Changing Carbohydrate Partitioning in 6-Year-Old Coniferous Trees after Prolonged Exposure to Cement Dust

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Z. Naturforsch. **52c**, 586–594 (1997); received March 20/June 6, 1997

Conifers, Dust Pollution, Carbohydrates, Partitioning

Two-year-old seedlings of *Picea abies* L., *P. glauca* L., *P. mariana* L., *Pinus sylvestris* L. and *Pseudotsuga menziesii* L. were planted in a sample plot influenced by high concentrations of cement dust, and in an unpolluted (control) area in 1990. In 1994, the six-year-old trees were dug up in the pre-bud-break period. A comparative analysis of soluble sugars (glucose, fructose, sucrose, maltodextrines), starch and hemicelluloses contents was carried out and the changes in carbohydrate partitioning were estimated. A decrease in the total content of soluble sugars, mainly of glucose, fructose and maltodextrines, was observed in polluted trees, especially in roots, stems and buds, while the sucrose content increased in different organs. Fluctuations in glucose and fructose contents in roots were in good correlation with these sugars in needles and maltodextrines in stems and shoots. Changes in starch and hemicellulose partitioning between different organs of trees were modest and their directions were highly dependent on species.

Introduction

Balanced allocation of carbon between immediate use and storage is essential not only for plant growth but also for survival during stress (Chapin, 1991; Geiger and Servaites, 1991). Ample information is available about deviations in the assimilation of carbon and its partitioning within plants under the influence of acidic air pollutants (Mooney *et al.,* 1987; Koziol *et al.,* 1988; Kozlowski *et al.,* 1991; Oren and Zimmermann, 1989; Dickson and Isebrands, 1991; Mandre and Klõšeiko, 1996). However, little is known about carbon assimilation and carbohydrate partitioning in plants under alkaline types of air pollutants and dust pollution impact.

Dust pollution is known to affect several physiological processes linked to carbon metabolism in plants (Farmer, 1993). Steinhübel (1962) compared starch reserve changes in common holly leaves and those treated with foundry dust. He concluded that the critical factor in starch formation is light absorption by the dust layer, whereas the influence on transpiration or overheating of leaf tissue are of minor significance. Possibly, the chemical composition and pH of dust are the factors most strongly affecting the metabolism of carbohydrates in plants subjected to dust pollution. Czaja (1961) showed that in case of the surface pH value up to 10 of *Beta vulgaris* leaves, the leaf cells starts to plasmolyse one week after the application of cement dust, with an irregular distribution of chloroplasts and halt of starch formation. Iliescu (1981) ascertained that alkaline dust from the electric filters of a cement plant, applied to *Begonia* sp., rapidly inhibits the formation of reducing sugars. Studies of the annual carbohydrate dynamics in the needles of Norway spruce incrusted with cement dust showed that in winter the content of soluble sugars may be 20–30% lower than in unpolluted trees, but the seasonal dynamics of starch is notably lower than control from April to July (Mandre, 1995a). Obviously, light shortage under the dust cover is of great importance in carbon assimilation and photosynthates content in plants.

The objective of this study was to detect changes in partitioning of carbohydrates in different coniferous species under high pollution impact of alkaline dust emitted from a cement plant. Our results should contribute to a better understanding of the physiological background of response reactions of conifers to air pollution.

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Materials and Methods

Plant material and environmental conditions

Our investigations were carried out on six-year-old trees of Scots pine (*Pinus sylvestris* L.), Norway spruce (*Picea abies* L.), white spruce (*P. glauca* L.), black spruce (*P. mariana* L.) and Douglas-fir (*Pseudotsuga menziesii* L.) in field conditions.

In 1990, 25–40 two-year-old genetically similar and homogeneous in habitus seedlings from each species were planted in two sample plots located in similar climatic conditions in Northeast Estonia.

The experimental sample plot was situated in the vicinity of the cement plant of Kunda (longitude 26°30' E, latitude 59°20' N). The main damaging factor for trees in this sample plot was apparently technological dust, which constitutes 87–91% of the total emission; SO_2, NO_x, CO and other gaseous pollutants make up the remaining 9–13% (Raukas, 1993; Estonian Environment 1993, 1994; Estonian Environment 1994, 1995). The dust from the electric filters has many components, but the following substances are predominant: 40–50% CaO; 12–17% SiO_2; 6–9% K_2O; 4–8% SO_3; 3–5% Al_2O_3; 2–4% MgO;1–3% Fe_2O_3, including Mn, Zn, Cu, V, As, Ba, Pb, etc. (Raukas, 1993). Dust had a pH value of approximately 12.3–12.6. The high dust concentration in the air for over 30 years has brought about alkalization of soil (pH 8.1) of this territory. During the vegetation period, pH values of 7.5–8.1 of precipitation were measured whereas the pH of snow water exceeded 10 (Mandre *et al.*, 1992; 1994).

