SEASONAL CHANGES IN CARBOHYDRATE CONCENTRATION AND COMPOSITION OF DIFFERENT TISSUE TYPES OF PINUS RADIATA TREES

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ABSTRACT

Seasonal variations of the non-structural carbohydrates, glucose, fructose, sucrose, cyclitols, and quinic and shikimic acids and starch were studied in buds, foliage of different ages and crown positions, stem wood and bark, and roots of **Pinus radiata** D. Don trees. The trees were either 12 years old from seed or rooted cuttings of two clones, growing in a fertile site at Rotorua. Of all the carbohydrates analysed, starch showed the most consistent patterns of accumulation and depletion, although the periods when starch concentration peaked differed with tissue type. In foliage, bark, and buds the proportion of carbohydrate present as starch was low, but in roots starch concentrations were similar to those of soluble carbohydrates. Soluble carbohydrates (glucose, fructose, sucrose, cyclitol, quinic and shikimic acids) were present in high concentrations throughout the year, although these also showed compositional changes with season and tissue type. Total non-structural carbohydrate contents were estimated to constitute some 2.8% of the total biomass of a tree.

Carbohydrate compositions and concentrations of the soluble fractions in foliage were found to be similar to published data for **Pinus sylvestris** L. and **Pinus taeda** L. However, starch contents differed by at least four-fold between **P. sylvestris** (24% of total dry weight) and **P. radiata** (6%); the lower starch levels in **P. radiata** foliage appear to result from its continuous growth habit in New Zealand.

Keywords: carbohydrates; saccharides; cyclitols; sugar acids; starch; buds; foliage; stems; roots; **Pinus radiata**.

INTRODUCTION

Most of the work published on the carbohydrates of mature trees has been carried out on Northern Hemisphere horticultural or forest species (Kozlowski & Keller 1966) which are dormant for several months each year. Their annual growth cycle is associated with a build-up of carbohydrates during autumn and rapid depletion in late spring and summer when conditions favour growth. However, this might not be so evident with a species such as *Pinus radiata* in New Zealand where growth continues throughout the year (Rook 1985).

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Although the insoluble carbohydrate, starch, is generally recognised to be the most important storage form in trees (Priestley 1962; Kozlowski & Keller 1966; Ford & Deans 1977), work by Ericsson *et al.* (1978), Cranswick & Zabkiewicz (1979), Chung & Barnes (1980a, b), has demonstrated that other carbohydrates can also constitute a major proportion of the total non-structural carbohydrates present and must be included in any estimates of carbohydrates available for growth. In *P. radiata* tissue, these are the monosaccharides (glucose and fructose), sucrose, cyclitols, sugar alcohols, and quinic and shikimic acids (Cranswick & Zabkiewicz 1979).

Concentrations of the different carbohydrates can vary with type of tissue, growing conditions, and season of the year (Kozlowski & Keller 1966; Ericsson 1980; Adams *et al.* 1986). Often the tissues with the greatest concentration of carbohydrates constitute only a small proportion of the total biomass and therefore the carbohydrates present make up a small part of the total amount in the tree. In relating growth to carbohydrate supply it is necessary to estimate total amounts of carbohydrate from carbohydrate concentrations in the different parts of the tree and the biomass of those parts.

This study examined seasonal changes in composition and concentration of the non-structural carbohydrates of different tissue types of 12-year-old *P. radiata.* Total amounts of carbohydrate available for growth per tree were estimated. The results for *P. radiata* were compared with data for other pine species which have a more limited annual period of growth and lower productivities.

EXPERIMENTAL

Plant Material

Pinus radiata trees, approximately 20 m in height and growing in a stand at the Long Mile experimental site, Forest Research Institute, Rotorua (lat. 38° 10′ S; long. 176° 16′ E) were 12 years old when sampled. This stand was established to allow intensive growth studies in *P. radiata* to be carried out and the results readily extrapolated to the main experimental site at Puruki, 30 km south of Rotorua (Beets & Brownlie 1987). The stock planted consisted of rooted cuttings of known clones (850.451 and 850.455) and seedlings of a controlled-pollination cross (55 × 121). The stand was approximately 1 ha in area and had been thinned to approximately 500 stems/ha 3 years previously. The 14 trees sampled were of similar size (Table 1) and dominance class. Two trees of Clone 850.451 and four of seedling origin were located along the edge of the stand and again within the main part of the stand. Trees of Clone 850.455 were present only near the middle of the stand. At the end of the study, the 14 sample trees were felled and measurements taken of dbh, diameter below green crown, total height, and green crown length (Table 1).

Collection of Samples

Samples of foliage, bud, stem, and root tissue (Table 2) were collected each month for a year, with the exception of January. The "bark" samples of the stem consisted of tissues external to the expanding xylem cells, i.e., a composite sample consisting of cambium, phloem, and bark. The wood was divided by annual growth rings into individual years, from 1- to 4-year-old xylem; wood older than 4 years was not analysed.

