Reprinted from

Canadian Journal of Forest Research

Réimpression du

707684

Journal canadien de la recherche forestière

Seasonal changes in energy allocation by white oak (*Quercus alba*)

S. B. McLaughlin and R. K. McConathy, R. L. Barnes, and N. T. Edwards

Volume 10 • Number 3 • 1980

Pages 379-388

National Research Council Canada
Conseil national de recherches Canada

Seasonal changes in energy allocation by white oak (*Quercus alba*)[1]

S. B. McLaughlin and R. K. McConathy
Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, TN, U.S.A. 37830
R. L. Barnes
School of Forestry and Environmental Studies, Duke University, Durham, NC, U.S.A. 27706
AND
N. T. Edwards
Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, TN, U.S.A. 37830

Received January 24, 1980[2]
Accepted April 28, 1980

McLaughlin, S. B., R. K. McConathy, R. L. Barnes, and N. T. Edwards. 1980. Seasonal changes in energy allocation by white oak (*Quercus alba*). Can. J. For. Res. **10**: 379–388.

Seasonal patterns of change in lipids, sugars, starch, labile (ethanol soluble) constituents, holocellulose, and lignin were studied in six forest-grown white oak (*Quercus alba* L.) trees. Contents of metabolically active constituents in leaves, twigs, branches, boles (upper and lower), and roots (support and small lateral) were used to construct whole-tree budgets of energy allocation. [^{14}C]Sucrose was also concurrently supplied to the study trees to follow the fate and efficiency of utilization of food reserves. Results showed that white oak rapidly mobilized and replaced food reserves during the critical period of canopy generation in the spring. Starch was more important as a reserve food than lipids or sugar. Large fluctuations in starch in roots in spring and fall suggested a bimodal belowground growth pattern. Labile constituents showed the most pronounced seasonal changes and dominated the calculated whole-tree energy flux patterns. Rapid decline in labile compounds in early spring and a parallel increase in holocellulose suggested a possible pattern of mobilization and resupply of stored reserves associated with in cell wells. This possibility was supported by a concurrent shift of labile ^{14}C to nonlabile ^{14}C in tissues. Canopy generation was calculated to have cost ≤ 17.7 kg of glucose (1.6 g glucose/g of canopy) of which 13 kg appeared to have come from within the canopy.

McLaughlin, S. B., R. K. McConathy, R. L. Barnes et N. T. Edwards. 1980. Seasonal changes in energy allocation by white oak (*Quercus alba*). Can. J. For. Res. **10**: 379–388.

Une étude des variations saisonnières en lipides, sucres, amidon, composés labiles (fraction soluble dans l'éthanol), holocelluloses et lignine est effectuée sur six chênes blancs (*Quercus alba* L.) provenant de peuplements forestiers. Les contenus en composés métaboliquement actifs dans les feuilles, rameaux, branches, parties supérieure et inférieure du tronc et racines principales et latérales permettent d'établir les bilans énergétiques pour l'arbre entier. Un apport de sucrose, marqué au ^{14}C, montre l'évolution et l'efficacité d'utilisation des réserves nutritives. D'après les résultats, le chêne blanc mobilise et remplace rapidement ses réserves nutritives au printemps, pendant la période critique de fermeture du couvert forestier. L'amidon constitue un matériel de réserve plus important que les lipides ou les sucres. Le contenu amylacé des racines subit, au printemps et à l'automne, de fortes fluctuations, lesquelles suggèrent un type bimodal de croissance racinaire. Les composés labiles montrent les variations saisonnières les plus prononcées et prédominent dans le calcul des flux énergétiques. Au début du printemps, une baisse rapide des composés labiles accompagnée d'une augmentation des holocelluloses, suggèrent une voie possible de mobilisation des réserves (probablement des hémicelluloses), emmagasinées dans les parois cellulaires. Le passage du ^{14}C d'une forme labile à une forme non-labile dans les tissus viendrait confirmer cette hypothèse. Le coût énergétique pour la fermeture du couvert forestier est évalué comme étant ≤ 17.7 kg de glucose (1.6 g de glucose/g de couvert), desquels 13 kg semblent provenir du couvert même.
[Traduit par le journal]

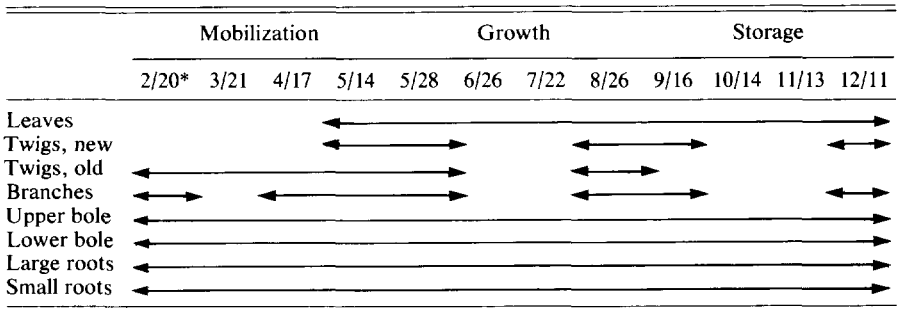
Introduction

Fluctuations in food reserves of forest and horticultural trees are of great interest to physiologists for several reasons. From a mechanistic standpoint the often well-defined patterns of change in the primary storage reserves, carbohydrates, fats, or protein have led to increased understanding of the relationship of phenological change to movement and utilization of available energy resources (Kramer and Kozlowski 1979). From a possibly more pragmatic stance these changes provide a basis for estimating and in some cases regulating the availability of energy to do the work of growth, reproduction, and tissue repair. This information is particularly relevant to understanding factors influencing growth and competition in deciduous forests. Here annual costs of regeneration of the foliar canopy represent a substantial investment of the energy available to the tree. These costs may achieve special significance where other energy costs have been magnified by biotic or abiotic stress.

