

Effects of coppicing on the root and stump carbohydrate dynamics in birches

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Abstract. Whole birch stems were cut off in order to determine how coppicing affects root and stump starch, glucose, fructose and sucrose concentrations and their correlation with shoot regeneration capacity. The *Betula pubescens* Ehrh. and *B. pendula* Roth studied included intact trees, trees that had been coppiced 8 years earlier, trees coppiced at the beginning of the experimental season, and birches that had been coppiced twice, 8 years earlier and at the beginning of the experimental season. Carbohydrate accumulation differed between 8 years earlier coppiced and intact trees. Recent coppicing clearly decreased the starch and sugar concentrations of the roots, which were often highest in the thin roots. The concentrations of these compounds in the stumps were always low, although the carbohydrate concentrations of stumps, in particular, correlated with shoot regeneration capacity. Starch was the most labile of the carbohydrates measured and most clearly reacted to coppicing. Differences in starch- and sugar-reserve dynamics indicate a difference between these birch species in the use and replenishing of root and stump reserves. This information may also be of help when the effects of other stresses, for example, severe animal damage or burning, on the regrowth of young birch stands are estimated.

Introduction

Carbohydrates, especially starch, are the most important reserve compounds in trees (Kozlowski et al. 1991), for example, in *Betula pendula* (Piispanen and Saranpää 2001b). In perennial parts of deciduous trees, concentrations of reserve carbohydrates, in particular starch and sucrose (Nelson and Dickson 1981), but not glucose and fructose (Keller and Loeschner 1989), normally have a seasonal cycle, which includes well-known changes in concentrations during the growing season (Essiamah and Eschrich 1985; Kozlowski et al. 1991; Piispanen and Saranpää 2001a,b). A decrease in carbohydrate reserves as a consequence of spring growth has been observed in both stems (Abod and Webster 1991) and roots of birch (Abod and Webster 1991; Johansson 1993), after which the reserves normally are replenished by photosynthesising leaves, and conversions from starch to sugars occur in the autumn.

To recover after damage, a plant needs viable meristems and carbon reserves. After total removal of above-ground shoots, the stump and root reserves are the only source of carbon for regeneration. Then the amount of root reserves is of major importance for the success of shoot regeneration (e.g., FitzGerald and Hoddinott 1983; Kays and Canham 1991; Dickmann and Pregitzer 1992; Bowen and Pate

1993). Even the carbon of very fine distal roots may be of primary importance, although the distance of a root from a sink is important for its value as a reserve source, as this affects the cost of transport (Vogt and Bloomfield 1991). However, when shoots are being regenerated, the assimilates produced by new leaves soon become the major supplier of carbohydrates to the growing sprouts as well as to depleted root reserves (Kauppi et al. 1990). The effects of removal of above-ground plant parts on root and stump carbohydrate dynamics and their duration are still poorly known, especially in birches, although sprouting has long been important in traditional coppice management of northern woodlands and in forest succession. The aim of this study was to improve our knowledge of changes occurring during the growing season in the non-structural carbohydrate concentrations of *B. pendula* and *B. pubescens* roots and to study the effect of coppicing on concentrations of these compounds. On the other hand, to explain regrowth after coppicing, the role of the stump as a carbohydrate reservoir was investigated as well as possible correlations between carbohydrate concentrations in the root and stump and sprouting parameters.

Material and methods

Betula pendula Roth (origin of seeds: Pohjois-Savo T3-80-17) and *B. pubescens* Ehrh. (origin of seeds: Punkaharju G1-80-369) were sown 9 years before these experiments. At the age of one year the seedlings were moved from a greenhouse and planted in an experimental field at the Botanical Gardens of the University of Oulu, Oulu, Finland (65°N, 25°E), where the length of the growing period is on average 148 days (Finnish Meteorological Institute 2003). Birches were planted by species in rows (Figure 1). At the time of planting, 8 years earlier, the entire above-ground stem had been cut off from 15 *B. pendula* and 30 *B. pubescens* seedlings; 30 of the *B. pendula* seedlings had been left intact. The former will be referred to as 'sprout-origin' and the latter as 'intact' or 'seed-origin' trees (the size of the sample trees is in the Table 1). Birches were grown in a mixture of peat, sand and compost soil (1:1:1). The depth of the growth medium was 40 cm, and under it there was a sand layer. The spacing of the trees was 1.5 m × 1.6 m.