TABLE 1—Height, diameter, and green crown lengths of sample trees of rooted cuttings (Clones 850.451 and 850.455) and seedling (Sdg) origin

Tree type	dbh (cm)	Total ht (m)		Height to base of green crown (m)	Stem diameter at base of green crown (cm)
		1977	1978		
451	33.3	18.6	20.7	4.8	26.5
451	28.5	17.9	19.7	5.1	22.0
451	27.8	19.0	21.9	5.4	22.8
451	19.5	17.5	19.4	7.8	14.5
455	28.2	18.1	19.9	3.6	25.8
455	29.0	20.1	21.4	6.0	22.0
Sdg	28.2	18.0	20.5	5.2	23.7
Sdg	24.4	18.8	20.5	8.5	17.8
Sdg	22.9	19.0	20.9	6.5	18.7
Sdg	24.3	17.9	20.1	6.7	19.5
Sdg	28.1	18.0	20.0	7.7	21.1
Sdg	25.0	16.4	18.6	2.6	23.5
Sdg	23.3	17.4	19.6	7.3	17.3
Sdg	22.9	17.6	19.7	6.7	17.4
Average	26.1	18.2	20.2	6.0	20.9

Lateral roots were harvested from a 20 × 20 × 20-cm volume of soil taken approximately 0.5 m from the base of the genotype sampled that month. The roots were separated into "coarse roots" (> 5 mm diameter) and "fine roots". The latter were somewhat arbitrarily separated into forked mycorrhizal and unbranched fine roots. Pollen was collected immediately prior to its release in September.

Material sampled from each genotype was kept separate. The samples were frozen in liquid nitrogen immediately on harvesting, and kept frozen until they were freeze-dried (over 48 hours). Separate sub-samples were used to determine tissue oven-dried weights. The freeze-dried material was ground to pass through a 40-mesh sieve, then stored in sealed glass jars at 4°C. The pollen was air dried over silica gel for 48 hours then stored in sealed jars at 4°C.

Carbohydrate Analyses

Soluble saccharides, cyclitols, and sugar acids were extracted from the ground, freeze-dried, plant tissue with 60% ethanol as described by Cranswick & Zabkiewicz (1979). Duplicate tissue samples were used. Sucrose, glucose, fructose, quinic and shikimic acids, myoinositol, sequoyitol, pinitol, and pinpollitol, were quantified by gas-liquid chromatography (GLC) of their trimethylsilyl derivatives. The tissue residue was retained for starch analysis, using a modification of the method of Haslemore & Roughan (1976), and after hydrolysis the component glucose units were determined colorimetrically.

TABLE 2—Collection of samples by tissue type, position, number, and frequency

Tissue sampled	Position	Types of sample	Number	Frequency
Foliage	Sun crown	(i) 0- to 1-yr-old (ii) 1- to 2-yr-old (iii) 2- to 3-yr-old	Four trees of seedling genotype and two trees of each clone per stand location*.	Monthly , when present Monthly Monthly, when present
	Shade crown	(i) 0- to 1-yr-old (ii) 1- to 2-yr-old (iii) 2- to 3-yr-old	Four trees of seedling genotype and two trees of each clone per stand location*.	Monthly , when present Monthly Monthly , when present
Buds	Sun crown	(i) Terminal 3 cm of first-order branches	Buds from two trees per genotype group	Monthly
Stem	Breast height	(i) Bark, phloem, cambium (ii)1-yr-old xylem (iii) 2-yr-old xylem (iv) 3-yr-old xylem (v) 4-yr-old xylem	Increment cores from two trees per genotype	Monthly
Roots	Close to base of stem, 0 to 20 cm soil depth	(i) <5 mm dia. unbranched (ii) <5 mm dia. branched (iii) 5 to 10 mm dia.	One tree per genotype group	Monthly
	Close to base of stem	Increment cores (0.5 cm dia.) from anchoring roots	Seedling genotype only; one tree	Monthly

* Trees of Clone 850.455 were not available from the location of edge of stand.

Statistical Analyses of Carbohydrate Concentration Data

Concentrations of different types of carbohydrate are expressed on a dry weight basis, i.e., milligrams carbohydrate per gram dry weight of tissue.

Foliage: Analyses of variance were undertaken on the data of 1- to 2-year-old foliage for concentrations of total carbohydrate, quinic and shikimic acids, cyclitols, monosaccharides, sucrose, and starch individually as well as total, against sampling date, genotype, and location in stand. Estimates of variation and the corresponding first-order

interactions were calculated. Current-years foliage was not replicated by crown position and, as 3-year-old foliage was not consistently present, it was not included in the analysis.

Buds: As only one bud per tree per genotype was analysed each month, it was possible to analyse statistically only for variation due to sampling date and genotype, but not variation within genotype.

Roots: Analyses of variance carried out on the root carbohydrates were similar to those for foliage. The main effects were time of sampling, genotype, and root type. All root types (coarse, mycorrhizas, and unbranched fine) were included in the single analysis.

Bark and xylem: There was insufficient replication to allow any statistical analyses of these tissue samples.

