the fact that organic acids in peat soils form stronger complexes with Sr (Nisbet & Shaw 1994). Coughtrey and Thorne (1983) reported that plant grown under dry conditions generally take up less Cs than when grown under humid conditions. The nutrient status of the soil plays an important role for uptake, especially in natural and semi-natural ecosystems, and the highest transfer factor for Cs was found in peat-like, nutrientpoor soils. The lowest transfer factor for Sr was connected with a soil rich in calcium (Carini 2001). The physical form of radio-nuclides in the soil is another factor, which has an effect on plant uptake. Our studies (III, IV) as well as the study by Sandalls et al. (1990), demonstrated that ^{137}Cs deposited 20 to 30 years ago was much less available for uptake than the relatively newly deposited Cs from the Chernobyl accident.

Species difference is another factor that influences root uptake and transport of Cs and Sr within the plant. This is mainly due to differences in rooting depth, ion uptake capacity and mycorrhizal associations. As roots grow, their surfaces come into close contact with nuclide ions. The larger the root systems the larger the contact area. In general, woody plants have larger root systems than annual plants. However, the relatively deep root distribution in woody plants could reduce the root uptake since in the normal case both Cs and Sr are mostly found in the upper 0-10 cm soil layer (Rosén et al. 1999, Forsberg 2000). Plant species differ considerably in the number of cation exchange sites in their root cells (Carini 2001). In general, the CEC of dicotyledonous species is much greater than of monocotyledonous species (Carini 2001). Ion transport across cell membranes in the roots depends on membrane properties, which results in different plants having distinct Cs uptake characteristics (White & Broadley 2000). Grasses in general, including cereals, take up less Cs than dicotyledons. Among the dicotyledons, cabbage, lettuce and legumes are known to have high uptake rates of radio-nuclides (Coughtrey & Thorne 1983). The corresponding values for fruit plants are of the same order or lower than those from green vegetables (Carini 2001). Dwarf shrub communities dominated by common heather (*Calluna vulgaris*) generally showed higher Cs uptake than grass-dominated communities (Salt & Mayes 1993). As mentioned above, other studies have shown differences in the concentration of ^{137}Cs in a number of boreal plant species (Nylén 1996) and also in coniferous and deciduous tree species (McGee et al. 2000). Considering the uptake of Sr, Coughtrey & Torne (1983) reported that legumes had a much higher affinity for Sr than grasses. Other authors have observed that many vegetables have higher Sr uptake than cereals, with lettuce and cabbage in particular having high uptake rates (Nisbet & Shaw 1994, Paasikallio et al. 1994). Carini (2001) showed that shrubs transfer more Sr from soil to fruit than annual plants and trees. However, data on uptake of Cs and Sr in woody plants are limited. The results from the present study as well as from the study by Sennerby-Forsse et al. (1993) show that *Salix* readily takes up Cs and Sr.

Mycorrhiza is another factor that is believed to enhance uptake of radio-nuclides (Clint & Dighton 1992), especially in forest plant species (Nikolova et al. 2000). The reason for this might be that metal ions form complexes with the chitin of the fungal cell wall and this facilitates the uptake of radio-nuclides (Streit & Stumm 1993). A common observation is that mycorrhizal associations are less developed in nutrient-rich soils (Marschner 1995), which may partly explain the lower uptake rate in agricultural crops growing in richer soils than in forest soils, which are usually poorer.

The uptake ability of radio-nuclides is also related to different agricultural practices. It has been shown that soil ploughing markedly decreases the transfer of ^{137}Cs from soil to plant (Rosén 1996). Management measures such as fertilisation of contaminated soils might increase the content of competing cations in the soil and affect the uptake of Cs and Sr. In one of our studies (III), potassium fertilisers reduced the uptake of Cs. Similar results from K-application have been reported by Lembrechts (1993) and Rosén (1996). Both Cs and K are monovalent and relatively similar in size and can effectively replace each other at the exchangeable sites in the soil and in the root. Thus, K-fertilisers can be applied in order to increase the pool of exchangeable potassium in the soil, thereby causing a reduction in the ratio of Cs:K in the soil solution. The uptake of Cs by plants is most efficient at low K concentration in the soil and K-fertilisation of soils already high in K has little effect on Cs uptake (Shaw 1993, Rosén 1996, Smolders et al. 1996). This observation agrees well with the results presented in paper III, which showed no clear differences in ^{137}Cs uptake in plants supplied with 80 or 240 kg K/ha. High levels of Ca in the soil can also reduce the uptake of Cs (Lembrechts 1993). The reason for this observation could be that Ca increases both pH and the cation exchange capacity of the soil. Different forms of N-fertilisers might affect the uptake rate of ^{137}Cs. NH_4^+-N was shown to enhance transfer of Cs from soil to plant (Cremers et al. 1990). However, Lembrechts (1993) and Campbell & Davies (1997) showed that NH_4^+ could compete with the alkali cations and in this way limit the amount of Cs taken up by plants. Phosphorus fertilisation caused a 50% reduction on ^{137}Cs uptake in food crops (Robison & Stone 1992). A possible explanation of this observation could be that P suppressed mycorrhizal infections, thereby reducing the uptake of ^{137}Cs (Robison & Stone 1992).

Lime and other calcium-containing minerals applied to soils cause the Sr: Ca ratio to decrease and hence the uptake of Sr. Thus, soils with a low Ca status show that the greatest benefit from lime applications by marked reductions in Sr uptake by plants (Milbourn 1960, Lembrechts, 1993). There are data in the literature showing that P and S could reduce the availability of Sr in the soil solution (Nisbet 1993). According to Lembrechts (1993) the addition of K-fertilisers can also reduce the transfer factor of Sr by 20%. Kwaratskhelia et al. (1967) reported that the uptake of ^{90}Sr by plants decreased after addition of ammonium sulphate, while nitrate additions stimulated uptake.