Some of the *B. pubescens* trees and the seed-origin *B. pendula* trees were coppiced to a 5-cm stump at the beginning of the experimental season (1st June) and some were left uncut (Table 2). Moreover, all the sprout-origin *B. pendula* trees were left uncut. The first samples were collected in connection with coppicing (1st June, when leaves had started to grow). Other sampling dates were 22nd June, which corresponds to midsummer (leaves were of full-size), and 15th August, the end of summer (leaves had started to become yellow).

On each of the sampling dates both the dormant and the activated basal buds located on the stumps were counted; and the numbers and lengths of the sprouts were measured. Dormant and activated buds as well as sprouts were determined as previously (see Kauppi et al. 1988b; Paukkonen and Kauppi 1998). Sprouting percentages were determined as in Paukkonen and Kauppi (1998).

X	<u>4/2</u>	X	X	<u>5/2</u>	X			X	X	X	<u>2/2</u>	<u>1/2</u>	X	X	X	X	X		
<u>4/2</u>	<u>4/3</u>	<u>5/3</u>	X	<u>4/1</u>	X			X	<u>3/3</u>	X	X	<u>1/3</u>	<u>2/3</u>	<u>1/1</u>	X	X	X	X	
	<u>4/2</u>	<u>4/3</u>	X	<u>5/3</u>	X		X	X	<u>3/2</u>	X	(x)	<u>2/3</u>	<u>1/1</u>	X	X	X	X	X	
	<u>4/3</u>	<u>5/3</u>	X	<u>4/1</u>	X		X	X	(x)	<u>3/2</u>	X	X	<u>1/3</u>	<u>2/2</u>	<u>1/2</u>	X	X	X	X
	<u>4/1</u>	X	<u>5/2</u>	X			X	X	(x)	<u>3/3</u>	X	X	<u>1/1</u>	<u>1/3</u>	<u>2/2</u>	X	X	X	X
	<u>5/2</u>	X	<u>5/3</u>	X			X	X	(x)	<u>3/1</u>	X	<u>3/2</u>	X	<u>1/2</u>	<u>2/3</u>	<u>1/3</u>	X	X	
	<u>4/3</u>	X	<u>4/2</u>	X			X	X		<u>3/3</u>	X	<u>3/1</u>	(x)	<u>1/1</u>	<u>2/2</u>	<u>1/2</u>	X	X	
	X	X	<u>5/2</u>	X	<u>4/3</u>		X	X	X	<u>3/3</u>	<u>3/2</u>		<u>2/2</u>	<u>1/1</u>	<u>2/3</u>	X	X		
	X	<u>5/3</u>	X	<u>5/2</u>			X	X	X	<u>3/1</u>	X		<u>1/3</u>	<u>2/3</u>	<u>1/2</u>				
	X	<u>4/1</u>	X	<u>4/2</u>			X	X	X	X	X								
	X	<u>4/1</u>	X				X	X	X	X	X								

Figure 1. Growing order of the sampled birch trees. The first number of a figure pair refers to the plant type: 1 – intact *B. pendula*, 2 – intact *B. pendula*, coppiced on 1st June of the experimental growing season, 3 – sprout-origin, 8 years earlier coppiced *B. pendula*, 4 – sprout-origin, 8 years earlier coppiced *B. pubescens*, 5 – sprout-origin, 8 years earlier coppiced *B. pubescens* coppiced a second time on 1st June of the experimental growing season. The second number refers to the sampling date: 1 – 1st June, 2 – 22nd June, 3 – 15th August. X – birch tree of same age but different type, not sampled, (x) – dead tree. Birches from empty places had been sampled earlier. Underlining, bold, rasters and regular font are used to make it easier to differentiate between the samplings.

Table 1. Lengths and diameters with standard error of mean (SE) of sampled *B. pendula* and *B. pubescens* trees and the number of stems in an individual with SE. Measurements were made at the end of May just before the first sampling

Species	Origin	Length(SE), m	Diameter(SE), cm	Number of stems(SE)	n
<i>B. pendula</i>	Seed	4.61(0.13)	5.7(0.2)	1.0(0.0)	25
<i>B. pendula</i>	Sprout ¹	4.01(0.19)	5.0(0.3)	1.1(0.1)	11
<i>B. pubescens</i>	Sprout ¹	3.45(0.11)	3.7(0.2)	1.3(0.1)	26

¹Coppiced 8 years before this experiment.

Table 2. Origins, treatments, numbers and sampling dates of *B. pendula* and *B. pubescens* trees used in this experiment. Coppicing refers to the treatment made on 1st June of the experimental growing season

Species	Origin	Coppicing	Number of sampled trees		
			1st June	22nd June	15th August
<i>B. pendula</i>	Seed	No	}5 ²	5	5
<i>B. pendula</i>	Seed	Yes		5	5
<i>B. pendula</i>	Sprout ¹	No	3	4	4
<i>B. pubescens</i>	Sprout ¹	No	}5 ²	5	5
<i>B. pubescens</i>	Sprout ¹	Yes		5	5

¹Coppiced 8 years before this experiment.