Calculation of total amounts of non-structural carbohydrate per tree: Height, diameter, and green crown length measurements of the trees sampled are presented in Table 1. Based on the average tree dimensions and height growth increments for ages 11 to 12 years (Table 1), data from 8-, 9-, and 10-year-old thinned stands of *P. radiata* from Kaingaroa Forest (Table 1 of Madgwick *et al.* 1977) were extrapolated to provide estimates of oven-dry weights of stem wood, branches, stem bark, and foliage of the sample trees in this study. The weight of the stump and roots > 5 mm diameter for each tree was estimated from Equation 2 of Jackson & Chittenden (1981); this equation was developed from data on individual trees of *P. radiata* of similar size to the trees in our study. The weight of roots < 5 mm diameter was estimated from data of Santantonio & Santantonio (1987) for a similar-aged stand of *P. radiata* with a stocking of 570 stems/ha at Puruki.

Carbohydrate content was calculated from the weight of the biomass component multiplied by the average carbohydrate concentration of that biomass component over the period November to March. These component carbohydrate contents were summed to estimate total amount of non-structural carbohydrate per tree.

RESULTS

Carbohydrate Composition in Different Tissues

All types of *P. radiata* tissue analysed, except pollen, consistently had shikimic and quinic acids, the cyclitols (pinpollitol, pinitol, sequoyitol, and myoinositol), monosaccharides (glucose and fructose), disaccharide (sucrose), and starch. Pollen had the four cyclitols and glucose, sucrose, and starch. The tissue composition peaks were pollen with the highest proportion of sucrose, developing foliage with the highest proportion of acids, and roots with the highest proportion of starch (Fig. 1). These data are presented as average values for the period November to March to represent the carbohydrate composition of the tissue types during that part of the year when there is a high demand for carbohydrates for growth and respiration (Table 3).

There were significant differences in composition with time of year. For example, starch constituted a major proportion of the total non-structural carbohydrate pool in the foliage, roots, and bark in early summer, i.e., October to December, and a small proportion in autumn, i.e., March to May, as can be seen in Fig. 2.

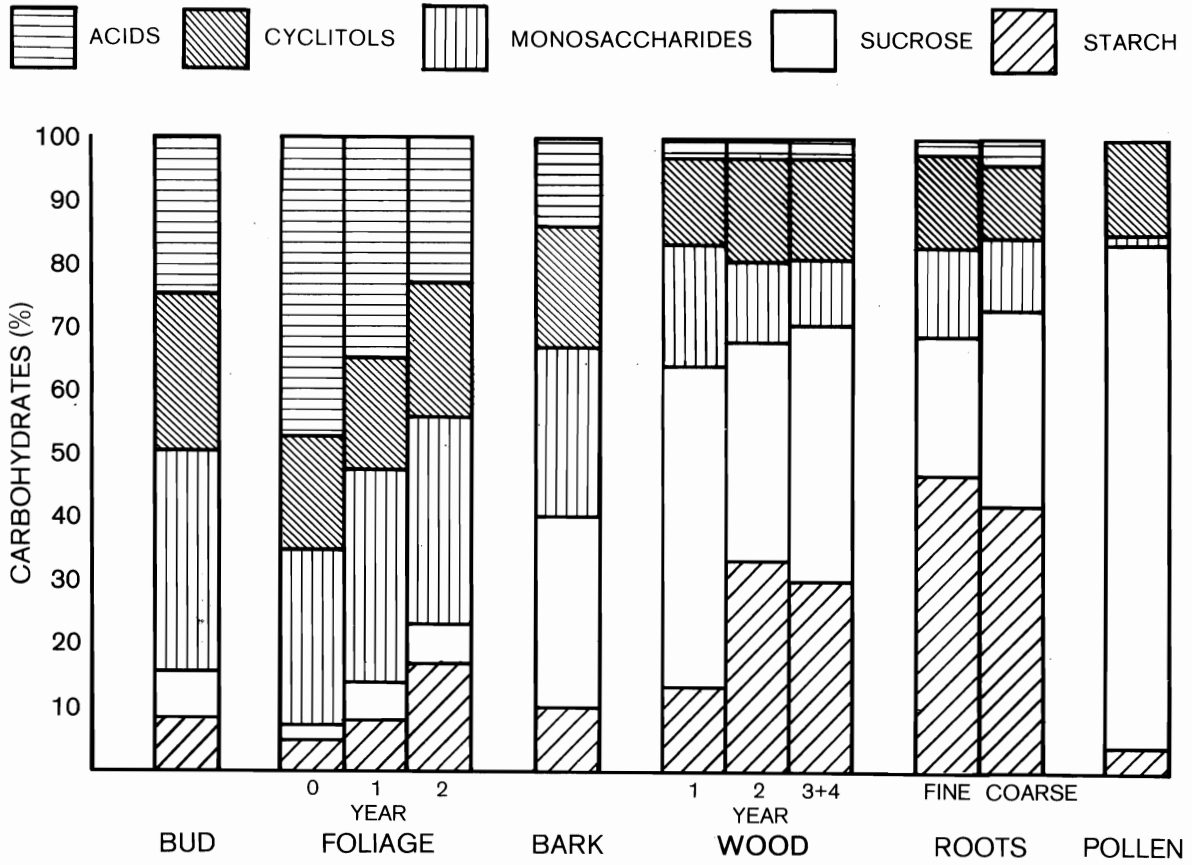


FIG. 1—Average percentage composition of non-structural carbohydrates, by tissue type, for **P. radiata** (November to March period).