The dust load on the experimental sample plot was approximately 600–2400 g$\times$m$^{-2}\times$year^{-1} depending on the velocity and direction of winds. The total dust emission from the cement plant is shown in Fig. 1.

Control sample plots were situated on the relatively unpolluted territory of Lahemaa National Park about 34 km west from the cement plant, opposite to prevailing winds (longitude 26°00' E, latitude 59°31' N). The pH of rainwater measured during the investigation period was 6.1–6.6 and that of meltwater 6.7–7.0. The humic horizon of soil had pH 3.6–4.2.

In late April – early May 1994, before bud break, 6–10 six-year-old trees of each species were dug up and the roots, stems, shoots, needles of shoots and stems, and buds were separated for the assessment of carbohydrates. We used only one-year-old needles and shoots, because they are the most important source of photosynthate for the new needles and shoots during the pre-bud-break period and during their first weeks of development (Ziemer, 1971; Ericsson, 1978).

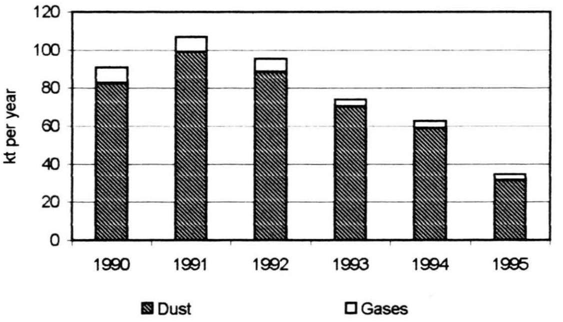

Fig. 1. Emission of dust and gaseous pollutants into the atmosphere from the cement plant in Kunda in 1990–1995.

Extraction and biochemical measurements

Total soluble sugar and starch concentrations were estimated using the methods recommended by Arasimovich and Ermakov (1972), Ferenbaugh (1976) and Marshall (1984). The separated parts of 6–10 trees were immediately fixed in boiling ethanol and dried in the air. 1–5 g of dried and homogenized plant material was used for repeated extraction of soluble sugars with 80% ethanol, centrifuged and the soluble supernatant was collected. All the residue that remained after the removal of soluble sugars was dried, followed by gelatinization in distilled water and digestion with 35% perchloric acid (Ferenbaugh, 1976; Marshall, 1984). The extraction of hemicelluloses was carried out by the acid hydrolysis (2% H_2SO_4) method, recommended by Arasimovich and Ermakov (1972) and Sofronova and Chinenova (1987). The soluble sugar, starch and hemicelluloses extracts obtained were individually reacted with anthrone reagent (0.1% anthrone in 72% sulphuric acid) to produce a blue-green coloration and their absorbances were measured at 620 nm (Ferenbaugh, 1976; Peace *et al.*, 1995). Concentrations were calculated using glucose curves as standard.

Detailed analysis of soluble carbohydrates glucose, fructose, sucrose and maltodextrines was carried out using the enzymatic method according to Steen and Larsson (1986). Oven dried sample (50 mg) was extracted in acetate buffer (5 ml, pH 5.0), sucrose was subsequently hydrolysed with 74 mM H_2SO_4 and maltodextrines with amyloglycosidase (Boehringer Cat. No 102 857). Glucose-6-phosphate dehydrogenase (Boehringer Cat. No 737 275) indicator reaction was applied to reduce NADP within the substrate formed in extractions and isomerisation of fructose (via phosphoglycose isomerase (Boehringer Cat. No 127 396, diluted 1+24) reaction) phosphorylation of glucose (via hexokinase (Boehringer Cat. No 737 275) reaction), absorbance of NADPH at 340 nm was measured spectrophotometrically.

The correlation matrix of Pearson *r* and the significance (*P*) of the correlation between parameters, the regression trendlines and *R*-squared values and standard deviations from the mean were calculated using the packages Statgraphics and MS Excel 5.0.