²On 1st June the original situation of these two treatments was the same.

At every sampling date, starch, sucrose, glucose and fructose samples were collected from the stumps, from the coarse lateral roots (diameter 3–30 mm) just next to the stump, and from the thin lignified lateral roots (diameter 1–3 mm) 50–60 cm from the stump. Fine roots were not sampled because here only

long-living structural roots were under investigation. Samples were dug with a shovel from whole the soil layer (0–40 cm), and birch roots were separated from other roots and washed rapidly. The samples was sawn from the stumps. Wood and bark were not separated. Then the samples were cut into small pieces, dried in an oven (60 °C), and ground into powder, which was then stored at room temperature before analyses were performed. The sugars were extracted in water, and the starch in dimethylsulphoxide, after which the carbohydrates were quantified by an enzymatic method as a percentage of dry weight. Glucose and fructose were analysed as phosphates using hexokinase, glucose-6-phosphate dehydrogenase and phosphoglucose isomerase suspensions. Starch was hydrolysed by amyloglucosidase and sucrose by fructosidase and they were analysed then as glucose. Principles of the tests are found in Bergmeyer and Bernt (1974), Beutler (1978) and Bergmeyer (1984). An exact procedure of the assay is presented in the booklet of Boehringer Mannheim GMBH, Biochemica (1989). The standards and test-combinations (for starch Cat. No. 207748 and for sugars Cat. No. 716260) were purchased from this firm. The inner enzymatic activity of the tissues was eliminated using sample blanks. Two independent parallel samples were treated and measured in the same manner.

The results of the carbohydrate analyses were calculated with the SPSS GLM procedure. If the conditions of parametric test were fulfilled, pairwise comparisons were made with the LSD-test, and if not, with the Tamhane test. For SPSS correlation procedures the total carbohydrate concentration was calculated by adding together the concentrations of individual sugars and starch.

Results

Starch

In all root samples the starch concentration was low at the beginning of June, after which the starch concentration increased significantly by midsummer in the roots of intact *B. pendula* (Figure 2(a)). After that starch decreased significantly to a very low level by the middle of August. Also in *B. pendula* coppiced 8 years earlier, the starch concentration of the roots increased from 1st June to midsummer, and continued to increase until 15th August (Figure 2(b)). On the other hand, in both types of sampled roots, *B. pendula* coppiced on 1st June of the experimental season always had a very low starch concentration (Figure 2(c)). The starch concentration of *B. pendula* stumps was always low (Figure 2). Starch concentration of coarse roots was significantly higher than that of stump in sprout-origin trees on 22nd June (Figure 2). Also coppicing, whether performed recently or 8 years earlier, decreased the starch concentration of *B. pendula* in both stump and roots when the concentration is compared to that of intact trees (Figure 2).

As in *B. pendula*, also in *B. pubescens* the starch concentration of the stumps was always low. In the roots the starch concentration increased from 1st June to 15th August in *B. pubescens* trees coppiced 8 years earlier (Figure 3(a)). In *B. pubescens*