TABLE 3—Mean carbohydrate contents of different tissues from radiata pine of seedling origin sampled between November and March. All sugar levels expressed as mg/g dry wt

Tissue type	Acids		Cyclitols				Monosaccharides		Sucrose	Starch
	Shikimic acid	Quinic acid	Pin-pollitol	Pinitol	Sequoyitol	Myoinositol	Glucose	Fructose		
Bud	38.0	19.7	3.1	41.1	11.8	3.2	51.1	31.0	17.3	20.2
Foliage: 0- to 1-yr	53.1	37.3	3.6	23.3	4.5	4.5	29.7	23.0	4.7	10.1
1- to 2-yr	44.5	17.1	3.4	20.5	1.1	7.2	34.6	25.9	9.9	14.8
≥ 2 yr	22.7	11.4	3.9	21.7	1.4	4.7	25.7	23.0	9.5	25.6
Bark/Cambium/Phloem	3.7	7.5	1.0	10.6	1.3	2.4	14.2	7.4	23.8	8.0
Wood: 0- to 1-yr	0.2	0.4	0.2	2.3	0.3	0.8	2.2	1.1	10.2	2.7
1- to 2-yr	0.1	0.5	0.2	2.3	0.2	0.4	1.3	1.1	6.5	6.3
2- to 3-yr	0.2	0.3	0.1	1.9	0.2	0.4	1.2	0.6	6.9	5.1
Roots: Coarse >5 mm dia.	0.5	1.9	0.3	4.3	0.9	0.7	3.8	2.7	17.5	24.0
Main root	0.7	1.6	0.3	3.6	0.4	1.0	4.1	2.4	9.4	11.9
Fine branched	0.3	0.6	0.8	3.6	1.1	0.4	3.6	1.9	9.0	18.6
Fine unbranched	0.5	0.9	0.3	6.2	1.7	0.7	4.6	2.6	11.3	32.5
Pollen*	0	0	0.8	19.5	0.5	1.0	1.6	0	111.8	5.7

* Sampled September only

Carbohydrate Concentrations in Different Tissues

Concentrations of the carbohydrates analysed varied both by tissue type (Table 3) and with season of the year (Fig 2 and 3). The variations in amounts of the different carbohydrates between months were in fact generally significant for all tissue types except for the total carbohydrates and acids in the foliage (Tables 4, 5, and 6).

Buds and foliage contained high concentrations of all soluble carbohydrate components, especially quinic and shikimic acids (Fig. 2 and 3). Older foliage contained lower total carbohydrate concentrations, while bark and fine roots had concentrations less than 10 mg/g dry weight of tissue (Fig. 4). Although concentrations of the individual classes of carbohydrates differed (Table 3), the patterns of carbohydrate

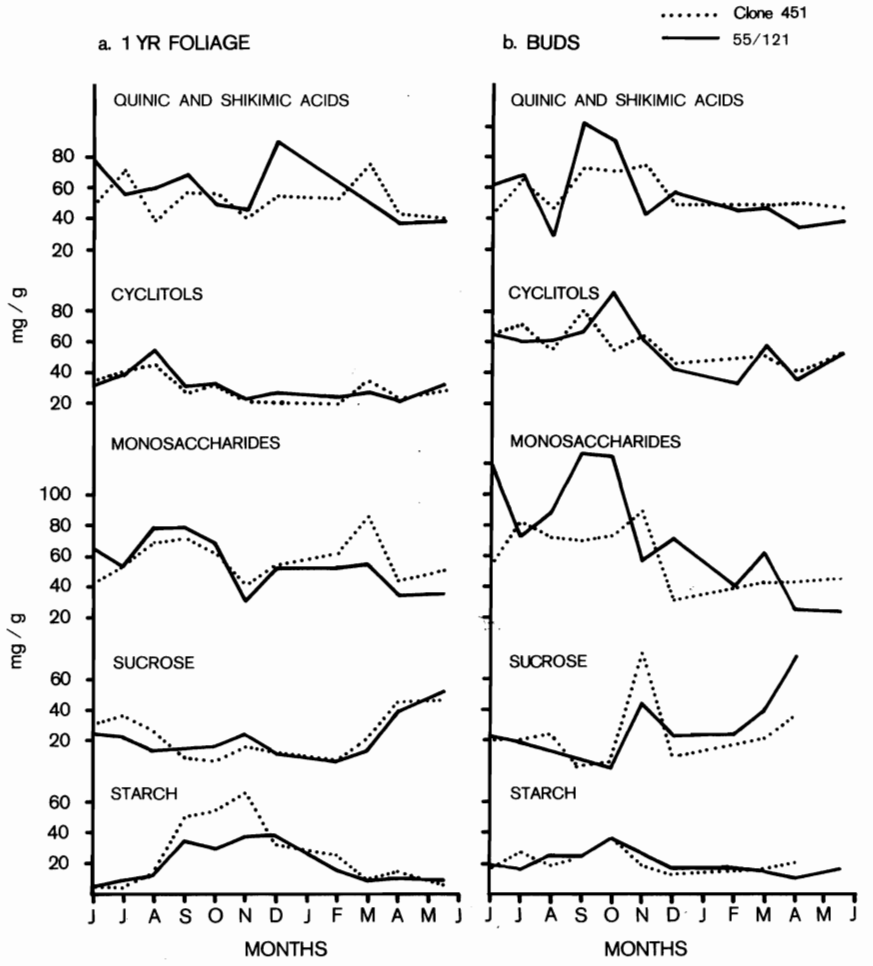
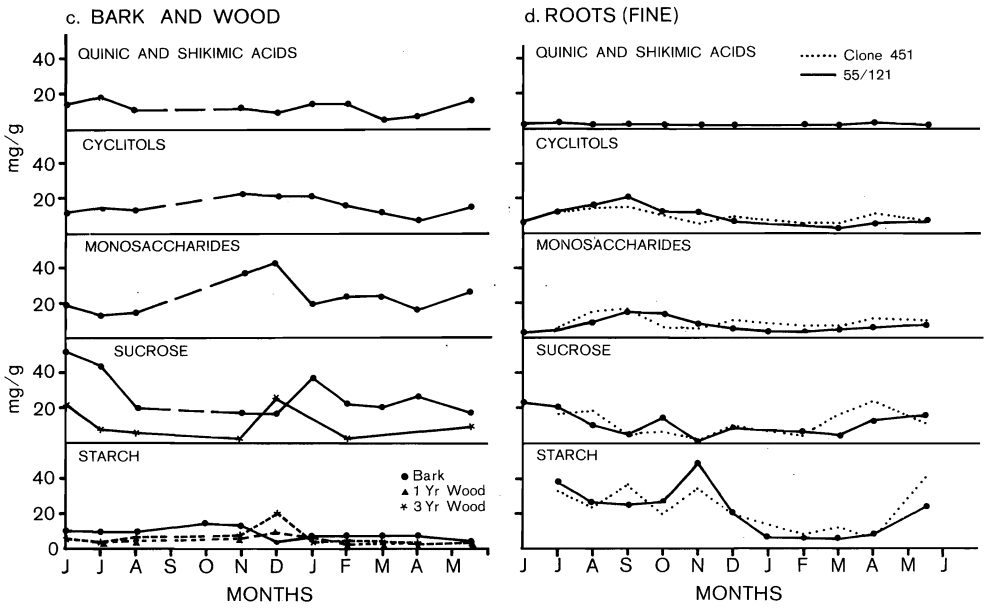