Table I. Averaged content (mg×g^{-1}) of different fractions of carbohydrates in organs of six-year-old coniferous trees (in parentheses, ± SD; *n*=6 for roots, stems, shoots and stem needles; *n*=10 for shoot needles; and *n*=3 for buds).

Species	Organs	Soluble sugars		Starch		Hemicellulose		$\frac{\text{Soluble sugars}}{\text{Starch+hemicellulose}}$	
		Control	Polluted	Control	Polluted	Control	Polluted	Control	Polluted
Picea abies	Root	62*(12.1)*	15*(1.2)*	88*(4.0)*	82*(5.3)*	125*(10.8)*	102*(14.1)*	0.29	0.08
	Stem	59*(4.9)*	31*(2.4)*	78*(6.3)*	46*(5.2)*	113*(13.7)*	82*(7.4)*	0.31	0.24
	Shoot	67*(5.2)*	52*(10.1)*	91*(4.7)*	54*(1.6)*	113*(30.4)*	86*(5.7)*	0.34	0.37
	Stem needles	106*(6.9)*	124*(15.2)*	136*(16.1)*	103*(8.7)*	150*(13.5)*	130*(9.7)*	0.37	0.53
	Shoot needles	112*(6.5)*	118*(9.4)*	141*(9.4)*	112*(7.1)*	176*(12.4)*	117*(11.0)*	0.35	0.52
	Bud	92*(6.5)*	53*(2.9)*	51*(2.0)*	37*(5.3)*	89*(22.5)*	67*(8.3)*	0.67	0.52
	Average	**83**	**66**	**98**	**72**	**127**	**97**	**0.39**	**0.38**
P. glauca	Root	37*(2.9)*	40*(3.8)*	43*(8.0)*	59*(4.7)*	97*(6.1)*	97*(6.1)*	0.26	0.26
	Stem	45*(3.2)*	47*(3.3)*	49*(4.1)*	50*(5.2)*	97*(13.2)*	106*(9.2)*	0.32	0.30
	Shoot	64*(2.4)*	48*(5.5)*	74*(9.3)*	58*(3.8)*	93*(3.1)*	87*(9.2)*	0.38	0.33
	Stem needles	110*(7.7)*	110*(4.9)*	97*(7.3)*	95*(5.9)*	113*(10.5)*	125*(11.8)*	0.53	0.50
	Shoot needles	102*(7.1)*	90*(5.4)*	109*(12.0)*	95*(9.0)*	128*(8.3)*	107*(7.8)*	0.43	0.45
	Bud	76*(1.6)*	38*(2.2)*	41*(6.3)*	49*(1.7)*	91*(9.2)*	82*(6.2)*	0.58	0.29
	Average	**72**	**62**	**69**	**67**	**103**	**101**	**0.43**	**0.35**
P. mariana	Root	45*(4.1)*	12*(0.9)*	72*(4.9)*	71*(4.0)*	115*(5.8)*	99*(7.6)*	0.24	0.07
	Stem	54*(5.5)*	11*(0.9*	*53(2.8*	*50(2.5)*	90*(4.2)*	87*(7.3)*	0.38	0.08
	Shoot	91*(7.1)*	39*(2.2)*	72*(7.1)*	57*(4.8)*	91*(4.1)*	93*(5.0)*	0.56	0.26
	Stem needles	118*(5.7)*	100*(3.0)*	112*(12.5)*	108*(10.9)*	133*(6.9)*	128*(7.4)*	0.48	0.42
	Shoot needles	107*(5.4)*	91*(5.4)*	118*(7.2)*	95*(11.8)*	146*(20.4)*	125*(11.1)*	0.41	0.42
	Bud	90*(11.1)*	61*(8.5)*	53*(6.8)*	47*(1.7)*	105*(7.3)*	90*(2.7)*	0.58	0.44
	Average	**84**	**52**	**80**	**71**	**113**	**104**	**0.44**	**0.28**
Pseudotsuga menziesii	Root	30*(2.3)*	18*(1.3)*	93*(8.1)*	87*(5.4)*	129*(11.4)*	115*(8.5)*	0.14	0.09
	Stem	61*(4.5)*	13*(1.7)*	109*5.6)*	34*(3.7)*	136*9.1)*	79*(4.9)*	0.25	0.12
	Shoot	46*(3.5)*	31*(3.2)*	93*(8.1)*	70*(8.4)*	116*(9.1)*	93*(9.9)*	0.22	0.19
	Stem needles	79*(11.5)*	*70(4.8)*	116*8.7)*	111*(13.3)*	159*(8.8)*	129*(9.1)*	0.29	0.29
	Shoot needles	84*(7.7)*	65*(4.8)*	126*(11.1)*	110*(10.7)*	171*(16.7)*	123*(9.7)*	0.28	0.28
	Bud	68*(3.2)*	30*(1.8)*	63*(6.4)*	39*(2.1)*	102*(5.1)*	101*(3.0)*	0.41	0.21
	Average	**61**	**38**	**100**	**75**	**136**	**107**	**0.27**	**0.20**
Pinus sylvestris	Root	34*(2.4)*	43*(3.6)*	83*(6.0)*	92*(12.3)*	124*(11.1)*	88*(5.7)*	0.16	0.23
	Stem	54*(3.9)*	56*(2.9)*	41*(6.8)*	65*(4.2)*	88*(8.0)*	81*(9.5)*	0.42	0.39
	Shoot	57*(5.4)*	38*(3.4)*	56*(2.7)*	50*(3.9)*	83*(4.5)*	89*(7.8)*	0.41	0.28
	Stem needles	86*(6.7)*	84*(7.1)*	87*(7.7)*	100*(17.4)*	122*(8.2)*	123*(8.8)*	0.42	0.38
	Shoot needles	77*(6.2)*	76*(10.3)*	84*(3.8)*	77*(6.3)*	119*(6.1)*	114*(5.9)*	0.38	0.40
	Bud	90*(1.5)*	88*(2.9)*	61*(6.0)*	56*(3.9)*	93*(9.7)*	96*(6.2)*	0.58	0.58
	Average	**66**	**64**	**68**	**73**	**105**	**100**	**0.39**	**0.37**