Weather conditions can affect the uptake and distribution of radio-nuclides in plants. Low precipitation affects mineral nutrient acquisition, and hence uptake of radio-nuclides, negatively as well as the turnover of soil organic matter (Carini 2001). Rain may reduce the leaf concentration of Cs through leaching (IV, Peter et al. 1969), while wind might increase the rate of transpiration and in this way increase the content of Sr in leaves.

Concentration of ^{137}Cs in ashes after combustion

In the present study (IV), the concentration of ^{137}Cs was higher in the fly ash than in the bottom ash. This is in agreement with studies by Ravila & Holm (1994) and Hedvall (1997). The concentration of ^{137}Cs was about 900 Bq/kg in fly ash and about 100 Bq/kg in bottom ash in this study, which is well below the safety limit for ash established by the Swedish Radiation Protection Institute, *i.e.* 5000 Bq/kg (Hubbard & Möre 1998). In Sweden, the ashes should be recycled back to the site after combustion in order to use the ashes as fertiliser and as a method of adjusting pH to prevent nutrient imbalances after harvest. It is therefore important that the concentration of radio-nuclides in the ashes does not exceed the safety limit.

Implications for practical management

Macro-nutrients

Salix plantations are generally harvested during winter, when all leaves have been shed. This management practice is considered economical from an N point of view, since leaves constitute the most N-rich plant organ. Towards the end of the growing season, 150 kg N or more per ha is tied up in the leaf biomass of a high-yielding *Salix* plantation (Christersson 1986, Ericsson 1994). However, stem harvest during the dormant season coincides with the time when the stem N content is at its maximum (paper I, Bollmark et al. 1999). Thus, removal of only stems from a *Salix* plantation still implies that up to 50 percent of the leaf N content will be lost at each harvest as a consequence of withdrawal of easily mobile nutrient elements prior to leaf fall. According to the results in paper I, significant losses of leaf P will also occur at each harvest. The leaf contents of K and Mg are also recycled in the plant. The efficiency of withdrawal of these elements from senescing leaves was low in the present study. However, our findings together with literature data suggest that the amount of K and Mg originating from the leaves and lost at stem harvest can be negatively correlated with the K and Mg availability in the soil. Ca is an immobile plant nutrient and most part of this element in the leaves will be returned to the soil at leaf fall. However, stem wood and bark in *Salix* are rich in Ca (Ericsson 1984). Considerable amounts of this element will therefore be removed on each harvest occasion in a high yielding *Salix* plantation. This will harm the long-term productivity unless countermeasures such as liming are undertaken. In eucalyptus plantations, which are also characterised by high productivity and short rotations, loss of Ca via stem harvest is regarded as a threat to the long-term productivity of the site (Pereira et al. 1994). The emission of S from the use of fossil fuels has significantly decreased during recent decades (Information from the Swedish Board of Agriculture). As a result, shortage of S in agricultural crops is now becoming a problem. Thus, the need for S application to short rotation willow crops should not be over looked.

If we want to optimise yields and nutrient balances in practical *Salix* plantations we have to think about the best time for harvesting. However, as described below, the two practises proposed have their difficulties and risks.

1. Most of the plant material used in *Salix* plantations is of southern origin and is adapted to longer nights for the induction of growth cessation and frost hardiness. The leaves are often shed green as a consequence of exposure to subzero temperatures and the efficiency of nutrient withdrawal prior to leaf abscission is reduced. This means that the recycling of nutrients is less efficient in these plants and more nutrients remain at the growing site. However, the risk for frost damage during autumn is high when using these clones.

2. From a nutrient balance points of view, the harvest operation in a *Salix* plantation should take place after growth cessation before the easily mobile nutrients are retranslocated from the leaves, but after the export of carbohydrates from the leaves to the perennial organs. This would require that the leaves be mechanically removed from the stems at harvest and left at the site. However, the timing of such an operation is not easy, since the ideal phenological stage is hard to detect by eye, and will vary from year to year because of normal fluctuations in climate. Furthermore, harvest operations on unfrozen soil are not recommendable since this activity may cause soil compaction.

The nutrient status of a *Salix* plantation influences the efficiency of nutrient withdrawal from senescing leaves. Plants grown on highly fertile soils, or well-supplied with fertilisers, tend to be less efficient in this respect and a greater fraction of the nutrients therefore remains at the site after harvest. Also the initiation of frost hardiness is often delayed in plants with a high N-status. A proper matching of the plant material to both soil fertility and the climatic conditions at the site is therefore desirable. *Salix* plantations have a high proportion of nutrient-rich bark, and in order to avoid nutrient losses the ashes after burning of harvested stems should be recycled to the field. When utilising radio-nuclides-contaminated soils for *Salix* plantations the ashes should be returned to sites already contaminated.

Based on the results obtained in this study and data from the literature, we propose that the assessment of autumnal changes in leaf nutrient composition can be used as a tool for determining which elements are in low supply at a particular site. The use of soil data is important but the interpretation of soil data is often difficult, especially from sandy soils, and a combination of the soil data with leaf nutrient status would give a better estimation of the need for fertilisers. Also more research concerning the plant material, the breeding potential and technical development concerning harvesting machinery is needed.

Radio-nuclides

The strong interaction between the chemically related elements Cs/K and Sr/Ca offers great possibilities to manipulate the uptake of these radio-nuclides. In soils low in K, the transfer of Cs from soil to plants can be significantly reduced by K-fertilization. However, addition of K to plantations growing on K-rich soils has a limited effect on Cs uptake (paper III, Rosén 1996). If removal of Cs from contaminated sites is the operational goal, addition of K should be kept at a minimum in order to increase the Cs:K ratio in the soil solution and thereby to increase the uptake of Cs. The uptake of Cs and Sr differs between different plant species, and it is of considerable interest to prevent these radio-nuclides from entering the food chain through growing crops that do not accumulate Cs and Sr. In contrast, remediation of contaminated areas should be done using plants that accumulate large amounts of Cs and Sr. From this study, it is evident that the concentration of Cs in *Salix viminalis* roots and leaves is far higher than in stems. Thus, larger amounts of Cs can be removed from the site if leaves are included in the harvest. As already pointed out, such a harvest procedure should not be carried out before the stores of carbohydrates in the roots have been adequately filled (II, Bollmark et al. 1999). Removal of both the below- and aboveground biomass at the time of harvest from the field would significantly increase the transport of Cs from contaminated soils. Based on the same reasoning as for Cs, Sr accumulates in leaves to a much greater extent than in roots and stems. If removal of Sr from contaminated soils is the operational goal, harvest of both stems and leaves is recommendable.