FIG. 2—Seasonal changes in carbohydrate concentrations (mg carbohydrate/g tissue dry weight) by tissue type for two genotypes of **P. radiata** trees. Genotypes were (1) seedling origin, and (2) rooted cuttings of Clone 850.451. Tissue types are (above) (a) foliage, (b) buds; (facing page) (c) bark, (d) roots.



accumulation and depletion were similar for all root types. The data for roots presented in Fig. 2 are for the fine roots < 5 mm only; concentrations of individual carbohydrates by root type are given in Table 3.

In general, the seasonal trends of concentrations of quinic and shikimic acids, cyclitols, and monosaccharides had two minima occurring in spring (November) and autumn (May) and two maxima occurring in winter (August) and summer (February) (Fig. 2).

The greatest starch concentrations were observed in the older foliage and root tissues; in spring and early summer starch concentrations of 60 mg/g dry weight tissue were recorded in the 1- to 2-year-old foliage and a low of 5 mg/g in early winter (Fig. 2). In contrast, starch levels of fine roots were high during winter and early spring then declined rapidly. The proportion of starch in roots was higher than in 1-year-old foliage and there was an increase in starch in foliage during spring (Fig. 3).

The values of total non-structural carbohydrates (Fig. 4) are average concentrations during the period of most active growth, i.e., November to March, and are samples from the trees of seedling origin. Buds have the greatest carbohydrate concentrations and older xylem the least. Carbohydrate concentrations decreased with age for the foliage and xylem tissue types.

Effect of Foliage Age and Crown Position

Generally, soluble sugar concentrations decreased and starch levels increased with increasing foliage age, but it was not possible to separate the significant interaction between age and crown position. Upper crown 0- to 1-year-old foliage had greater soluble carbohydrate levels than both the lower 0- to 1-year-old foliage and all the