Average was calculated as the average content of carbohydrates in all the studied organs.

Results and Discussion

Our investigations were carried out in late April and early May when buds of trees did not yet show any important morphological changes, but metabolic processes had already activated in trees by that time. It has been indicated by several studies that evergreen conifers accumulate starch gained from net photosynthetic activity during spring before bud break (Ericsson, 1980; Mattson and Troeng, 1986; Sofronova, 1985) and that a relatively large quantity of foliar carbohydrates may be accumulated in conifers (Amundson *et al.,* 1993, 1995; Mandre, 1995a; Wallin *et al.,* 1996). Comparing five coniferous species, we found that starch, which is practically absent in both buds and needles in winter, had already increased before bud break in all young trees, as had the content of hemicellulose. It is known that seasonal dynamics of soluble sugars tends to decrease in the pre-bud-break period (Sofronova, 1985; Mandre, 1995a; Wallin *et al.,* 1996). Still, their content in young conifers, as studied by us, was the highest in needles and buds but low in roots, stems and shoots (Table I).

Regression analysis showed a relationship between the starch content and that of the soluble sugars ($R^2=0.58$, $P<0.001$), and an interdependence of starch and hemicelluloses ($R^2=0.85$, $P<0.001$) in coniferous trees. A dependence was found also between the starch content and the amount of maltodextrines ($R^2=0.50$, $P<0.001$).

Before bud break, in young six-year-old control trees the content of soluble sugars averaged 6–8.5%, that of starch 6.8–10% and hemicellulose 10.5–13.5% of dry weight, varying in different species between indicated levels. According to the average content of carbohydrates, the examined species may be ranged as follows:

Soluble sugars: black spruce > Norway spruce > white spruce > Scots pine > Douglas-fir;

Starch: Douglas-fir > Norway spruce > black spruce > white spruce > Scots pine;

Hemicelluloses: Douglas-fir > Norway spruce > black spruce > white spruce > Scots pine.

The starch and hemicelluloses contents were found to be higher and that of soluble sugars lower in Douglas-fir than in other species. This allows us to suggest a more intensive assimilation Douglas-fir at that period and thus its higher readiness for bud break.

Sofronova and Chinenova (1987) claim that a certain decrease in soluble sugars before bud break takes place mostly on the account of sucrose and fructose, which is compensated by a proportional increase in glucose content. Our studies, however, show the predominance of fructose and glucose among soluble sugars in different coniferous species directly before bud break, while the sucrose content is relatively low (Table II). The ratio between insoluble polysaccharides and soluble sugars changes in favour of the former by the end of April and early May (Table I).