Because of their large size and associated maintenance demands, mature forest trees consume sig-

[1]Research supported by the Eastern Deciduous Forest Biome, US-IBP, funded by the National Science Foundation under Interagency Agreement AG-199, DEB76-00761 with the U.S. Department of Energy under contract W-7405-eng-26 with Union Carbide Corporation. Publication No. 1555, Environmental Sciences Division, Oak Ridge National Laboratory.
[2]Revised manuscript received April 24, 1980.

TABLE 1. Sampling schedule for biochemical analysis of white oak tissues. Two trees were studied during each growth phase; 5 mCi of ^{14}C was administered at the beginning and trees were harvested at the end of each phase



*Month/day.

nificant amounts of photosynthate in the myriad physiological processes linking gross photosynthetic production and net annual growth. Kira (1975), for example, has estimated production efficiencies (net/gross production) of world forests to range from 0.21 to 0.68. Evans (1975) has stressed the need to characterize allocation processes as a means of understanding the basis of productive potential.

Considerable progress towards attaining this objective has been made as a result of the calculations of the energetics of tissue biosynthesis by Penning de Vries (1974). More recently Chung and Barnes (1977) have used these calculations and the biochemistry of loblolly pine tissue to estimate energy expenditures for new shoot growth (needles plus axes). In this paper we have used a similar approach with large forest-grown white oak trees. Our primary objective was to characterize changes in whole-tree energy levels and relate these changes to calculated expenditures for tissue growth and maintenance. To do this we have followed monthly changes in pools of available energy reserves for seven tissue types of a dominant eastern deciduous forest species, white oak (*Quercus alba*). Tissue analysis and tree harvesting were scheduled to characterize three critical phenological stages in the annual growth cycle. These were (1) mobilization for canopy production, (2) production and growth, and (3) storage and leaf fall.

Methods

Sampling procedures

Six codominant white-oak trees in a second-growth mixed deciduous stand were selected for study. The stand was located on a ridgetop site (elevation 370 m) on the Oak Ridge Reservation in East Tennessee, U.S.A. The trees ranged in height from 15 to 20 m ($\bar{X}$ = 18 cm) and in diameter (dbh) from 22 to 30 cm ($\bar{X}$ = 26 cm). A sampling and harvest scheme was devised to permit a variety of tissue types to be collected from two trees over each of three sampling intervals as shown in Table 1. On each interval initiation date (February 12, May 12, and September 12) two trees were stem tagged with 5 mCi (1Ci = 37 GBq) [U-^{14}C]sucrose by the trough-uptake method as described by McLaughlin et al. (1977). One week later and at three subsequent 1-month intervals tissues were collected from the leaves (when present), twigs, branches, bole (two positions), and roots (two size classes) for biochemical and radiochemical analysis. Radiochemical analyses included differentiation of tissue ^{14}C activity into labile (ethanol soluble) and nonlabile constituents. Only data from the initial 3-month interval will be presented in this report. Biochemical analysis involved characterization of tissue levels of lipids, starch, soluble sugars, holocellulose, and residual materials (mostly lignin). At the end of each 3-month sampling interval, the two study trees were harvested for additional chemical analyses and a determination of biomass distribution between the tissue types. Stumps and associated roots were excavated with a back hoe. Data from the monthly analyses were then used to construct whole-tree budgets for each tissue constituent.

Tissues from the canopy were collected with the use of a truck-mounted extension ladder and a pole pruner. Because of reach limitations, leaf and branch samples collected in this manner were restricted to the bottom two-thirds of the canopy. Branch samples were 50–75 mm in diameter and twig and leaf samples consisted of terminal and adjoining shoots. Bole samples consisted of two 5-mm diameter increment cores collected from opposite sides of the tree both at approximately 150 cm above ground level (lower bole) and at a point just below the insertion point of the lowest live branch (upper bole). The cores included all tissues from the outer phloem inward to the pith. The two cores (at each height) were composited to represent lower and upper bole positions, respectively. "Large root" samples were taken as cores from large support roots around the base of the bole. Small roots were sampled at distances up to approximately 2 m from the tree base and consisted of roots ≤1 cm in diameter which had been identified and numbered before sampling began. Approximately three such roots and associated fine lateral roots were collected at each sampling date. Tissue subsamples from both roots and branches were composited for biochemical analysis.

Biochemical analyses

Tissue samples were frozen with dry ice in the field immediately after harvesting. They were subsequently treated with liquid nitrogen in the laboratory to stop enzyme activity. The samples were then blended in 30 mL of $CHCl_3$ for 5 min and stored until processed further. The processing sequence and the identity of constituent analyses are outlined below.

Lipids were determined gravimetrically after evaporating the $CHCl_3$ over a hot water bath.

Soluble carbohydrates were determined on the lipid-insoluble residue by extracting it with 80% ethyl alcohol in a Soxhlet apparatus for 2 h. Extracts were decolorized with activated charcoal, filtered, and analyzed for soluble carbohydrates by the colorimetric method of DuBois *et al.* (1956).