Conclusions

1. The internal dynamics of macro-nutrients in leaves, stems and roots of coppiced *Salix dasyclados* and *Salix viminalis* followed the same principal pattern in response to seasonal changes. Plants cultured under high availability of nutrients had i) higher concentrations of all macro-nutrients, ii) a delay of leaf senescence and dormancy, iii) an earlier growth start and a more vigorous growth in the following year, and iv) contained less starch compared with Low-Nutr plants. Between 40-50% of N and about 60% of P was withdrawn from the leaves prior to abscission and stored mainly in the aboveground perennial organs. Retranslocation was observed in K and S but only under low nutrient conditions.

2. Starch proved to be an abundant nutrient, particularly in roots during most of the seasons. The amount as well as the size of starch grains fluctuated markedly during the seasons, being mainly found in phloem- and cortex cells and to some degree also in xylem parenchyma cells. The fact that we failed to observe re-synthesis processes during early spring indicates that this stage may be very short in *Salix*. The root starch in coppiced plants decreased more rapidly than in intact plants, indicating that starch reserves in roots are important for early phases of

growth and that coppicing had an increasing effect on the sink strength for internal carbohydrate reserves.

3. The accumulation of ^{137}Cs and ^{90}Sr differed between plant organs and during different seasons. The ^{137}Cs concentration in leaves decreased from summer to autumn whereas the ^{90}Sr concentration in leaves increased during the same period. The fine roots had the highest Cs concentration, while the Sr concentration was highest in leaves. The low transfer rate of Cs to the stem wood resulted in levels well below the safety limits of ^{137}Cs in the ashes after burning. Therefore, fast-growing *Salix* coppicing systems exhibited promising features for utilisation of contaminated agricultural soils.

Future perspectives

Energy forestry was introduced in Sweden more than 20 years ago (Sirén et al. 1984), and has an average yield of about 10 tonnes per hectare and year in practical plantations (Christersson 1999). A much higher growth potential, *i.e.* 20-35 tonnes dry matter per hectare and year has been reported from several studies in Sweden and other countries (Ericsson 1984, Christersson 1987). These results show that there is great potential for biomass production in this species. However, maximising coppice production is more complicated than was first believed since many different factors influence growth. Besides genetic improvement, increasing pest- and disease resistance and frost hardiness in the plant material are vital for the achievement of sustainable high yields. The present fertilisation schemes focus mainly on conventional N-P-K fertilisers. Although several studies have been published concerning plant-nutrient relationships many questions still remain. For example, there is growing interest in micro-nutrients, which have been shown to play an important role in plant resistance to disease and root-stress (Welch 1995). There are also reports on the lanthanide series of elements from atomic number 57 to 71, indicating increased crop yields and improved product quality from applications of fertilisers including these elements (Istvan & Benton 1997). It would be interesting to investigate the effects of these elements on fast-growing *Salix* plants.

Salix species as well as clones of the same species differ in capacity to accumulate heavy metals (Landberg & Greger 1994). Therefore, there is reason also to believe that the capacity of *Salix* spp. to take up and store Cs and Sr may vary among species and clones. Further studies may therefore allow selection of more effective genotypes for restoration of radio-contaminated sites. Further investigation of how repeated harvesting may influence the uptake and distribution of radio-nuclides in the individual plant is needed to increase our knowledge and understanding of the transfer and cycling of Cs and Sr in coppice plantations. As a result of the Chernobyl accident, vast areas of agricultural land became wasteland; in the area of Belarus alone, there are more than 260,000 ha of agricultural land that are now non-cultivated (Ipatyev et al. 1999). Afforestation of this area with fast-growing *Salix* species for energy might be a simple and safe way to utilise this land, provided that the health risks involved in the handling and burning of contaminated wood are properly evaluated.

References

Adams, M.B., Allen, H.L. & Davey, C.B.1986. Accumulation of starch in roots and foliage of loblolly pine (*Pinus taeda* L.): effects of season, site and fertilisation. *Tree Physiology 2*, 35-46

Åhman, B. & Åhman, G. 1994. Radio-caesium in Swedish reindeer after the Chernobyl fallout: Seasonal variations and long-term decline. *Health Physics 66*, 503-512.

Alriksson, B. 1997. Influence of site factors on *Salix* growth with emphasis on nitrogen response under different soil conditions. Ph. D. thesis. Swedish University of Agricultural Sciences, *Acta Universitatis Agriculturae Sueciae: Silvestria 47*. ISSN 1401-6230.

Bell, J.N.B., Minski, M.J. & Grogan, H.A. 1988. Plant uptake of radio-nuclides. *Soil Use and Management 4 (3)*, 76-84.

Bernier, B. 1984. Nutrient cycling in *Populus*: A literature review with implications in intensively managed plantations. *Canadian Forest Service, Ottawa, IEA/ENFOR Report 5*. 46 pp.

Bollmark, L. 2000. Accumulation and mobilisation of nutrient reserves in *Salix viminalis*. Ph. D. thesis. Swedish University of Agricultural Sciences, *Acta Universitatis Agriculturae Sueciae: Silvestria 155*. ISSN 1401-6230.

Bollmark, L., Sennerby-Forsse, L. & Ericsson, T. 1999. Seasonal dynamics and effects of nitrogen supply rate on nitrogen and carbohydrate reserves in cutting-derived *Salix viminalis* L. plants. *Canadian Journal of Forest Research 29*, 85-94.