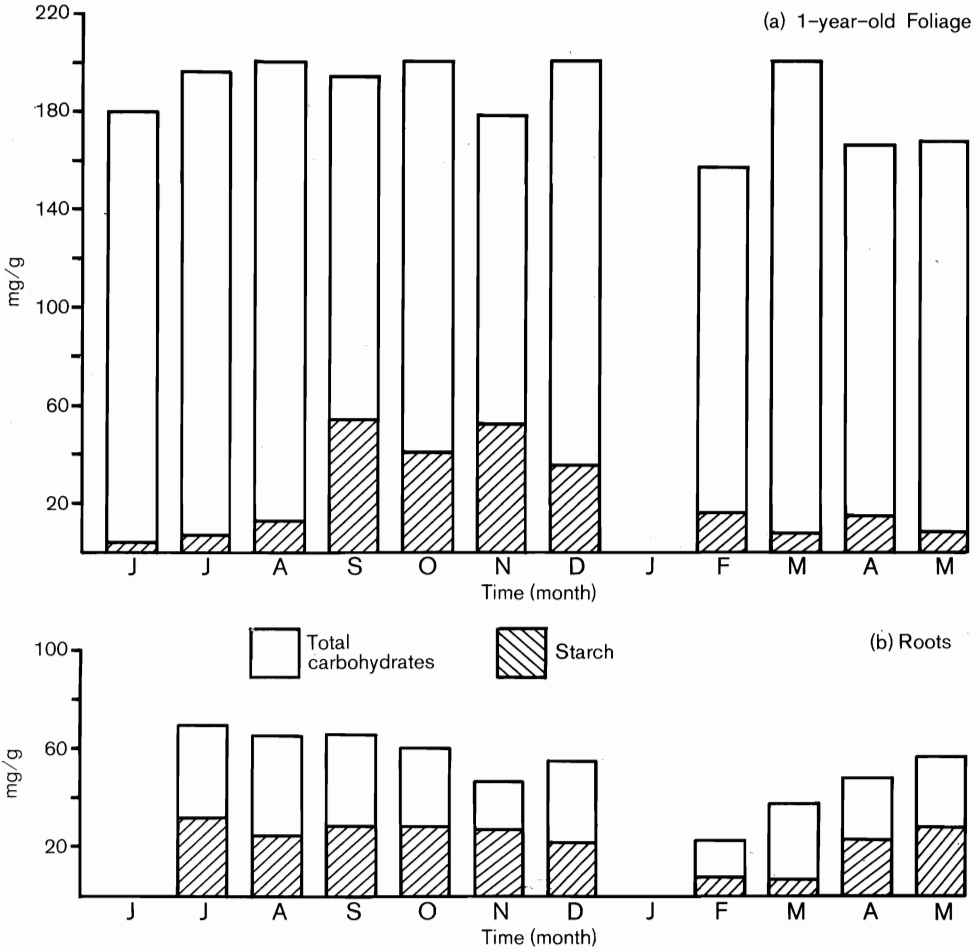


FIG. 3—Changes in total non-structural carbohydrate concentrations (mg carbohydrate/g tissue dry weight) and starch with time for (a) 1- to 2-year-old foliage, and (b) roots (mean value for all types).

1- to 2-year-old foliage. The reverse trend appeared with starch concentrations – upper 0- to 1-year-old foliage had the least starch and upper 1- to 2-year-old foliage had the greatest (Table 7).

Position of Tree in Stand

Foliage was sampled from trees located (a) within the stand, and (b) along the edge of the stand. Although all carbohydrate classes except for sucrose were present in slightly higher concentrations in the edge trees than in the mid-stand trees, the

TABLE 4—Analyses of variance: Concentrations of carbohydrates of 1- to 2-year-old foliage

Source of variation	Total carbohydrates		Acids		Cyclitols		Monosaccharides		Sucrose		Starch	
	df	MS	df	MS	df	MS	df	MS	df	MS	df	MS
Sampling time	10	1032	10	338	10	279**	10	714*	10	826***	10	1423***
Genotype	1	159	1	1158*	1	28	1	121	1	79	1	102
Stand location	1	18	1	196	1	85	1	565	1	411	1	0
Time x genotype	10	1138									10	157**
Time x location	10	1036					10	318	10	332**	10	80
Genotype x location									1	344		
Residual	11	387	32	181	32	31	22	173	20	82	11	26

* 5% level of significance
** 1% level of significance
*** 0.1% level of significance

differences were not significant (Table 4). Total soluble carbohydrate concentrations of the 1- to 2-year-old foliage were 184.8 and 186.1 mg/g for mid- and edge-trees respectively and starch levels were similar, i.e., 23.0 and 22.9 mg/g respectively.

TABLE 5—Analyses of variance: Concentration of carbohydrates of buds

Source of variation	df	Acids MS	Cyclitols MS	Monosaccharides MS	Starch MS
Sampling time	10	856*	333*	1426*	110***
Genotype	1	8	185	462	2
Residual	11	242	95	416	17

* 5% level of significance
*** 0.1% level of significance

TABLE 6—Analyses of variance: Concentrations of carbohydrates of roots

Source of variation	df	Total Carbohydrates MS	Acids MS	Cyclitols MS	Mono-saccharides MS	Sucrose MS	Starch MS
Sampling time	9	1864***	5.4**	69***	78***	318**	664***
Genotype	2	696	1.9	18	21	13	385
Root type	2	1271*	20.1***	72**	52*	80	427*
Time x genotype	18	419	1.2	19	35*	89	159
Time x root type	18	593	1.8	15	17	86	289*
Genotype x root type	4	398	0.3	4	37	86	85
Residual	36	305	1.6	10	16	78	123

* 5% level of significance
** 1% level of significance
*** 0.1% level of significance

TABLE 7—Concentrations of different classes of carbohydrate (mg/g) for different ages of foliage from upper and lower crown positions

	Crown position	0- to 1-year-old	1- to 2-year-old
Acids	Upper	88.0	25.0
	Lower	48.0	31.8
Cyclitols	Upper	48.3	27.2
	Lower	33.3	36.4
Monosaccharides	Upper	59.6	46.6
	Lower	50.0	50.6
Starch	Upper	16.6	40.2
	Lower	36.8	39.2