Starch was determined on a portion of the 80% ethanol-insoluble residues from the soluble carbohydrate analyses following the glucose oxidase method of Ebell (1969).

Labile extractives (ethanol soluble) were determined gravimetrically by comparing the ovendry weights of $CHCl_3$-extracted residues before and after the extraction with 80% ethanol.

Holocellulose was determined as chlorite holocellulose after acid hydrolysis of a portion of the 80% ethanol-insoluble residue in a mixture of glacial acetic acid and sodium chlorite (1 mL/3 g) using the procedures described in Browning (1967).

Residual materials were determined by subtracting values for lipids, starch, labile extractives, and holocellulose from total sample weights. The major component of this fraction was probably lignin.

Construction of allocation budgets

To follow tissue-level and tree-level changes in biochemical constituents, tissue contents, on a percent dry weight basis, were multiplied by the biomass of each tissue determined at harvest. Since individual trees varied in total biomass from 251 to 726 kg, it was necessary to normalize the data. Comparisons between trees over the entire 10-month study interval were made possible by adjusting all whole-tree data on a weight proportional basis to expected contents in a 410 kg hypothetical tree. Thus it was possible to follow fluctuations in the pool size of tissue constituents and relate these to the total amount of those constituents in the sample trees. To convert the fluctuations in levels of constituents to energy changes, the biochemical energetic equivalence relationships of Chung and Barnes (1977) were applied. Expressed in terms of the energy requirements for synthesis of a gram of a constituent from glucose, the glucose requirement factor (GRF) allows one to convert tissue contents of relevant biochemical species to total energy availability within that tissue. In this study, we used GRF ratios from Chung and Barnes (1977) as follows: lipids, 3.02; nitrogeneous compounds, 1.58; organic acids, 1.48; and carbohydrates, 1.18. For ethanol extractable constituents, a class which comprises sugars, amino acids, organic acids, low molecular weight phenols, some of the more polar pigments, and oxygenated isoprenols, an energy conversion factor of 1.2 g of glucose per gram constituent weight was used. This factor was determined by averaging the composition-weighted energy contributions of these components in loblolly pine shoots as determined by Chung and Barnes (1977). These relationships were used directly with tissue analyses to calculate seasonal fluctuations in whole-tree energy reserves. The requirements for synthesis of new leaf and twig tissue in the canopy were based on more detailed biochemical analysis of synthesis requirements for shoots of loblolly pine by Chung and Barnes (1977). These authors calculated that 1.57 g of glucose was required to synthesize 1 g of typical shoot biomass of loblolly pine. We have used this same figure for calculating the energetic requirements of new canopy formation in white oak.

Results

Variations in tissue levels and in total pools of lipids, sugars, starch, labile extractives (ethanol soluble), holocellulose, and residuals over the 10-month study interval are shown in Table 2. Data are recorded as mean tissue contents (percent dry weight) for the entire study, as the range of monthly mean content of each constituent, and as the range of percentages of the total tree content of a constituent found in each specific tissue type. Although we collected tissues from a total of six trees, only two trees were sampled on any single date. For this reason we have not attempted to statistically test differences in constituent contents between tissues or dates, but rather have highlighted the more obvious gradients and the nature of seasonal trends.

In general, tissues showed a gradient in mean content of the more metabolically active constituents, such as lipids, sugars, starch, and labile constituents. Highest values were found in the youngest tissues, leaves, twigs, and small roots. Lowest values of these constituents were found in the structural support tissues. Average tissue lignin content followed a similar trend but holocellulose, as would be expected, was highest in the older tissues, which have a higher proportion of nonliving cells.

In spite of its generally lower content of metabolically active tissues, the lower bole contained the largest quantity of metabolically active constituents. This was, of course, primarily attributable to the high percentage of total biomass included in this tissue class. Starch and labile constituents showed the greatest overall range in tissue contents throughout the study.

Whole-tree levels of each of the four nonstructural constituents which comprise the major energy reserves of the tree showed two- to three-fold changes during the study. The temporal distribution of these changes is shown in Fig. 1. Since branch and twig samples were not collected on all sample dates, these data are expressed as total content of each constituent in leaves (when present),

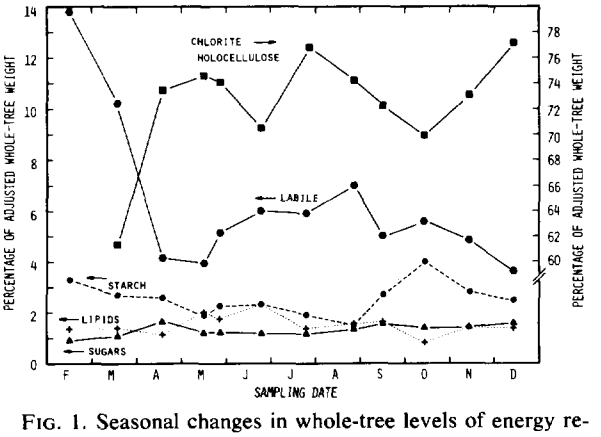


FIG. 1. Seasonal changes in whole-tree levels of energy reserves of white oak.