Bonical, A., Haddad, G. & Gagnaire, J. 1987. Seasonal variations of starch and major soluble sugars in different organs of young poplars. *Plant Physiology and Biochemistry 25*, 451-459.

Buysse, J., Van Den Brande, K. & Merckx, R. 1995. The distribution of radiocesium and potassium in spinach plants grown at different shoot temperatures. *Journal of Plant Physiology 146*, 263-267.

Campbell, L.S. & Davies, B.E. 1997. Experimental investigation of plant uptake of caesium from soils amended with clinoptilolite and calcium carbonate. *Plant and Soil 189*, 65-74.

Cannell, M.G.R. 1989. Physiological basis of wood production: A review. *Scandinavian Journal of Forest Research 4*, 459-490.

Carini, F. 2001. Radionuclide transfer from soil to fruit. *Journal of Environmental Radioactivity 52*, 237-279.

Champigny, M.L. 1985. Regulation of photosynthetic carbon assimilation at the cellular level: A review. *Photosynthesis Research 6*, 273-286.

Chapin, F.S. & Kedrowski, R.A. 1983. Seasonal changes in nitrogen and phosphorus fractions and autumn retranslocation in evergreen and deciduous taiga trees. *Ecology 64*, 376-391.

Chapin, F.S., Schulze, E-D. & Mooney, H.A. 1990. The ecology and economics of storage in plants. *Annual Review of Ecology and Systematics 21*, 423-427.

Christersson, L. 1986. High technology biomass production by *Salix* clones on a sandy soil in southern Sweden. *Tree Physiology 2*, 261-272.

Christersson, L. 1987. Biomass production by irrigated and fertlized *Salix* clones. *Biomass 12*, 83-95.

Christersson, L. 1999. Theoretical background to and practical utilization of short-rotation and energy forestry. In: L. Christersson & S. Ledin (Eds.), *Short-rotation crops for energy purposes*, p. 5-19. Proceedings of the first meeting of IEA, Bioenergy, Task 17, Uppsala, Sweden, 4-6 June, 1998. Rapport 64, Swedish University of Agricultural Sciences.

Christersson, L., Sennerby-Forsse, L. & Zsuffa, L. 1993. The role and significance of woody biomass plantations in Swedish agriculture. *The Forestry Chronicle 69*, 687-693.

Clarkson, D.T. & Hanson, J.B. 1980. The mineral nutrition of higher plants. *Annual Review of Plant Physiology 31*, 239-298.

Clint, G.M. & Dighton, J. 1992. Uptake and accumulation of radio-caesium by mycorrhizal and non-mycorrhizal heather plants. *New Phytologist 121*, 555-561.

Coughtrey, P.J. & Thorne, M.C. 1983. *Radio nuclide distribution and transport in terrestrial and aquatic ecosystems (vol. 1),* p. 93-127, 321-346. Rotterdam: Balkema.

Coughtrey, P.J., Carini, F. & Venter, A. 2001. Conclusions and recommendations. *Journal of Environmental Radioactivity 52*, 309-314.

Cremers, A., Elsen, A., de Preter, P. & Maes, A. 1988. Quantitative analysis of radio-caesium retention in soils. *Nature 335*, 247-249.

Cremers, A.A., Elsen, E., Valcke, J., Wauters, F.J., Sandalls, F.J. & Gaudern, S.L. 1990. The sensitivity of upland soils to radio-caesium contamination. In: G. Desmet, P. Nassimbeni & M. Belli (Eds.) *Transfer of Radio-nuclides in Natural and Semi-natural Environments*, p. 238-248. Elsevier, London.

Danfors, B., Ledin, S. & Rosénqvist, H. 1998. *Short-rotation willow coppice-growers manual.* Swedish Institute of Agricultural Engingeering. Uppsala, Sweden, 40 pp.

Day, P.R. 1965. Particle fraction and particle size analysis. In: C.A. Black, D.D. Evans, J. L. White, L.E. Ensminger, & F.E. Clark (Eds.) *Methods of soil analysis, Part 1 Agronomy 9,* 914-926.

De Preter, P., van Loom, L., Maes, A. & Cremers, A. 1991. Solid/liquid distribution of radio-caesium in boom clay. A quantitive interpretation. *Radiochimica Acta 52/53*, 299-302.

Devell, L., Gntay, S. & Powers, D.A. 1996. *The Chernobyl reactor accident source term. Development of a consensus view.* One decade after Chernobyl: Summing up the consequences of the accident. Vienna 8-12 April. IAEA CN-63/155. Vienna.

Dickmann, D. & Pregitzer, K.S. 1992. The structure and dynamics of woody plant root systems. In: C.P. Mitchell, J.B. Ford-Robertson, T. Hinckley & L. Sennerby-Forsse (Eds.) *Ecophysiology of short rotation forest crop*s, p. 95-123. Elsevier Applied Science, London.

Dickson, R. E. 1991. Assimilate distribution and storage. In: A. S. Raghavendra (Ed.) *Physiology of trees,* p. 51-85. John Wiley and Sons, Inc. New York/ Chichester/ Brisbane/ Toronto/ Singapore.

Dumat, C. & Staunton, S. 1999. Reduced adsorption of caesium on clay minerals caused by various humic substances. *Journal of Environmental Radioactivity 46*, 187-200.

Edvardsson, K. 1991. Fallout over Sweden from the Chernobyl accident. In: L. Moberg (Ed.) *The Chernobyl Fallout in Sweden,* p. 47-66. Swedish Radiation Protection Institute.

Egner, H., Riehm, H. & Domingo, W.R. 1960. Untersuchungen über die chemische Bodenanalyse als Grundlage für die Beurteilung des Nährstoffzustandes der Böden. II. Chemische Extraktionsmethoden zur Phosphor und Kaliumbestimmung. *The Annals of the Royal Agricultural College of Sweden. No. 26*, 199-215.