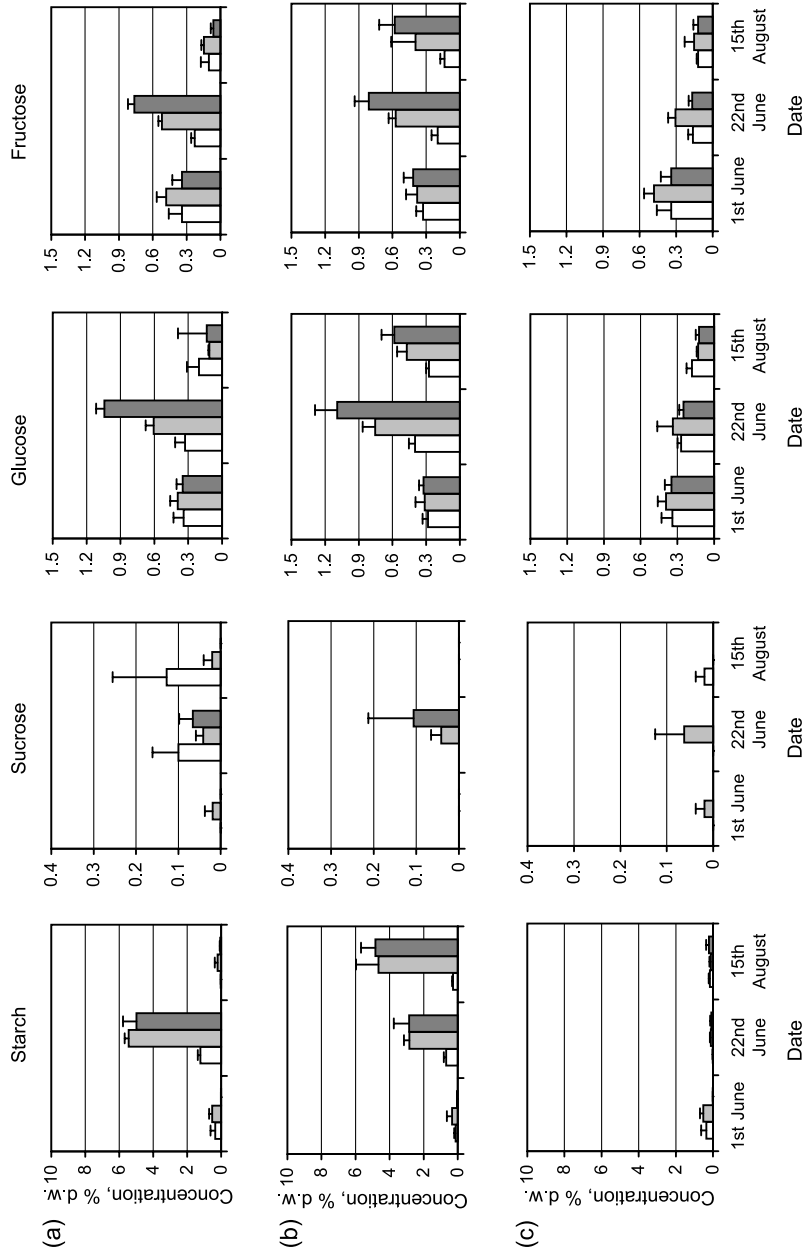


Figure 2. Concentrations of measured carbohydrates (% of dry weight) of *B. pendula* trees: (a) intact, (b) coppiced 8 years earlier, and (c) coppiced on 1st June of the sampling season. Samples of 1st June are the same in (a) and (c) sections. Bars – \pm SE (standard error of mean), white column – stump, light grey column – coarse roots, dark grey column – thin roots.

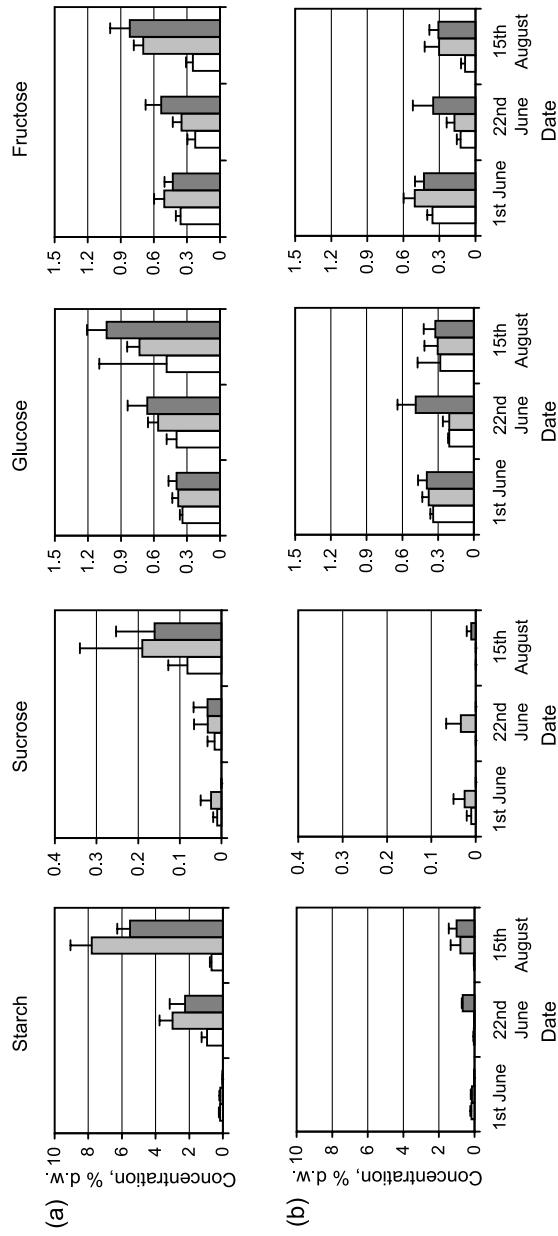


Figure 3. Concentrations of measured carbohydrates (% of dry weight) of *B. pubescens* trees: (a) coppiced 8 years earlier, and (b) coppiced 8 years earlier and on 1st June of the sampling season (twice coppiced). Samples of 1st June are the same in (a) and (b) sections. Bars – \pm SE (standard error of mean), white column – stump, light grey column – coarse roots, dark grey column – thin roots.