TABLE 2. Means and ranges in composition of biochemical constituents of mature white oak tissues during an 11-month study interval

Tissue (wt.%/1 SD)		Biochemical composition					
		Lipids	Sugar	Starch	Labile	Holocellulose	Lignin
Leaves	Mean*	8.7^{15}	4.5^{15}	1.2^{15}	21.5^{15}	36.0^{15}	32.7^{15}
(2.8/0.5)	Range†	6.0-12.2	2.4-7.4	0.3^{2}-1.7	18-26	32^{2}-38	25^{2}-37
	% of total‡	12-24	5.3-20	<0.1-2.7	11-18	0.9-1.7	2.8-7.5
Current	Mean	6.3^{9}	5.1^{9}	3.4^{9}	14.3^{9}	50.9^{9}	25.3^{9}
twigs	Range	4.1-11.9	3.0-10.7	0.9^{2}-5.9	9.5^{2}-23	48-59^{2}	21-27^{2}
(0.5/0.1)	% of total	1.3-4.3	1.5-1.8	0.2-4.3	1.4-2.1	0.3-0.5	0.8-0.9
Old	Mean	3.8^{11}	2.8^{11}	4.0^{11}	9.9^{11}	60.9^{7}	24.4^{7}
twigs	Range	2.0-5.9	1.5^{2}-4.5	1.5-6.3	5.5-20	56-67	20-30
(2.2/0.4)	% of total	4.4-11	3.5-15	2.0-4.6	1.3-3.5	1.8-1.9	3.9-7.5
Branches	Mean	1.6^{13}	2.8^{11}	3.4^{13}	7.1^{13}	71.7^{11}	18.2^{11}
(9.2/2.6)	Range	1.3-1.9	1.9-3.5	1.0-5.2	1.3^{2}-16	65^{2}-76	16-28^{2}
	% of total	11-17	3.5-15	2.0-4.6	2.7-4.3	4.4-12	13-29
Upper	Mean	1.3^{23}	1.0^{23}	2.4^{23}	6.6^{23}	75.6^{19}	15.4^{19}
bole	Range	0.8-2.2	0.5-1.8	1.2-8.0	2.2-14.5	74-79	14^{2}-18
(11.8/1.7)	% of total	8.9-15	6.2-17	9.2-13	8.7-61	14-16	10.7-10.9
Lower	Mean	1.0^{24}	0.8^{24}	1.7^{24}	5.6^{24}	78.6^{20}	14.8^{20}
bole	Range	0.3-1.6	0.5-1.8	1.0-2.8	1.5-19.0	73-85	11-20
(47.2/4.1)	% of total	13-42	22-53	19-61	21-80	46-56	37-61
Large	Mean	1.8^{23}	2.0^{22}	3.9^{23}	5.6^{23}	68.6^{20}	20.3^{20}
root	Range	0.4-4.0	1.4-2.4	2.0-8.6	3.9-7.2	59-80	15-27
(20.8/1.3)	% of total	11-36	20-39	18-58	21-22	24-22	20-37
Small	Mean	2.6^{24}	3.6^{24}	4.8^{23}	10.0^{23}	54.2^{20}	29.5^{20}
roots	Range	1.4-4.5	1.4-3.7	1.2-9.0	5.3-15.1	46-59	26-34
(5.3/1.7)	% of total	7.5-19	7.0-18	4.0-15	1.8-3.8	5.0-3.3	11-14

*Mean ^{N} content (percent tissue dry weight) for each constituent during the entire study. The sample number is shown as a superscript (N).

†Range in average content (percent tissue dry weight) for monthly samples. Data are minimum-maximum means for monthly averages representing 12 sample dates. Each is an average for two trees except for single valued "means" indicated by a superscript 2.

‡Range in percent of whole-tree content of each constituent contained in each tissue type. Values were determined on the dates when respective minimum and maximum tissue levels were recorded. Data are two-valued means except as indicated in footnote †.

upper and lower bole, and large and small roots. Collectively these tissues, referred to as adjusted whole-tree weight, represent an average of 88% of the total tree weight. Labile extractives showed the widest fluctuations during the study with a sharp 67% decline in early spring, preceding and during the period of canopy regeneration. A general increase in compounds in this category occurred during the middle of growing season followed by a gradual decline during the final three months. Tissue starch levels showed an approximately 30% decline during the time of budbreak and remained generally depressed during midseason. A gradual buildup in this constituent occurred in late summer with a peak in October followed by a late season decline. Sugar showed a gradual 50% increase from a low of 1.0% in February to a high of 1.5% in April just prior to bud burst. Lipids showed a similar threefold increase from a February minimum of 0.5% to a midsummer maximum of 2.3% of total tree weight.

Seasonal fluctuations of constituents within individual tissues were more pronounced than whole-tree contents (an expected consequence of mobilization, translocation, and storage). Fluctuations

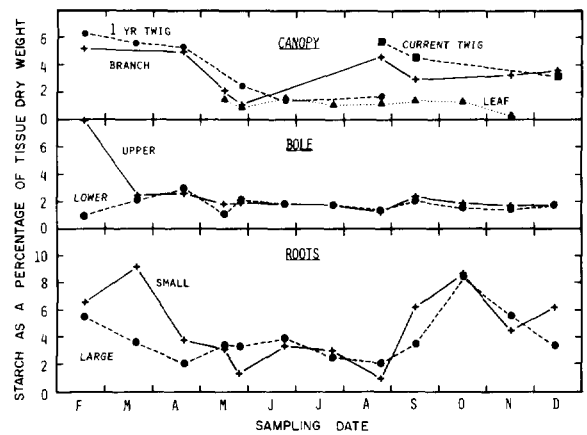


FIG. 2. Seasonal changes in tissue contents of starch.