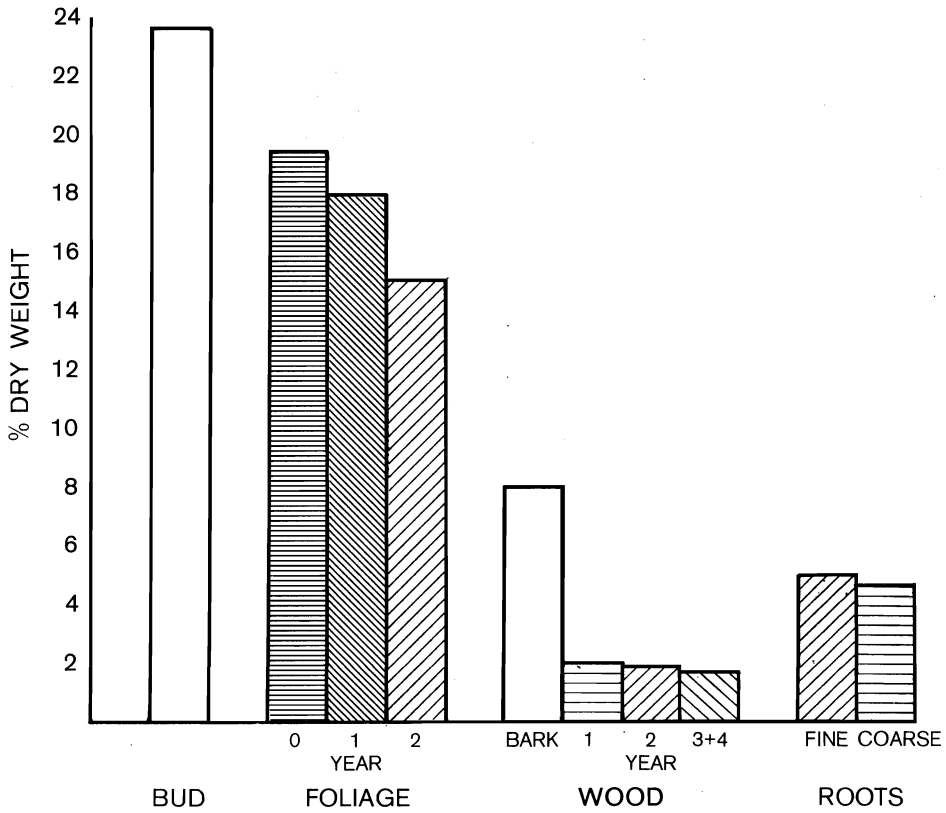


FIG. 4—Total non-structural carbohydrate concentration by tissue type. Values are averages for period November to March and were obtained from **P. radiata** trees of seedling origin.

Genotype

Data from two types of tree material, i.e., seedling origin and rooted cuttings of Clone 850.451 are given in Fig. 2. Generally, genotype did not appear to be an important variable in determining carbohydrate concentration. In 1- to 2-year-old foliage, quinic and shikimic acids varied significantly (5% level) with genotype (Table 4). Trees of Clone 850.451 had greater starch levels than trees of seedling origin, but interpretation of these data is confounded by a significant interaction between sampling time and genotype (Table 4). Buds did not show any significant effect of genotype (Table 5). Three genotypes (Clones 850.451 and 850.455 and seedling origin) were included in the root analysis but again genotype was not a significant variable (Table 6).

Carbohydrate Content per Tree

Most of the non-structural carbohydrates are present in the stem, coarse root, and foliage biomass components (Table 8). These 12-year-old *P. radiata* trees had approximately 2.8% of their total biomass dry weight as non-structural carbohydrates and approximately two-thirds of this was in the form of soluble carbohydrates.

TABLE 8—Approximate soluble carbohydrate and starch contents per tree by component type

	Dry weight* (kg/tree)	Soluble carbohydrates (g/tree)	Starch (g/tree)
Stem wood	135	1670	780
Live branches	30		
Stem bark	12	530	100
0- to 2-yr-old needles	10	1300	100
≥2-yr-old needles	2	220	30
Roots > 5 mm dia	47	910	840
< 5 mm dia	8	130	200
Total	244 kg	4760 g	2050 g

* Based on stand with 500 stems/ha, basal area of 27 m^2/ha, and height of 20 m at age 12 (from Table 1).

DISCUSSION

This study indicates that genotypic differences in carbohydrate composition within *P. radiata* are minor. Ericsson *et al.* (1978) recorded the presence of glucose, fructose, sucrose, myoinositol, pinitol, quinic and shikimic acids in needles of adult *Pinus sylvestris.* Although Ericsson (1980) quantified concentrations of starch, saccharides, and cyclitols, he did not quantify the acids which are the most abundant class of soluble carbohydrate in developing and young foliage of *P. radiata* and are a major component of old foliage (Fig. 1). Chung & Barnes (1980a) observed concentrations of quinic and shikimic acids of up to 6.5% of the total dry weight of foliage of 15-year-old *P. taeda.* Current year's foliage of *P. radiata* had 9.5% as acids, and 2-year-old foliage 3.8% (Fig. 1). Soluble carbohydrates, other than these acids, comprised up to 10% of the dry weight of foliage of *P. taeda* (Chung & Barnes 1980a) and of *P. sylvestris* (Ericsson 1979); this is of a similar order to that observed in *P. radiata.* It would appear that the soluble carbohydrates in foliage of *P. radiata, P. taeda,* and *P. sylvestris* are similar in concentration and in the classes of carbohydrates present. Because of the manner in which the tissue samples were defined and bulked these studies on *P. sylvestris* and *P. taeda* did not allow the soluble carbohydrates of other tissues to be compared with the data obtained for *P. radiata.*