Elowson, S. 1999. Willow as a vegetation filter for cleaning of polluted drainage water from agricultural land. *Biomass and Bioenergy 16*, 281-290.

Epstein, E. 1972. *Mineral nutrition of plants: Principles and perspectives*. John Wiley & Sons. Inc., New York.

Erdei, L. & Trivedi, S. 1991. Caesium/potassium selectivity in wheat and lettuce of different K^+ status. *Journal of Environmental radioactivity 138*, 696-699.

Ericsson, T. 1981. Growth and nutrition of three *Salix* clones at low conductivity solutions. *Physiologia Plantarum 52*, 239-244.

Ericsson, T. 1984. *Nutrient cycling in willow*. Canadian Forestry Service, Ottawa, IEA/ENFOR, Report 5. 32pp.

Ericsson, T. 1994. Nutrient dynamics and requirements of forest crops. *New Zealand Journal of Forestry Science 24(2/3)*, 133-168.

Ericsson, T. 1995. Growth and shoot: root ratio of seedlings in relation to nutrient availability. *Plant and Soil 168-169*, 205-214.

Ericsson, T. & Lindsjö, I. 1981. The influence of pH on growth and nutrition of some energy forest tree species. *SEFP, Techn. Rep. No. 11*. 13 pp.

Ericsson, T. & Ingestad, T. 1988. Nutrition and growth of birch seedlings at varied relative phosphorus addition rates. *Physiologia Plantarum 72*, 227-235.

Ericsson, T. & Kähr, M. 1993. Growth and nutrition of birch seedlings in relation to potassium supply rate. *Trees, Structure and Function 7*, 78-85.

Ericsson, T. & Kähr, M. 1995. Growth and nutrition of birch seedlings at varied relative addition rates of magnesium. *Tree Physiology 15*, 85-93.

Eriksson, B. 1992. Climate. In: Å Clason & B. Granström (Eds.) *Agriculture - Swedish National Atlas*, p. 14-21. SNA Förlag, Stockholm.

Essiamah, S. & Eschrich, W. 1985. Changes of starch content in the storage tissues of deciduous trees during winter and spring. *IAWA Bulletin 6 (2)*, 97-106.

von Fircks, H. 1994. Frost resistance in *Salix*. Ph.D. thesis. *Swedish University of Agricultural Science. Report No. 67*. 78 pp. ISSN 0384-422x.

Fjell, I. 1985. Preformation of root primordia in shoots and root morphogenesis in *Salix viminalis*. *Nordic Journal of Botany 5*, 357-376.

Ford, E.D. & Deans, J.D. 1977. Growth of Sitka spruce plantation: Spatial distribution and seasonal fluctuations of lengths, weights and carbohydrate contents of fine roots. *Plant and Soil 47*, 463-485.

Forsberg, S. 2000. Behaviour of ^{137}Cs and ^{90}Sr in agricultural soils. Ph. D. thesis. Swedish University Agricultural Science, *Act Universitatis Agriculturae Sueciae: Agraria 212*, 46 pp. ISSN 1401-6249.

Francis, C.W. 1978. *Radio-strontium movement in soils and uptake in plant*. Technical Information Center, US Dept. of Energy.

Fredriksson, L., Lönsjö, H. & Eriksson, Å. 1969. Studies on plant accumulation of fission products under Swedish conditions, X. Absorption of ^{90}Sr and ^{137}Cs from soil by vegetable crops. *FOA rapport C 4387-28,* March 1969.

Glavac, V. & Jochheim, H. 1993. A contribution to understanding the internal nitrogen budget of beech (*Fagus sylvatica L.*). *Tree 7*, 237-241.

Hedvall, R. 1997. *Activity Concentrations of Radio-nuclides in Energy Production from Peat, Wood Chips and Straw*. Ph.D Thesis, Lund University, Sweden. 65 pp.

Howard, B.J., Johanson, K., Linsley, G.S., Hove, K., Pröhl, G. & Horyna, J. 1996. Transfer of radio-nuclides by terrestrial food products from semi-natural ecosystems to humans. In: *Modelling of radionuclide interception and loss processes in vegetation and of transfer in semi-natural ecosystems,* p. 49-79. Second report of the VAMP Terrestrial Working Group, Vienna: IAEA.

Hubbard, L.M. & Möre, H. 1998. Strålskyddskonsekvenser från ^{137}Cs vid användning av biobränsle i stora anläggningar. *Swedish Radiation Protection Institute SSI rapport: 98, 15*. 31 pp. ISSN 0282-4434.

IAEA 1987. *Handbook of parameter values for the prediction of radionuclide transfer in the terrestrial and freshwater environment.* 2nd draft March 1987. IAEA, Vienna.

Ingestad, T. & Lund, A.-B. 1986. Theory and techniques for steady state mineral nutrition and growth of plants. *Scandinavian Journal of Forest Research 1*, 439-453.

Ipatyev, V., Bulavik, I., Baginsky, V., Goncharenko, G. & Dvornik, A. 1999. Forest and Chernobyl: Forest ecosystems after the Chernobyl nuclear power plant accident: 1986-1994. *Journal of Environmental Radioactivity 42*, 9-38.

Istvan, P. & Benton, J.J. 1997. Rare earth elements In: *The handbook of trace elements* 223 pp. Boca Raton, Fla. St. Lucie Press.

Johanson, K.J., Bergström, R., von Bothmer, S. & Kardell, L. 1991. Radio-caesium in Swedish forest ecosystems. In: L. Moberg (Ed.) *The Chernobyl Fallout in Sweden,* p. 477-486. Swedish Radiation Protection Institute, Stockholm.

Jonsson, A., Ericsson, T., Eriksson, G., Kähr, M., Lundkvist, K. & Norell, L. 1997. Interfamily variation in nitrogen productivity of *Pinus sylvestris* seedlings. *Scandinavian Journal of Forest Research 12*, 1-10.

Josefsson, W. 1995. Solar Radiation. In: B. Raab and H. Wedin, (Eds.) *Climate, Lakes and Rivers*, p. 40-43. Swedish National Atlas. SNA Förlag, Stockholm.