trees that had also been coppiced at the beginning of the experimental season, the starch concentration of both types of roots and that of the stumps remained low throughout the growing season (Figure 3(b)). Starch concentrations were mostly significantly higher in the roots of once than of twice coppiced *B. pubescens* trees (Figure 3(a))

Sucrose

Sucrose concentration in the roots and stumps of all trees was very low at every sampling date. There were several samples of both sprout-origin and intact *B. pendula* for which no sucrose could be measured (Figure 2); and owing to the large deviations, no statistically significant differences were observed. In intact trees, the sucrose concentration was highest in the stumps, while in trees coppiced 8 years earlier, no sucrose was measured in the stumps. In trees coppiced at the beginning of the sampling season, no sucrose was found in the thin roots.

In *B. pubescens* the sucrose concentrations were slightly higher than those in *B. pendula*, and the deviations were large. In *B. pubescens*, in all the organs sampled sucrose was observed at least once during the growing season regardless of treatment (Figure 3), and recent coppicing decreased slightly the concentration compared to those coppiced 8 years earlier although no significant differences were observed.

Fructose and glucose

In all samples fructose and glucose were observed in clearly smaller concentrations than starch but in larger concentrations than sucrose. In addition, in any given sample the concentrations of both sugars were almost the same. The trends for these two sugars were the same in trees that had been treated alike, although the trends differed slightly between species. In intact *B. pendula* and in trees of the same species coppiced 8 years earlier the concentrations of fructose and glucose were highest in midsummer, after which in some cases the concentrations decreased by 15th August to even lower levels than on 1st June (Figures 2a,b). At midsummer (22nd June), these sugars were found remarkably in the thin roots. In *B. pendula* trees coppiced at the beginning of the sampling season the concentrations of fructose and glucose remained at the same level during the whole sampling period, decreasing slightly (Figure 2(c)). The concentrations of fructose and glucose were higher in roots than in stumps of *B. pendula* especially on 22nd June (Figure 2), and in thin roots of recently coppiced birches concentrations were lower than in other *B. pendula* trees; coarse roots of sprout-origin uncoppiced *B. pendula* had higher glucose concentration than the intact ones (Figure 2).

Stumps of *B. pubescens* contained less fructose and glucose than the roots did (Figure 3(a)). In *B. pubescens*, coppiced 8 years before sampling, the concentrations of fructose and glucose were highest in the middle of August (Figure 3(a)). In

Table 3. Average number and standard error of mean (\pm SE) of (a) dormant buds, (b) activated buds, and (c) sprouts, and (d) average length of sprouts, cm (\pm SE), and (e) proportion of sprouting buds, %, of *B. pendula* and *B. pubescens*. Coppicing refers to the treatment made on 1st June of the growing season during which the experiment was performed

	Species	Origin	Coppicing	1st June	22nd June	15th August
(a)	<i>B. pendula</i>	Seed	No	2.6(2.6)	0	0
	<i>B. pendula</i>	Seed	Yes	2.6(2.6)	0	0
	<i>B. pendula</i>	Sprout	No	2.0(2.0)	7.0(3.6)	0
	<i>B. pubescens</i>	Sprout	No	16.0(9.7)	11.2(7.3)	0
	<i>B. pubescens</i>	Sprout	Yes	16.0(9.7)	0	0
(b)	<i>B. pendula</i>	Seed	No	0.4(0.4)	0	1.0(0.3)
	<i>B. pendula</i>	Seed	Yes	0.4(0.4)	0	1.2(1.2)
	<i>B. pendula</i>	Sprout	No	0.3(0.3)	0	2.5(2.2)
	<i>B. pubescens</i>	Sprout	No	5.2(4.7)	1.2(1.2)	2.8(2.2)
	<i>B. pubescens</i>	Sprout	Yes	5.2(4.7)	1.4(1.4)	0.6(0.4)
(c)	<i>B. pendula</i>	Seed	No	0	0	5.2(5.2)
	<i>B. pendula</i>	Seed	Yes	0	0	0
	<i>B. pendula</i>	Sprout	No	0	0	1.0(1.0)
	<i>B. pubescens</i>	Sprout	No	0	0.8(0.8)	0.3(0.3)
	<i>B. pubescens</i>	Sprout	Yes	0	25.4(10.7)	8.8(2.0)
(d)	<i>B. pendula</i>	Seed	No	0	0	3.2(3.1)
	<i>B. pendula</i>	Seed	Yes	0	0	0
	<i>B. pendula</i>	Sprout	No	0	0	9.7(9.7)
	<i>B. pubescens</i>	Sprout	No	0	2.2(2.2)	0.8(0.8)
	<i>B. pubescens</i>	Sprout	Yes	0	6.2(0.8)	30.9(6.9)
(e)	<i>B. pendula</i>	Seed	No	0	0	84
	<i>B. pendula</i>	Seed	Yes	0	0	0
	<i>B. pendula</i>	Sprout	No	0	0	40
	<i>B. pubescens</i>	Sprout	No	0	6	11
	<i>B. pubescens</i>	Sprout	Yes	0	95	94