The carbohydrate partitioning between different organs of trees is relatively similar in different species. The content of soluble sugars is the highest in needles and buds and fairly low in roots. Starch shows the highest values in needles. Its content is relatively high also in shoots but low in buds. Hemicellulose is the highest in needles and roots in the pre-bud-break period, but the lowest in buds (Table I).

It has been shown that plants respond to stress by changes in carbon assimilation and in the partitioning of carbon and other resources within the plant. Cement dust, covering the plant organs above ground, acts as a light-selecting filter reducing penetration of photosynthetically active parts of the spectrum (Borka, 1980), rising the temperature of plant tissues (Flückiger *et al.,* 1978) and transpiration intensity (Singh and Rao, 1981). Alkalization of the growth substrate due to cement dust inhibits the assimilation of several necessary nutrient elements. As a result, imbalance of nutrients develops in the plant: Ca and K accumulate in tissues in large amounts, while the availability of Mn, Mg and N is hindered in polluted trees (Mandre, 1995b). Some earlier experimental works on the pigment system indicated reduced photosynthesis and bleaching of leaves under dust pollution impact (Manning, 1971; Borka, 1980). Alkaline cement dust causes a decrease of chlorophyll *a* and other photosynthetic pigments in one-year-old needles of Norway spruce and Scots pine (Ricks and Williams, 1974, 1975; Mandre and Tuulmets, 1995). All these processes are closely related to carbohydrate metabolism and cause changes in carbohydrate content and partitioning.

Our data indicate that cement dust decreases the content of carbohydrates in conifers while the intensity of changes varies in different species. The

Table II. Averaged content of soluble sugars (mg×g^{-1} dw) in different organs of polluted by cement dust and unpolluted six-year-old coniferous trees in the pre-bud-break period (n=3; in parentheses, ± SD).