Rook (1985) plotted starch contents of 1- to 2-year-old needles of *P. sylvestris* (data from Ericsson 1979) against data for *P. radiata* foliage of a similar age and showed that, whereas *P. sylvestris* had starch contents up to 24% of the dry weight, *P. radiata* had concentrations less than 6%. In both species foliage starch concentrations reached

their maxima in late winter to early spring. Starch concentrations of fine roots of *P. sylvestris* were of the order of four to nine times greater than those of *P. radiata* (cf. Ericsson & Persson 1980). It should be appreciated that no systematic sampling of the roots was carried out in our study and the classification of roots into branched and unbranched fine, and coarse, was somewhat arbitrary. There was no indication that the carbohydrate composition differed between branched and unbranched fine roots but, because of the magnitude of the estimated storage capacity of roots generally, more intensive examination would appear warranted.

The quantity of non-structural carbohydrates present in a *P. radiata* tree was estimated as 2.8% of the total biomass, i.e., 6.8 kg for a tree of 244 kg dry matter. No attempt was made to take into account seasonal changes in growth as the intent was only to provide an estimate at the first-order level of the non-structural carbohydrates present. Weights of the biomass components were based on height and diameter measurements of the sample trees which were then used to extrapolate data from Madgwick *et al.* (1977), Jackson & Chittenden (1981), and Santantonio & Santantonio (1987) to provide estimates of the dry weights for the different components. Weight tables for *P. radiata* grown in Australia (Dargavel 1970) estimate the total biomass of a similar-sized tree as 276 kg, i.e., 13% greater. This estimate of total non-structural carbohydrates is of value in showing the importance of the stem and roots in their capacities to store carbohydrates despite the fact that carbohydrate concentrations in these tissues were not high. This estimate is also of value in understanding *P. radiata's* response to adverse environmental conditions or pathogen attack.

A cautionary note, however, should be included regarding these estimates. The carbohydrate concentrations used were mean values calculated from November to March, i.e., part of the year when there was a high demand for carbohydrates in growth and respiration. No xylem samples older than 4 years were analysed and the mean concentration was extrapolated to xylem up to 12 years of age; this undoubtedly overestimates carbohydrate content of that component. On the other hand, there were no separate data for branch xylem and bark and so it was assumed that all branch material had a similar composition to the stem xylem, which would under-estimate carbohydrate content of that component. It was also assumed that all foliage over 1 year old has the same composition as that of 1- to 2-year-old foliage in Table 3. Madgwick *et al.* (1977) indicated that there were only small amounts of foliage older than 2 years in the 10-year-old stand and this agrees with our observations. Despite these extrapolations, the accuracy of the estimate of non-structural carbohydrates present in trees can be regarded as reasonable.

The non-structural carbohydrate content of a tree depends on the balance between the rates of carbohydrate production in photosynthesis and use of these carbohydrates in growth and respiration. Grace *et al.* (1987) reported that for *P. radiata* growing at Puruki the rate of photosynthesis of a whole tree crown in the long summer days of November to January is approximately three times that of the shorter winter days of June-July. Even on a deep fertile soil with adequate water availability throughout the year there was a decrease in photosynthesis by some 20% between January and February, and in other drier sites in New Zealand greater reductions occur (D. Rook, unpubl. data).

Pinus radiata grows throughout the year at Rotorua (Rook 1985). The periods of most active growth are shoot extension from September to December (Rook & Whyte 1976; Jackson *et al. 1976),* shoot radial growth from December to May (Jackson *et al.* 1976), needle growth from September to February (Rook *et al.* 1987), and fine root production from April to August and from September-October to December (Santantonio & Santantonio 1987). Quantification of seasonal dry matter increments of the individual biomass components as well as total for entire trees is now being attempted (Rook *et al.* 1985); growth of these biomass components requires appropriate levels of photosynthate supplies. However, rates of photosynthesis and total growth may not be synchronised on a daily or weekly basis so concentrations of non-structural carbohydrates can be expected to vary with time as indicated in Fig. 2 and 3.

Starch concentrations of foliage are high preceding and in the early stage of the more active part of the growing season. Starch in particular appears to reflect in a general manner where there is a surplus of carbohydrates over current demands for growth and respiration. Starch determinations have been used as the sole indicator of carbohydrate status in many studies (e.g., Ford & Deans 1977; Adams *et al.* 1986) and our study agrees with the use of starch as a reliable indicator of the carbohydrate status of a tree. It is interesting to note that the low total carbohydrate concentrations in February coincide with the warmest temperatures of the year and high rates of growth and so demands for carbohydrates would be very high (Rook 1985).

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