twice coppiced *B. pubescens* the concentration of glucose remained constant during the growing season, but the amount of fructose decreased in stumps (Figure 3(b)). Stumps contained less fructose and glucose than roots in August (Figure 3) and recent coppicing decreased their concentrations (Figure 3).

Bud activation and shoot regeneration

In the *B. pendula* trees investigated the average number of buds was 2.6 at most (Table 3(a and b)), and the buds also sprouted at random (Table 3(c)), as none of the trees coppiced at the beginning of the experimental season sprouted, and only one each of the seed- and the sprout-origin uncut trees sprouted by 15th August. The length of the sprouts remained small (Table 3(d)) but the sprouting percentage was high (Table 3(e)) depending on the low number of buds.

Table 4. Significant correlations observed between sprouting indicators and total non-structural carbohydrate concentrations (TC) of roots and stumps of *B. pendula* and *B. pubescens*. Coppicing refers to the treatment made on 1st June of the growing season during which the experiment was performed

Species	Origin	Coppicing	Date	Comparison	<i>r</i>	<i>p</i>	<i>n</i>
<i>B. pendula</i>	Seed	No	1st June	TC of stump/no. of dormant buds	0.994	0.006	4
<i>B. pendula</i>	Seed	No	1st June	TC of stumps/no. of activated buds	0.994	0.006	4
<i>B. pendula</i>	Seed	No	15th August	TC of coarse roots/no. of sprouts	0.964	0.036	4
<i>B. pendula</i>	Seed	No	15th August	TC of coarse roots/sprouting percentage	0.964	0.036	4
<i>B. pendula</i>	Sprout	No	15th August	TC of thin roots/no. of sprouts	0.953	0.047	4
<i>B. pubescens</i>	Sprout	No	22nd June	TC of all sampled organs/no. of activated buds	-0.895	0.040	5
<i>B. pubescens</i>	Sprout	No	22nd June	TC of all sampled organs/no. of sprouts	-0.895	0.040	5
<i>B. pubescens</i>	Sprout	No	22nd June	TC of coarse roots/no. of activated buds	-0.982	0.003	5
<i>B. pubescens</i>	Sprout	No	22nd June	TC of coarse roots/no. of sprouts	-0.982	0.003	5
<i>B. pubescens</i>	Sprout	No	22nd June	TC of coarse roots/sprouting percentage	-0.997	0.003	4
<i>B. pubescens</i>	Sprout	No	15th August	TC of coarse roots/no. of activated buds	0.957	0.011	5
<i>B. pubescens</i>	Sprout	Yes	22nd June	TC of coarse roots/no. of sprouts	-0.954	0.012	5

On the other hand, at the beginning of the experimental growing season, the numbers of dormant buds in *B. pubescens* were large but decreased during the course of the summer as the buds activated and sprouted (Table 3(a,b and c)). Two of the *B. pubescens* that were not coppiced at the beginning of the experimental growing season sprouted, and all of the *B. pubescens* trees coppiced for the second time at the beginning of the experimental growing season sprouted well. Both the length of the sprouts and the percentage of sprouting buds rose to a high level in the trees coppiced twice (Table 3(d and e)).

Some correlations were observed between sprouting indicators and total carbohydrate concentrations (TC) (Table 4). There was a difference between birch species, that is, in *B. pendula* correlations were positive, and of them those related to buds were found on 1st June and those related to sprouts on 15th August. In *B. pubescens* correlations were negative and they were found mainly on 22nd June; the only correlation observed on 15th August was positive. The correlations of *B. pubescens* related to both activated buds and sprouts but not dormant buds. Moreover, only one correlation was observed in recently coppiced birch, that is, in *B. pubescens* the number of sprouts correlated with the TC of coarse roots on 22nd June. In general, correlations of sprouting indicators were observed with the TC concentrations of coarse roots and stumps.