of starch in tissues were most well defined and seemingly most closely related to seasonally dependent phenological changes as shown in Fig. 2. A concurrent bimodal pattern was apparent in the lower bole and roots for this constituent. Major peaks occurred in February and in October, while a secondary peak was apparent in late July. Except

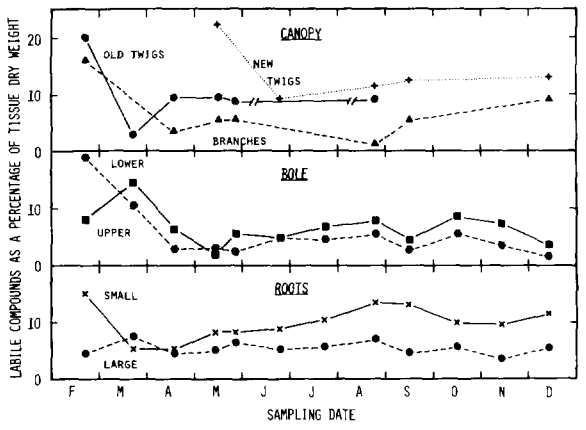


FIG. 3. Seasonal changes in tissue contents of labile (ethanol-soluble) compounds.

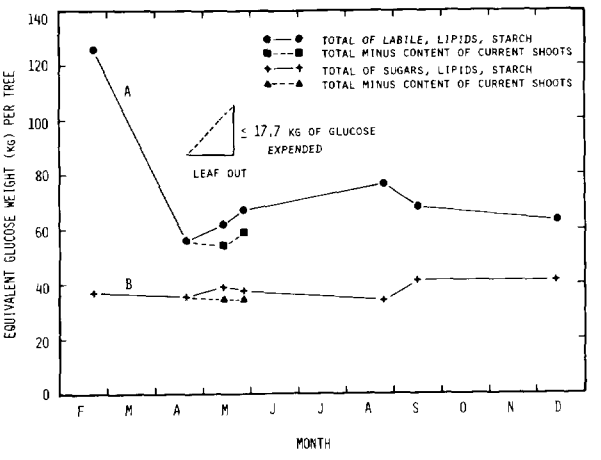


FIG. 4. Seasonal fluctuations in whole-tree energy levels. Data are expressed as total energy (in kilograms of glucose) present in two functional classifications of metabolically available compounds.

for February starch fluctuations in the upper bole mirrored those in the lower bole.

Fluctuations in labile constituents in individual tissues are shown in Fig. 3. These data show that the abrupt decline in this constituent in the spring, shown in Fig. 1, can be attributed to rather uniform decreases in all tissues except large roots. Changes were most abrupt in old twigs and small roots.

Seasonal changes in tissue contents of constituents with a major role in whole-tree energy supply were examined using energy conversion units (equivalent grams of glucose). Results of these calculations for starch, sugar, ethanol extractives (labile), and lipids, the constituents comprising the major energy reserves of trees, are shown in Table 3. Data are reported only for the months on which branch and twig tissues were sampled in addition to the routinely sampled bole and root tissues. Also included in Table 3 are energy sums of starch, lipids, and sugars, the constituents most typically reported in studies of fluctuation of tree energy reserves. These data are plotted in Fig. 4 as the summed whole-tree energy (equivalent to kilograms of glucose) in labile constituents (includes sugars), starch, and lipids (plot A) and as the sum of sugars, starch, and lipids (plot B).

An analysis of the energy changes in starch, lipids, and ethanol extractives in Table 3 shows an abrupt decline in total tree energy in the spring at the time of canopy regeneration. Whole-tree energy in February dropped by 57% to a level in May equivalent to approximately 54 kg of glucose. Although some recovery of this energy occurred during the subsequent growing season, the level apparent in February was not attained again during this study. The major cause of this drop was a sharp decline in ethanol-extractable constituents. Almost all of this occurred as a result of changes in twigs, branches, bole, and small roots (see Fig. 3). Starch and lipid levels actually showed a slight increase during this time.

An additional and somewhat different look at the energy status of the tree is provided by examining total energy in starch, soluble sugars, and lipids. This figure, which represents from 30% (February) to 75% (December) of the total energy reserves, shows a minimum in February prior to budbreak with maximum values during the late fall.

To examine the energy requirements for production of new growth (leaves and associated current-year branches), leaf and twig biomass determined at the May harvest were calculated and expressed in terms of glucose equivalents. Calculations again were based on an assumed comparability of tissue composition between white oak and loblolly pine (Chung and Barnes 1977). Based on an average normalized leaf and twig weight of 11.2 kg and a synthesis requirement of 1.57 g of glucose per gram of shoot biomass, we calculate that canopy synthesis costs for a 410 kg white oak tree would be 17.7 kg of glucose. This figure amounts to approximately 14% of the combined energy found in February in starch, ethanol extractives and lipids, and approximately 48% of that in starch, sugars, and lipids.

During the mobilization period (February to May) the energy depletion in starch and labile constituents of tissues of the upper canopy (including upper bole) amounted to approximately 13 kg of glucose, 74% of the total calculated to synthesize the new canopy. Depletion of energy in the root system equalled 7.2 kg of glucose.