Karavaeva, Y.N., Kulikov, N.V., Molchanova, I.V., Pozolotina, V.N. & Yushkov, P.I. 1994. Accumulation and distribution of long-living radio-nuclides in the forest ecosystems of the Kyshtym accident zone. *The Science of the Total Environment 157*, 147-151.

Kato, T. 1986. Nitrogen metabolism and utilization in citrus. *Horticulture Review 8*, 181-216.

Kozlowski, T.T. 1992. Carbohydrate Sources and Sinks in Woody Plants. *The Botanical Review 58(2)*, 109-223.

Kramer, P.J. & Kozlowski, T.T. 1979. *Physiology of woody plants*. Academic Press, New York/San Francisco/London, 811 pp.

Kwaratskhelia, N.T., Glonty, G.G., Arnautov, T.N. & Gamazova, E.K. 1967. The influence of some natural factors on the behaviour of radioactive strontium in soils. In: B. Åberg & F.P. Hungate (Eds.) *Radioecological concentration Processes*, p. 19-24. Proc. Int. Symp. Stockholm, 1966. Pergamon Press, Oxford.

Landberg, T. & Greger, M. 1994. Can heavy metal tolerant clones of *Salix* be used as vegetation filters on heavey metal contaminated land? In: P. Aronsson & K. Perttu (Eds.) Report from a symposium: *Willow Vegetation Filters for Municipal Wastewaters and Sludges - a Biological Purification System*, p. 133-144. SLU Info/Repro, Uppsala Sweden.

Lembrechts, J. 1993. A review of literature on the effectiveness of chemical amendments in reducing the soil-to-plant transfer of radio-strontium and radio-caesium. *The Science of the Total Environment 137*, 81-98.

Levitt, J. 1980. *Responses of plants to environmental stresses, Vol 1: Chilling, freezing, and high temperature stresses*. Academic Press, New York, 497 pp.

Linder, S. & Rook, D.A. 1984. Effects of mineral nutrition on carbon dioxide exchange and partitioning in trees. In: G.D. Bowen & E.K.S. Nambiar (Eds.) *Nutrition of Plantation Forest*, p. 211-226. Academic Press, New York.

Marschner, H. 1986. *Mineral nutrition of higher plants*. Academic Press, London. 674 pp.

Marschner, H. 1995. *Mineral nutrition of higher plants.* 2nd edn. Academic Press, London. 889 pp.

Mattsson, S. & Moberg, L. 1991. Fallout from Chernobyl and atmospheric nuclear weapons test. Chernobyl in perspective. In: L. Moberg (Ed.) *The Chernobyl fallout in Sweden,* p. 591-628. Swedish Radiation Protection Institute, Stockholm.

McDonald, A.J.S., Ericsson, A. & Lohammar, T. 1986. Dependence of starch storage on nutrient availability and photon flux density in small birch (*Betula pendula* Roth.). *Plant, Cell and Environment 9*, 433-438.

McGee, E.J., Synnott, H.J., Johanson, K.J., Fawaris, B.H., Nielsen, S.P., Horrill, A.D., Kennedy, V.H., Barbayiannis, N., Veresoglou, D.S., Dawson, D.E., Colgan, P.A. & McGarry, A.T. 2000. Chernobyl fallout in a Swedish spruce forest ecosystem. *Journal of Environmental Radioactivity 48*, 59-78.

Mehra, A. & Farago, M. 1994. Metal ions and plant nutrition. In: M. Farago (Ed.) *Plants and chemical elements: biochemistry, uptake, tolerance and toxicity,* p. 31-66. VCH Verlag, Weinheim, New York, Basel, Cambridge.

Melillo, J.M. 1981. Nitrogen cycling in deciduous forests. In: F.E. Clark & T. Rosswall (Eds.) *Terrestrial nitrogen cycles. Processes, ecosystem strategies and management impacts*, p. 427-442. Ecological Bulletines,No. 33, Stockholm.

Melin, J., Wallberg, L. & Suomela, J. 1994. Long term retention of caesium and strontium in Swedish Boreal Forest Ecosystems. *The Sciences of Total Environment 157*, 93-105.

Milbourn, G.M. 1960. The uptake of radioactive strontium by crops under field conditions in the United Kingdom. *Journal of Agricultural Science 55*, 273-282.

Millard, P. 1993. A review of internal cycling of nitrogen within trees in relation to soil fertility. In: M.A.C. Fragoso & M.L. van Beusichem (Eds.) *Optimization of Plant Nutrition*, p. 623-628. Kluwer Academic Publishers

Millard, P. 1996. Ecophysiology of the internal cycling of nitrogen for tree growth. *Zeitschrift für Pflanzenernährung und Bodenkunde 159*, 1-10.

Momoshima, N. & Bondietti, E.A. 1994. The radial distribution of ^{90}Sr and ^{137}Cs in trees. *Journal of Environmental Radioactivity 22*, 93-109.

Moore, R., Clark, W.D. & Stern, K.R. 1995. *Botany*, p. 475. Wim. C. Brown Publishers, Inc. ISBN 0-697-03775-4.

Nelson, E.A. & Dickson, R.E. 1981. Accumulation of food reserves in cottonwood stems during dormancy induction. *Canadian Journal of Forest Research 11*, 145-154.

Nikolova, I., Johanson, K.J. & Clegg, S. 2000. The accumulation of ^{137}Cs in the biological compartment of forest soils. *Journal of Environmental Radioactivity 47*, 319-326.

Nilsson, L.-O. & Ericsson, T. 1986. Influence of shoot age on growth and nutrient uptake patterns in a willow plantation. *Canadian Journal of Forest Research 16*, 185-190.

Nisbet, A.F. 1993. Effect of soil-based countermeasures on solid-liquid equilibria in agricultural soil contaminated with radio-caesium and radio-strontium. *The Science of the Total Environment 137*, 99-118.