Discussion

Carbohydrate dynamics was different in *B. pendula* coppiced eight years earlier than in intact *B. pendula* (Figure 2(a and b)). Kauppi et al. (1988a) observed that birch sprouts developed clearly faster than seedlings during their first three growing seasons. Thus coppicing performed 8 years earlier may play a role in carbohydrate dynamics, but also other explanations may exist, for example, the observation of Kauppi et al. (1990) (see also Tschaplinski and Blake 1995) that the leaves of sprouts have better photosynthetic capacity than those of the seed-origin shoots; they grow faster and also longer in the autumn. Other stresses, that is, cutting or burning (Harrington 1989; Bowen and Pate 1993) or insect attack (Kolb et al. 1992), have also been observed to deplete the carbohydrate reserves a significant length of time, two years, before the carbohydrate concentration is normal again (Kolb et al. 1992; Bowen and Pate 1993). In a short interval, for example, in this experiment, where the coppicing was performed at the beginning of the experimental season, the lack or small number of photosynthesising organs is the probable reason for the expected low carbohydrate concentrations of roots and stump of coppiced trees. Even partial defoliation during the growing season has been observed to affect the carbohydrate balances of the roots of *B. pendula* seedlings during the same growing season (Raitio et al. 1994). On the other hand, in tropical *Gliricidia sepium* (Jacq.) Walp., coppicing even in short 3–6 week rotations (Erdmann et al. 1993) or 50% shoot pruning every 2 months (Garcia et al. 2001) did not affect the concentrations of non-structural carbohydrates in the roots, while the concentrations in the above-ground plant parts changed significantly. Difference

in the length and temperature of growing season serve to explain the discrepancy in the results.

Although there were differences in treatments between *B. pendula* and *B. pubescens*, the results strongly suggest that the carbohydrate dynamics differed in *B. pendula* and *B. pubescens*, as the carbohydrate concentration of *B. pubescens* decreased less after recent coppicing (Figures 2(c) and 3(b)). *B. pubescens* sprouted both more and faster, mostly by midsummer, than *B. pendula*, which did not sprout until August (Table 3). This was expected because *B. pubescens* is known to be more resistant to changes caused by cutting off the whole stem (Paukkonen and Kauppi 1998) and is known to have better sprouting ability than *B. pendula* (Mikola 1942). It is also the more northerly species of the two included here and it is adapted to a shorter growing season than *B. pendula* (Gimingham 1984), more northerly species having a better capacity for vegetative reproduction by means of sprouts (Vaarama and Valanne 1973, Kallio et al. 1983). A comparable difference has been observed between two *Eucalyptus* species, as their sugar – but not starch – concentration decreased similarly after coppicing: in a susceptible *Eucalyptus* species the starch concentration even increased slightly, while in the resistant species it did not. This may have been due to the decrease in use of starch (Taylor et al. 1982). Difference in sprouting ability may also be due to the resource remobilization strategy, as for example, *Euptelea polyandra* Sieb. et Zucc needs large above-ground plant parts to sprout, while *Quercus serrata* Thunb. does not (Sakai and Sakai 1998), or due to the size of the stump, because although *Betula platyphylla* var. *japonica* Hara and *Quercus mongolica* var. *grosseserrata* Rehd et Wils. both sprouted after burning, they did it differently: the most seriously damaged the largest birches, but not the oaks, sprouted most (Masaka et al. 2000). A positive correlation between stump size and sprouting has also been observed by Johansson (1992) in *B. pendula* and *B. pubescens* and by Babeux and Mauffette (1994) in *Acer rubrum* L., and a negative correlation by Hytönen (1994) in *Salix* 'Aquatica'.

Correlations between carbohydrates and sprouting indicators were observed mainly in birches that were not coppiced at the beginning of the experimental season (Table 4). In seed-origin *B. pendula* clear correlations were found with numbers of buds on 1st June and with number and percentage of sprouts on 15th August. Instead, sprout-origin *B. pubescens* showed usage of carbohydrates for growth by midsummer, which come out in the negative correlations. Coppicing clearly disturbed the carbohydrate dynamics as only one correlation concerning recently coppiced birches was observed: it shows that carbohydrates of coarse roots are important for basal bud bursting and growing into sprouts. The long distance between the thin roots and sprouting buds, and the small biomass of the thin roots, which also means they contain a small absolute carbohydrate content, may diminish their importance as carbohydrate reservoirs, while this importance may increase if trees are coppiced several times. Coppicing has been found to change the character of the root system by increasing the number of fine roots at the expense of the coarse lateral roots (Bédéneau and Auclair 1989; Paukkonen and Kauppi 1998). Here the only significant correlation in which the thin lateral roots were involved, was observed in *B. pendula* coppiced 8 years earlier (Table 4). Thus, both shoot