		Glucose		Fructose		Sucrose		Maltodextrines		Glucose/Fructose	
Species	Organs	Control	Polluted	Control	Polluted	Control	Polluted	Control	Polluted	Control	Polluted
Picea abies	Root	9.7(*0.2*)	3.5(*0.2*)	8.9(*0.3*)	3.3(*0.3*)	1.4(*0.6*)	5.6(*0.6*)	21.5(*0.5*)	13.5(*0.6*)	1.1(*0.02*)	1.1(*0.03*)
	Stem	10.9(*0.7*)	8.0(*0.8*)	13.2(*0.8*)	7.6(*1.3*)	1.2(*0.5*)	12.5(*0.7*)	12.5(*0.6*)	9.3(*0.3*)	0.9(*0.00*)	1.1(*0.06*)
	Shoot	4.2(*0.1*)	3.1(*0.4*)	5.3(*0.1*)	2.1(*0.5*)	10.6(*1.2*)	7.1(*0.1*)	9.3(*0.3*)	5.1(*0.0*)	0.8(*0.00*)	1.5(*0.13*)
	Stem needles	15.9(*3.5*)	14.4(*0.7*)	14.4*3.6)*	11.1(*1.2*)	13.6(*1.0*)	21.4(*7.9*)	15.5(*2.4*)	17.8(*2.2*)	1.1(*0.04*)	1.3(*0.08*)
	Shoot needles	20.4(*1.0*)	15.2(*1.0*)	20.9(*1.4*)	12.0(*1.6*)	13.6(*2.8*)	17.9(*3.8*)	16.3(*0.7*)	20.0(*2.1*)	0.7(*0.02*)	1.3(*0.08*)
	Average	**12.2**	**8.8**	**12.5**	**7.2**	**8.1**	**12.9**	**15.0**	**13.1**	**0.91**	**1.23**
Picea glauca	Root	8.7(*0.3*)	9.3(*0.9*)	8.0(*0.5*)	8.8(*1.6*)	1.7(*0.5*)	9.2(*0.7*)	16.7(*0.6*)	5.3(*0.9*)	1.1(*0.03*)	1.1(*0.09*)
	Stem	5.1(*0.7*)	6.4(*0.4*)	5.4(*0.5*)	6.2(*0.6*)	1.4(*0.0*)	5.0(*0.0*)	7.1(*0.3*)	6.3(*0.2*)	0.9(*0.04*)	1.0(*0.03*)
	Shoot	8.8(*0.5*)	15.4(*3.1*)	6.4(*0.7*)	6.1(*0.8*)	1.9(*0.6*)	3.6(*0.4*)	3.0(*1.0*)	7.9(*1.7*)	1.4(*0.07*)	2.5(*0.18*)
	Stem needles	28.0(*1.6*)	23.3(*0.2*)	16.4(*0.9*)	13.5(*0.1*)	10.8(*3.8*)	15.8(*5.1*)	11.5(*2.3*)	8.6(*1.9*)	1.7(*0.00*)	1.7(*0.02*)
	Shoot needles	26.9(*0.8*)	19.3(*0.8*)	16.0(*0.0*)	14.1(*1.4*)	14.7(*2.5*)	21.2(*6.7*)	11.7(*2.6*)	7.4(*1.8*)	1.7(*0.06*)	1.4(*0.10*)
	Average	**15.5**	**14.7**	**10.4**	**9.7**	**6.1**	**10.9**	**10.0**	**7.1**	**1.36**	**1.54**
Pseudotsuga menziesii	Root	8.6(*0.2*)	2.9(*1.1*)	7.8(*0.7*)	2.5(*1.6*)	10.8(*0.4*)	6.3(*0.7*)	14.5(*0.7*)	9.8(*1.6*)	1.1(*0.24*)	1.2(*0.08*)
	Stem	6.3(*0.4*)	6.7(*0.5*)	5.9(*0.6*)	6.6(*0.6*)	1.5(*0.1*)	2.7(*1.3*)	9.9(*0.5*)	6.3(*0.6*)	1.1(*0.03*)	1.0(*0.04*)
	Shoot	6.5(*1.5*)	4.3(*0.9*)	7.0(*0.7*)	3.8(*1.1*)	4.4(*0.5*)	7.9(*0.5*)	12.7(*2.8*)	8.5(*0.3*)	0.9(*0.10*)	1.1(*0.11*)
	Stem needles	19.8(*0.7*)	16.3(*2.3*)	18.4(*1.1*)	12.8(*2.0*)	20.0(*1.5*)	8.2(*0.5*)	21.1(*2.8*)	11.5(*1.0*)	1.1(*0.03*)	1.3(*0.01*)
	Shoot needles	24.7(*2.4*)	15.6*1.2)*	21.1(*2.9*)	12.0(*1.2*)	9.7(*1.7*)	7.1(*0.9*)	18.1(*3.6*)	14.2(*1.6*)	1.2(*0.07*)	1.3(*0.04*)
	Average	**13.2**	**9.2**	**12.0**	**7.5**	**9.3**	**6.4**	**15.3**	**10.1**	**1.07**	**1.18**
Pinus sylvestris	Root	5.5(*0.5*)	15.1(*0.7*)	5.7(*0.5*)	15.3(*3.7*)	0.9(*0.3*)	5.5(*1.0*)	9.4(*0.7*)	10.8(*3.1*)	1.0(*0.00*)	1.0(*0.20*)
	Stem	6.5(*0.2*)	5.4(*0.2*)	5.4(*0.2*)	5.0(*0.3*)	0.6(*0.2*)	1.0(*0.3*)	2.5(*0.2*)	2.5(*0.3*)	1.2(*0.00*)	1.1(*0.02*)
	Shoot	9.8(*0.4*)	4.4(*0.6*)	10.5(*0.5*)	6.7(*0.9*)	1.9(*0.7*)	25.7(*2.4*)	1.5(*0.5*)	10.7(*0.9*)	0.9(*0.01*)	0.7(*0.02*)
	Stem needles	13.7(*0.2*)	23.2(*1.7*)	15.7(*0.2*)	25.2(*2.0*)	7.9(*0.5*)	13.4(*5.5*)	4.2(*1.7*)	7.8(*1.4*)	0.9(*0.02*)	0.9(*0.01*)
	Shoot needles	18.5(*2.5*)	28.8(*3.9*)	22.3(*3.7*)	29.4(*5.6*)	13.6(*1.4*)	11.1(*1.7*)	6.7(*1.4*)	3.8(*1.7*)	0.8(*0.03*)	1.0(*0.05*)
	Average	**10.8**	**15.4**	**11.9**	**16.3**	**5.0**	**11.3**	**4.8**	**7.1**	**0.96**	**0.93**

Average was calculated as the avarage content of carbohydraes in all the studied organs.

greatest changes are recorded in the content of soluble sugars, the average values being particularly low in Douglas-fir and black spruce. Soluble sugars seem to decrease relatively little in needles, but more in roots and stems, to some degree also in shoots and buds. The content of starch and hemicellulose decreases as well, but less in comparison with changes in soluble sugars (Table I, Fig. 2). Moreover, elevated starch and hemicellulose contents due to cement dust were recorded in roots and stems of white spruce and Scots pine. Certain increase of soluble sugars in stems and roots of these species causes also an increase in starch and hemicellulose storage. The ratio of soluble sugars to polysaccharides is below the control level in the trees grown under dust pollution and in alkalized environment, except for Norway spruce (Fig. 3).