Nisbet, A.F. & Shaw, S. 1994. Summary of a 5-year lysimeter study on the time-dependent transfer of ^{137}Cs, ^{90}Sr, ^{239,240}Pu and ^{241}Am to crops from three contrasting soil types: 1. Transfer to the edible portion. *Journal of Environmental Radioactivity 23*, 1-18.

Nylén, T. 1996. Uptake, turnover and transport of radio-caesium in boreal forest ecosystems. Ph. D. thesis. *Swedish University of Agricultural Sciences.* 41 pp. FOA-R-95-00242-4.3-SE. ISSN 1104-9154.

Öhman, M. & Nordin, A. 1998. A new method for quantification of fluidized bed agglomeration tendencies - a sensitivity study. *Energy & Fuels 12*, 90-94.

Paasikallio, A., Rantavaara, A. & Sippola, J. 1994. The transfer of cesium-137 and strontium-90 from soil to food crops after the Chernobyl accident. *The Science of the Total Environment 155*, 109-124.

Pereira, J.S., Madeira, M.V., Linder, S., Ericsson, T., Tomé, M. & Araújo, M.C. 1994. Biomass production with optimised nutrition in *Eucalyptus globulus* plantations. In: J. S. Pereira (Ed.) *Eucalyptus for Biomass Production,* p. 13-30. The State-of-the-Art. CEC, Brussels.

Perttu, K. & Aronsson, P. 1999. Fast growing, perennial crops as vegetation filters and CO_2 neutral fuels. *Proceedings, IEA Bioenergy, IUFRO Division 1.09/IEA Task 17, 03-07 March 1999, p. 83-87.*

Peters, L.N., Olson, J.S., & Anderson, R.M. 1969. Eight-year summary of plant-soil data on ^{137}Cs in a tagged appalachian forest dominated by *Liriodendron tulipifera. Oak ridge national laboratory,* ornl-TM-2737.

Ravila, A. & Holm, E. 1994. Radioactive elements in the forest industry. *The Science of the Total Environment 157,* 339-356.

Robison, W.L. & Stone, E.L. 1992. The effect of potassium on the uptake of ^{137}Cs in food crops grown on coral soils: Coconut at Bikini Atoll. *Health Physics, 62(6),* 496-511.

Rosén, K. 1991. Effects of potassium fertilization on caesium transfer to grass, barley and vegetables after Chernobyl. In: L. Moberg (Ed.) *The Chernobyl Fallout in Sweden,* p. 305-322. Swedish Radiation Protection Institute, Stockholm.

Rosén, K. 1996. Field studies on the behaviour of radio-caesium in agricultural environments after the Chernobyl accident. Ph. D. thesis. *Swedish University of Agricultural Sciences, Department of Radioecology. Report SLU-REK-78.* 65 pp. ISSN 0280-7963.

Rosén, K., Öborn, I. & Lönsjö, H. 1999. Migration of radio-caesium in Swedish soil profiles after the Chernobyl fallout in Sweden 1987-1995. *Journal of Environmental Radioactivity 46,* 45-66.

Rytter, L. & Ericsson, T. 1993. Leaf nutrient analysis in *Salix viminalis* energy forest stands growing on agricultural land. *Zeitschrift für Pflanzenernährung und Bodenkunde 156,* 349-356.

Rytter, R.-M. 1997. Fine-root production and carbon and nitrogen allocation in basket willows. Ph.D. thesis. Swedish University of Agricultural Science, *Acta Universitatis Agriculturae Sueciae: Silvestria 39,* 36 pp. ISSN 1401-6230.

Salt, C.A. & Mayes, R.W. 1993. Plant uptake of radio-caesium on heather moorland grazed by sheep. *Journal of Applied Ecology 30,* 235-246.

Sandalls, J., Gaudern, L. & Nason, P. 1990. Radio-caesium in herbage on upland pastures. In: G. Desment, P. Nassimbeni & M. Belli (Eds.) *Transfer of radio-nuclides in natural and semi-natural environments,* p. 511-518. Elsevier Applied Science.

Sauter, J.J. 1988. Temperature-induced changes in starch and sugar in the stem of *Populus x canadensis* "robusta". *Journal of Plant Physiology 132,* 608-612.

Sennerby-Forsse, L. & von Fircks, H.A. 1987. Ultrastructure of cells in the cambial region during winter harding and spring dehardening in *Salix dasyclados* Wimm. grown at two nutrient levels. *Trees, Structure and Function 1,* 151-163.

Sennerby-Forsse, L. & Johansson, H. 1989. *Handbook for Energy Forestry.* Swedish University of Agricultural Sciences, Uppsala, Sweden. 45 pp.

Sennerby-Forsse, L., Ferm, A. & Kauppi, A. 1992. Coppicing ability and sustainability. In: C.P. Mitchell, J.B. Ford-Robertson, T. Hinckley & L. Sennerby-Forsse (Eds.) *Ecophysiology of short rotation forest crops,* p. 146-184. Elsevier, London, New York.

Sennerby-Forsse, L., Melin, J., Rosén, C & Sirén, G. 1993. Uptake of radiocesium in fast-growing *Salix. Journal of Sustainable Forestry 1(3),* 93-105.

Sennerby-Forsse, L. & Zsuffa, L. 1995. Bud structure and resprouting in coppiced stools of *Salix viminalis* L., *S. eriocephala* Michx., and *S. amygdaloides* Anders. *Trees, Structure and Function 9,* 224-234.

SGAB 1986. *Swedish Geological Company. Map of ^{137}Cs kBq/m^2, Ground Surface Results from Aerial Surveys, May to October 1986.* Uppsala.

Sharkey, T.D. 1985. Photosynthesis in intact leaves of C3 plants: Physics, physiology and rate limitations. *Botanical Review 51,* 52-106

Shaw, G. 1993. Blockade by fertilisers of caesium and strontium uptake into crops: effects on the root uptake process. *The Science of the Total Environment 137,* 119-133.