TABLE 3. Seasonal changes in pools of constituents for whole white oak trees. Averaged data have been normalized and converted to equivalent mass of glucose using glucose equivalence ratios of 1.18 for starch, 1.00 for reducing sugars, 1.21 for labile constituents, and 3.02 for lipids

		Sampling date													
		February		April		May		May		August		September		December	
Constituent	Tree*	*C*†	*E*‡	*C*	*E*	*C*	*E*	*C*	*E*	*C*	*E*	*C*	*E*	*C*	*E*
Labile	1	61.8		9.7		14.2		18.2		27.6		20.8		18.0	
	2	54.7		24.0		21.2		25.6		32.3		22.5		18.5	
		$\bar{x}$ 58.3	93.9	$\bar{x}$ 16.9	27.2	$\bar{x}$ 17.7	28.5	$\bar{x}$ 21.9	35.1	$\bar{x}$ 30.0	48.0	$\bar{x}$ 21.7	34.9	$\bar{x}$ 18.3	29.4
Lipids	1	4.5		4.4		7.2		7.6		7.2		6.5		6.2	
	2	5.2		5.0		9.1		7.3		6.2		7.1		8.2	
		$\bar{x}$ 4.9	14.7	$\bar{x}$ 4.7	14.1	$\bar{x}$ 8.2	24.6	$\bar{x}$ 7.5	22.5	$\bar{x}$ 6.8	20.4	$\bar{x}$ 6.9	20.7	$\bar{x}$ 7.0	21.1
Starch	1	17.8		10.5		7.6		9.6		7.8		11.5		11.4	
	2	11.2		13.3		8.2		7.5		6.3		11.5		10.2	
		$\bar{x}$ 14.5	17.1	$\bar{x}$ 11.9	14.0	$\bar{x}$ 7.9	8.8	$\bar{x}$ 8.6	9.6	$\bar{x}$ 6.7	7.5	$\bar{x}$ 11.5	12.9	$\bar{x}$ 10.8	12.6
Sugar	1	5.7		4.4		5.2		5.7		5.3		8.2		5.5	
	2	4.2		9.5		5.2		5.4		6.2		7.1		7.9	
		$\bar{x}$ 5.0	5.0	$\bar{x}$ 7.0	7.0	$\bar{x}$ 5.2	5.2	$\bar{x}$ 5.6	5.6	$\bar{x}$ 5.8	5.8	$\bar{x}$ 7.7	7.7	$\bar{x}$ 6.7	6.7
Total A (labile, lipids, starch)			125.7		55.3		61.9		67.2		75.9		68.5		63.1
Total B (lipids, starch, sugar)			36.8		35.1		34.9		34.8		33.8		41.3		40.5

*Trees 1 and 2 sampled in February, April, and May; trees 3 and 4 in May and August; and trees 5 and 6 in September and December.
†*C*, constituent weight in kilograms for a 410 kg tree.
‡*E*, weight of glucose in kilograms with energy equivalent to that in *C*.

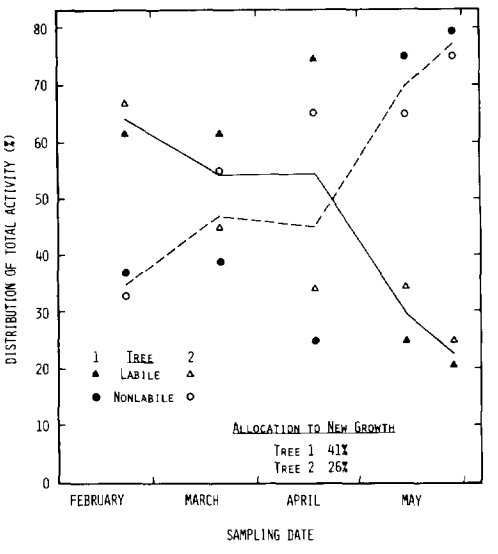


FIG. 5. Seasonal changes in apportionment of ^{14}C activity between labile and nonlabile tissue constituents of two white oak trees labelled with [^{14}C]sucrose on February 12 (trees 5 and 6).

Results of the radiochemical analyses of tissues collected during the transition from dormancy to canopy development are presented in Fig. 5. Plotted as changes in allocation of ^{14}C activity between labile and nonlabile fractions these data show a sharp increase in apportionment of supplied activity into the heavier molecular weight constituents of the nonlabile group. This is particularly evident in the spring as leafout occurs, resulting in incorporation of an average of 34% of the total ^{14}C activity into these rapidly developing sinks. Discrepancies between the two trees can be attributed largely to initial apportionment of the supplied activity. A much higher fraction of the initial ^{14}C label was directed belowground in tree 2 than in tree 1. At harvest approximately 43% of the activity in tree 2 was still in the belowground system, while only 3% remained belowground in tree 1.

Discussion

Woody plants employ rather well-defined annual strategies of managing food (energy) reserves (see reviews by Hepting 1945; Kramer and Kozlowski 1979; Ziegler 1964; Kozlowski and Keller 1966; and Zimmermann 1970). The seasonal patterns of the temperate forest climate produce alternating cycles of rapid growth and relative inactivity which are accompanied by corresponding periods of intense utilization or storage of food reserves. For this reason storage and mobilization of reserves play a significant role in the competitive strategies of temperate forest trees, particularly deciduous species.

Kramer and Kozlowski (1960, 1979) have grouped forest tree species into those which store food reserves predominantly as fats (primarily diffuse-porous species), predominantly as starch (primarily ring-porous species), and a third group which utilizes both storage forms. Regardless of the primary storage form, starch appears to be the predominant constituent of energy storage in roots of most tree species (Ziegler 1964).