origin and tree age may affect the carbohydrate dynamics of roots. On the other hand Kosola et al. (2002) did not find significant effect of root age or of root diameter on their sugar or starch concentrations. They studied young fine roots of poplar at the end of growing season, whereas we studied lateral roots of birches of different ages during the growing season. Thus, the results of our experiments are not directly comparable with those of Kosola et al. (2002). Johansson (1993) also did not find any significant differences in carbohydrate concentrations between roots of different diameter or different distance from the stump in his experiment with *B. pubescens* and *Populus tremula* L. Coppicing changes the balance between roots, as the primary root was the main carbohydrate reservoir of intact seedlings of *Ailanthus glandulosa* Desf, and the lateral roots played this role only after two or three cuttings (Bory et al. 1991). In young *B. pendula* seedlings the fine roots were observed to serve as the main carbohydrate reservoir (Abod and Webster 1991). Fine roots were not sampled in our research, however. Altogether, the above studies show about our insufficient knowledge of the carbohydrate economy in arboreal roots, especially concerning the significance of different root types as storage.

In our results starch was the most unstable of the measured carbohydrates (Figures 2 and 3), as noticed also Kosola et al. (2002). The differences in concentration were large, as the starch concentration of the roots increased rapidly by midsummer in plants that were not cut at the beginning of the experimental growing season. Cutting off the stem could be seen to affect both starch and sugar concentrations, but the effect on sugar was weaker than that on starch concentrations. Webb and Kilpatrick (1993) concluded that starch is the buffer between rapidly fluctuating amounts of photosynthesis products and ensuing translocation or growth processes. Thus, as observed also here (Figures 2 and 3) and by Erdmann et al. (1993), the treatments disturb the accumulation of starch more than that of soluble sugars. The very small concentration of sucrose both in the roots and stumps observed here (Figures 2 and 3), was also observed by Raitio et al. (1994). In their review article Loescher et al. (1990) say as their own opinion that 'sucrose is the major photosynthetic product in many plants and the main storage sugar, but its presence is limited in woody roots'. Further, they notice that glucose and fructose are commonly present in roots at higher concentrations than sucrose. This is well in accordance with our results. Recent measurements made by Mononen (2001) and Piispanen and Saranpää (2001a), also show that sucrose concentration is very low in the stem wood of birch during the growing season and higher in winter. It is possible that some other carbohydrates exist in birch roots instead of sucrose, as in stems of *B. pendula* small concentrations of raffinose have been found (Piispanen and Saranpää 2001a) and *Malus domestica* Borkh. cv. Gala roots contain sorbitol (Wang et al. 1998). However, the drop in the fructose and glucose concentrations of, in particular, seed-origin uncut *B. pendula* trees, and at the same time the decrease in starch concentrations in August with no comparable increase in sucrose concentration (Figure 2(a)) cannot be explained on the basis of this experiment, although the weaker photosynthetic capacity of the leaves of the seedlings than those of the sprouts (Kauppi et al. 1990; see also Tschaplinski and Blake 1995) may play a part in this, as the drop in fructose and glucose concentrations

was not as strong in sprout-origin *B. pendula* (Figure 2(b)), and was not observed at all in sprout-origin *B. pubescens* (Figure 3(a)). The difference of photosynthetic capacity between seedlings and sprouts may be the explanation also for the fact that sprout-origin birches, which were not coppiced at the beginning of the experimental growing season, increased their stump and root starch concentration until 15th August, while seed-origin trees did not (Figures 2(a and b) and 3(a)). This may lead to differences in carbohydrate dynamics between seedlings and sprouts continuing into winter, of which no measurements have yet been performed.

As only the well-regenerating birches, *B. pubescens* trees, were able to accumulate a little starch after recent cutting, the break in starch accumulation and the clear decrease in sugars in connection with the unsuccessful regeneration of the other trees, *B. pendula*, contribute to the difference between these two species in carbohydrate dynamics during vegetative regeneration. Differences were observed also between coppiced and intact plants. This information may be of help when the effects of other stresses on the growth of young birch, both *B. pendula* and *B. pubescens*, stands are estimated, for example, animal damage, burning, early frosts or very poor growing season.

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