Although the content of soluble sugars in the trees grown in polluted areas was lower than the control value, the dynamics of sugars of this fraction varies depending on the species and organ.

Alkaline dust deposited on trees and alkalized growth substrate caused a decrease in average glucose and fructose contents of 31 and 42%, respectively, in Norway spruce, 30 and 37% in Douglas-fir and only 5 and 7% in white spruce. In Scots pine, however, the contents of these sugars were 43 and 37% higher than in control trees. The average sucrose content increases in the trees grown in a polluted area, exceeding the control value by 59% in Norway spruce, by 126% in Scots pine and by 79% in white spruce, but being 31% lower in Douglas-fir (Table II), with the greatest changes observed in the roots.

The average glucose/fructose ratio is close to 1 in control plants but increases in polluted trees (Table II). This points to an increased share of glucose to glucose + fructose pool from other sources than sucrose (e.g. depletion of starch and malto-

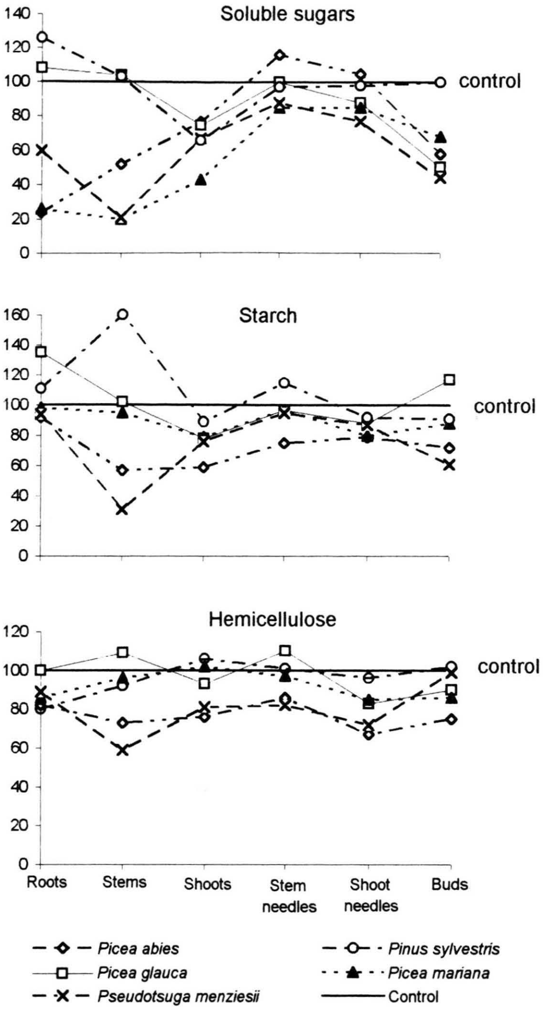

Fig. 2. Percentage from the control of the content of soluble sugars, starch and hemicelluloses in differfent organs of coniferous trees in the area affected by the cement plant. The content of carbohydrates in the control trees equals 100%; initial data in mg×g^{-1} dw are presented in Table I.

dextrines) in polluted trees, since sucrose breaking enzymes like sucrose synthase or acid invertase should not contribute to the formation of the glucose/fructose ratio higher than 1 (Hampp *et al.,* 1994). Deviations of the glucose/fructose ratio from the control value are essential in tree shoots and shoot needles (Fig. 3), i.e., in the organs directly affecting bud break or increasing the assimilating mass. Since an increase in sucrose in conifers is related to growing activity of sucrose phosphate synthase at certain growth stages of trees (Hampp *et al.,* 1994), it is suggested that this enzyme is activated in dust-polluted trees.

In most conifers affected by dust pollution maltodextrines, which constitute water soluble intermediate products in starch biosynthesis (Tohver, 1977), occur in smaller amounts than in trees from unpolluted areas. The dynamics of this value showed high species variability. Compared with control trees, Norway spruce contained 13%, white spruce 29% and Douglas-fir 34% less maltodextrines. In Scots pine grown in a polluted area, however, the maltodextrine content is 48% higher than in control trees (Table II).