The timing and duration of energy production and consumption also vary with life strategy (deciduous or evergreen) (Hepting 1945; Ziegler 1964) and with successional status (Marks 1975). Evergreen trees with the potential for significant photosynthetic production during the winter season (Waring and Franklin, 1979) show less pronounced fluctuations in energy reserves than deciduous species. In addition growth of tree canopies may occur as a typically single, rather rapid flush from a terminal bud (determinant or fixed growth) or as repeated flushes from lateral buds (indeterminant or free growth) throughout the growing season. Marks (1975) characterized the determinant strategy as typical of late successional deciduous species.

Our studies with mature white oak, a determinant, ring-porous species of late successional status, confirm the classification of *Quercus* as a "starch" tree by Kramer and Kozlowski (1960, 1979). In contrast to the results of Wargo (1976), we found rather similar levels of starch in small and large roots. Seasonal changes were also similar in the two size classes. Compared with lipids and sugars, starch reserves showed much more pronounced seasonal fluctuations than fats (Fig. 1). Tissues of the canopy and upper bole as well as roots had well-defined decreases in the spring which were concurrent with mobilization for tree growth (Fig. 2). Both small and large roots showed a rapid buildup of starch to very high levels (almost 9% of tissue weight) in late fall. The buildup and decline of starch in small roots in February-May and September-November corresponded well in time to measurements of rooting intensity of white oak determined in the field in Missouri by rhizotron studies (Teskey and Hinckley 1980). Changes noted in root starch in our study may then have reflected in part movement of carbohydrates to and storage in roots followed by subsequent utilization in growth of new tissues.

A somewhat unexpected finding of this study was the significance of labile (ethanol-soluble) constituents throughout the growing season (Fig. 1). Since this constituent group was determined gravimetrically (weight before minus weight after removal of ethanol extractable compounds), we have

only a functional identification of its constituents. Doubtlessly the relative amounts of sugars, amino acids, organic acids, phenols, and alkaloids comprising this class changed during the study; however, we consider this class a good general indicator of levels of active low molecular weight metabolites. The rapid drop in constituents in this class during the spring represented an approximate 10% change in whole-tree weight. A major portion of this change can be attributed to changes in the bole, branches and small roots as shown in Fig. 3. The initial increase in labile materials in the upper bole in March is suggestive of transport from the lower bole. Examination of our ^{14}C tissue analysis data, in fact, revealed the movement of approximately 12% of the total activity in the tree into the upper bole by March whereas none could be detected in February.

The spring decline in labile constituents corresponds well in both time and general magnitude to the sharp increase in chlorite holocellulose shown in Fig. 1. This relationship indicates that either the chemistry or the morphology of cell walls was changing or that new growth was initiated prior to growth of the new canopy. Chemical changes would involve redeposition of cell wall materials solubilized during winter months. Morphological changes might involve alterations of wall microstructure resulting in temporal changes in availability of cell wall associated constituents to ethanol extraction. We have no conclusive evidence for either possibility at this time.

There is evidence from the literature, however, to indicate that cell wall materials, particularly hemicelluloses, may serve as food reserves in trees. Although Hepting (1945) cites studies by Soblon (1904) and Schellenberg (1905) which showed that hemicellulose was a principal carbohydrate reserve of trees in winter, he concluded that the role of hemicellulose as a food reserve in trees had not been conclusively proven. More recently Kimura (1969) showed distinct seasonal fluctuations in hemicellulose in all tissues of 15-year-old *Abies*. Hemicellulose content showed a rapid buildup in early spring prior to active growth and a decline during the growing season. Fluctuations ranged from a maximum of 17% of tissue dry weight for needles to a minimum of about 7% for stems. Meyer and Splittstoesser (1971) found hemicellulose to be the primary storage form for carbohydrate reserves of seedlings of *Taxus*.

The buildup of chlorite holocellulose, which includes the hemicellulose fraction, which we found to occur in March in white oak, parallels the buildup of hemicellulose shown by Kimura (1969). It also corresponds well to the spring shift in ^{14}C activity from the labile to the nonlabile compartment as shown in Fig. 5. The two early season peaks in this component also correspond well to the bimodal early season pattern of stem growth by white oak in Missouri (Hinckley *et al.* 1976, 1979; and Dougherty *et al.* 1979). These studies also showed that stem growth can begin in Missouri in late March, as much as 3 weeks before the initiation of new leaf growth, a factor which may well explain our shift to higher levels of chlorite holocellulose in March. It is interesting to note that mid- and late-season changes in the holocellulose fractions are consistently opposite in direction from changes in starch content. The consistency of this trend suggests competitive uses of these constituents in storage or tissue synthesis, a possibility which cannot be substantiated from these data.

The pronounced changes in labile constituents with the onset of growth also dominate fluctuations in whole-tree energy reserves shown in Fig. 4. Based on conversion of tissue constituents to equivalent energy in glucose, whole-tree reserves in February ranged from approximately two (plot B) to seven (plot A) times the energy required for synthesis of the new canopy (17.7 kg of glucose). Springtime energy losses in plot A (which include labile constituents, lipid, and starch) exceed by a factor of 4 the energy needed for canopy generation. The magnitude of these changes strongly supports biochemical conversion of some components of the labile class to a nonlabile form as discussed previously. The shift from labile to nonlabile forms also explains the discrepancy between energy levels in February and December noted in plot A. Since this study covered a 10-month interval bracketing the growing season, we were unable to show a return to the high levels of labile components measured initially in February. The rapidity and magnitude of changes in this pool in March and April, however, indicate that such fluctuations are quantitatively and temporally feasible.