Shaw, G. & Bell, J.N.B. 1994. Plants and Radionuclides. In: M. Farago (Ed.) *Plants and chemical elements: biochemistry, uptake, tolerance and toxicity,* p. 179-220. VCH verlag, Weinheim, New York, Basel, Cambriadge.

Sirén, G., Perttu, K., Sennerby-Forsse, L., Christersson, L., Ledin, S. & Granhall, U. 1984. Energy Forestry. *Information on research and experiments at the Swedish University of Agricultural Sciences.* Swedish University of Agricultural Sciences, Deptartment of Ecology & Environmental Research, Energy Forestry Project, Uppsala, Sweden, 25 pp. ISBN 91-576-2034-2.

Sivak, M.N. & Walker, D.A. 1986. Photosynthesis in vivo can be limited by phosphate supply. *New Phytologist 102*, 449-512.

Skarlou, V., Nobeli, C., Anoussis, J., Haidouti, C. & Papanicolaou, E. 1999. Transfer factors of ^{134}Cs for olive and orange trees grown on different soils. *Journal of Environmental Radioactivity 45*, 139-147.

Smolders, E., Kiebooms, L., Buysse, J. & Merckx, R. 1996. ^{137}Cs uptake in spring wheat (*Triticum aestivum* L. Cv. Tonic) at varying K supply. *Plant and Soil 181*, 205-208.

Steen, E. & Larsson K. 1986. Carbohydrates in roots and rhizomes of perennial grasses. *New Phytologist 104*, 339-346.

Stepien, V., Brun, A., Botton, B. & Martin, F. 1991. Protein bodies in bark cells of *Populus x euramericana. C. R. Acad. Sci. Paris 313*, 153-158.

Strebl, F., Gerzabek, M.H. & Krag, V. 1995. Soil-plant transfer factors in forest ecosystems. In: *Proceedings of environmental impact of radioactive releases.* p. 716-718. Vienna IAEA.

Streit, B. & Stumm W. 1993. Chemical properties of metals and the process of bioaccumulation in terrestrial plants. In: B. Markert (Ed.) *Plants as Biomonitors. Indicators for Heavy Metals in the Terrestrial Environment*, p. 31-62. VCH Verlag, Weinheim, New York, Basel, Cambridge.

Suomela, J., Wallberg, L. & Melin, J. 1993. Methods for determination of strontium-90 in food and environmental samples by Cerenkov counting. *SSI report 93-11, Swedish Radiation Protection Institute, Stockholm;.*

Thorsteinsson, B., Tillberg, E. & Ericsson, T. 1990. Levels of IAA, ABA and carbohydrates in source and sink leaves of *Betula pendula* Roth.. *Scandinavian Journal of Forest Research 5*, 347-354.

Titus, J.S. & Kang, S.-M. 1982. Nitrogen metabolism, translocation and recycling in apple trees. *Horticultural Reviews 4*, 204-246.

Tromp, J. 1983. Nutrient reserves in roots of fruit trees, in particular carbohydrates and nitrogen. *Plant and Soil 71*, 401-413.

Van Bergeijk, K.E., Noordijk, H., Lembrechts, J. & Frissel, M.J. 1992. Influence of pH, soil type and soil organic matter content on soil-to-plant transfer of radio-caesium and strontium as analyzed by a nonparametric method. *Journal of Environmental Radioactivity 15*, 265-276.

Welch, R.M. 1995. Micronutrient nutrition of plants. *Critical Reviews in Plant Sciences, 14(1)*, 49-82.

Wetzel, S., Demmers, C. & Greenwood, J.S. 1989. Seasonally fluctuating bark proteins are a potential form of nitrogen storage in three temperate hardwoods. *Planta 178*, 275-281.

Wetzel, S., Sennerby-Forsse, L. & Burgess, D. 1995. Storage compounds in *Populus* cuttings in response to two different nitrogen regimes. In: L.O. Nilsson, R.F. Hüttl & U.T. Johansson (Eds.) *Nutrient uptake and cycling in forest ecosystems*, p. 677-685. Kluwer Academic Publishers.

White, P.J. & Broadley, M.R. 2000. Mechanisms of caesium uptake by plants. *New Phytologist 147*, 241-256.

Yelenosky, G. 1978. Cold hardening 'Valencia' orange trees to tolerate -6.7 °C without injury. *Journal of American Society of Horticultural Sciences 103*, 449-452.

Acknowledgements

First of all, I owe many thanks to my two supervisors Lisa Sennerby-Forsse and Tom Ericsson, who led me into the world of plant physiology and guided me in every possible way and during all stages of my studies. Thanks for their help, valuable advice, encouragement and friendship and without them this thesis would never have been finished.

I also wish to thank Klas Rosén, my supervisor in the last part of my study, for his help and co-operation.

I am deeply grateful to Prof. Sune Linder for giving me the opportunity to start my studies in Sweden. My time in Uppsala has not always been so easy but I certainly do not regret that I came here. I would like to thank Prof. Lars Christersson for giving me opportunity to start my work in the area of short rotation forestry. I also wish to thank Prof. Theo Verwijst for giving me the opportunity to finish this study.

Many thanks to my colleagues and friends in the Department of Short Rotation Forestry who has helped me in different ways throughout the years. Special thanks to the technical staff for their skilled assistance. I also would like to thank Prof. Kurth Perttu for valuable comments on the thesis.

Many thanks to Prof. Karl-Johan Johanson who let me share his knowledge in radioecology and also for his valuable comments on the manuscripts and thesis. I also wish to thank Nigel Rollison for linguistic suggestions.

Finally, I wish to thank my husband Heinrich for his love and whole-hearted support. He and my two daughters Anna and Linda have made my life meaningful and cheerful. I also would like to thank my parents, brothers and sisters, including their families, for their love and encouragement throughout my whole life.

This study was supported by the Swedish National Board of Industrial and Technical Development (NUTEK), the International Energy Agency (IEA) and the Swedish Radiation Protection Institute (SSI).