In general, carbohydrate synthesis and transport to other parts of plants is initially controlled within the leaf. Roots were found to be particularly sensitive to cement dust and to alkaliztion of the growth substrate (Mandre, 1995a) and the resulting changes in carbohydrate content correlate well with those in needles, shoots and stem: *r* values ranged from 0.82 to 1.0 for hexoses in needles and from 0.94 to 0.97 for maltodextrines in stem and shoot at a significance level $P<0.01$.

It was established that in the pre-bud-break period young conifers contained 23–30% carbohydrates in dry mass, most of this amount being starch and hemicellulose. The distribution of carbohydrates in the organism is determined by the functional properties and activity of the organs. Thus, in needles, serving as photosynthetic organs, the content of carbohydrates is much higher than in non-photosynthesizing roots and stem. Also, the carbohydrate content is different in stem needles and better illuminated shoot needles, being higher in the latter of spruces and Douglas-fir of the control area, but lower in the sample of the polluted area (Table I). This could probably be explained by the fact that shoot needles suffer from a relatively higher dust pollution load, since needles on the stem are placed vertically and therefore the dust falls down.

We may conclude that the assimilation processes, characterized by an increase and relatively high concentration of starch, which is low in buds and in needles in winter, have been activated in coniferous trees by the end of April and beginning of May. Dust pollution, however, includes a number of changes in the complex of soluble carbohydrates, particularly in roots and stem. Obviously, a decrease in glucose and fructose is com-

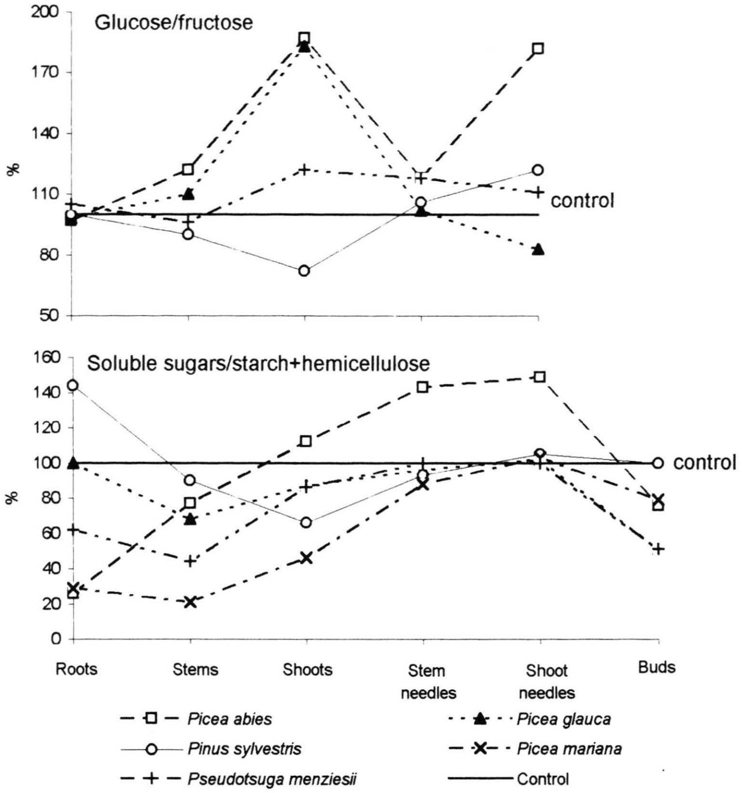

Fig. 3. Deviations from the control in the soluble sugars/polysaccharides and glucose/fructose ratios in coniferous trees grown in an area affected by a cement plant.

pensated by an increase in sucrose concentration due to starch decomposition in the organism. In general, air pollution reduces allocation to roots, which is in strong correlation with the changes of sugars in needles. Low carbohydrate reserves in stems and roots increase susceptibility to other stressors and decrease root growth (Dickson and Isebrands, 1991). The concentration of carbohydrates is also low in buds, which may hinder the development of new shoots and needles, as was documented earlier by Mandre and Ots (1995).

Acknowledgements

This research was supported by the Estonian Science Foundation. Dr. Göran Wallin from the University of Göteborg is gratefully acknowledged for the possibility of enzymatic analysis of sugars at the university laboratory. We are grateful to Kersti Poom and Liivi Tuulmets for technical assistance.

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