Recovery of the energy invested in canopy growth begins almost immediately and corresponds well to the rapid transition to self support of $^{14}CO_2$-labelled white oak leaves reported by McLaughlin *et al.* (1979) and McLaughlin and McConathy (1979). Based on plot A, recovery of the 17.7 kg investment in the new canopy is estimated to have occurred by approximately the end of June.

Whole-tree reserves of the more conventionally studied constituents, sugars, starch, and lipids (plot B, Fig. 4) showed remarkably little variation during the study. The decline associated with leaf-

out was approximately 3 kg of glucose, only 17% of the total expended aboveground. The seasonal pattern of plot B, however, shows a slight spring and midsummer depletion with a late season buildup.

Regardless of the energy summation used, however, our data indicate a rapid recovery of the energy invested in early season growth by white oak. Radiochemical data show that at least one third of reserve materials present in early spring were used in production of the new canopy. Rapid recovery of these losses intuitively fits the role of a late successional determinant species which must quickly attain its production potential to remain competitive.

In this study we have focused on the energy changes associated with a readily quantifiable expenditure in aboveground biomass. However, growth and maintenance respiration in the belowground system doubtlessly contributed to the energy losses in both spring and fall. Harris *et al.* (1975) found extensive production and turnover in small root biomass of *Liriodendron tulipifera* and estimated that on an annual basis energy allocation to belowground production equalled that for aboveground production. Changes in starch in small roots of white oak noted here and studies on small root elongation of white oak by Teskey and Hinckley (1980) support active metabolism of these tissues in both early spring and late fall. Energy decreases in white oak roots noted in spring in this study (7.2 kg) were about 55% of decreases in the upper crown (13 kg). Our radiochemical data for roots showed large discrepancies between the two trees, 3 and 43% of total remaining activity in trees 1 and 2, respectively, at the May harvest. We attribute these differences to previously mentioned differences in the initial distribution pattern of activity between the two trees. Such initial differences suggest more active growth of roots and hence a stronger belowground sink in tree 2 than in tree 1 at the time of tagging. Such a condition would result in a larger initial incorporation into belowground structural forms, and a lower availability of labile ^{14}C-labelled constituents for subsequent transport to aboveground sinks in this tree. Thus, in budgeting activity flow in trees, one must consider not only where the initial activity goes, but also the likely fate of the endogenous pools with which it initially equilibrates.

In summary, this study has examined the seasonal fluctuations in energy reserves of major tissue types of large field-grown white oak trees. Collectively these changes were used to characterize the energy allocation strategies of this species. Our results indicate a rapid mobilization and recovery pattern to be expected of a determinant late-successional species. The magnitude of the fluctuations in energy in the noncharacterized labile fraction, coupled with changes in the holocellulose fraction of cell walls, suggest the possibility of active participation of a cell wall component, probably hemicellulose, in the seasonal energy dynamics of white oak. Additional studies will be required to more clearly define the specific chemical species associated with these changes. Their potential significance to the allocation of energy by white oak and its potential physiological resilience is quite high.

BROWNING, B. L. 1967. Methods of wood chemistry. Vol. II. Interscience Publishers, New York, NY. pp. 395-396.

CHUNG, H., and R. L. BARNES. 1977. Photosynthate allocation in *Pinus taeda*. I. Substrate requirements for synthesis of shoot biomass. Can. J. For. Res. **7**: 106-111.

DOUGHERTY, P. M., R. O. TESKEY, J. E. PHELPS, and T. M. HINCKLEY. 1979. Net photosynthesis and early growth trends of a dominant white oak (*Quercus alba* L.). Plant Physiol. **64**: 930-935.

DUBOIS, M., K. A. GILES, J. K. HAMILTON, P. A. REBERS, and F. SMITH. 1956. Colorimetric method for determination of sugars and related substances. Anal. Chem. **28**: 350-356.

EBELL, L. F. 1969. Specific total starch determinations in conifer tissues with glucose oxidase. Phytochemistry, **8**: 25-36.

EVANS, L. T. 1975. Beyond photosynthesis—the role of respiration, translocation and growth potential in determining productivity. *In* Photosynthesis and productivity in different environments. *Edited by* J. P. Cooper. Cambridge University Press, New York, NY. pp. 501-507.

HARRIS, W. F., P. SOLLINS, N. T. EDWARDS, B. E. DINGER, and H. H. SHUGART. 1975. Analysis of carbon flow and productivity in a temperate deciduous forest ecosystem. *In* Productivity of world ecosystems. IBP General Assembly Symposium, Seattle, 1972. *Edited by* D. E. Reichle, J. P. Franklin, and D. W. Goodall. National Academy of Sciences, Washington, DC. pp. 116-122.

HEPTING, G. H. 1945. Reserve food storage in shortleaf pine in relation to little-leaf disease. Phytopathology, **35**: 106-119.

HINCKLEY, T. M., P. M. DOUGHERTY, J. P. LASSOIE, J. E. ROBERTS, and R. O. TESKEY. 1979. A severe drought: impact on tree growth, phenology, net photosynthetic rate and water relations. Am. Midl. Nat. **102**: 307-316.

HINCKLEY, T. M., D. R. THOMPSON, M. P. MCGINNIS, and A. R. HINCKLEY. 1976. Stem growth and phenology of a dominant white oak. *In* Proceedings of First Central Hardwood Forest Conference. *Edited by* J. S. Fralish, G. T. Weaver, and R. C. Schlesinger. Southern Illinois University, Carbondale, IL. pp. 187-202.

KIMURA, M. 1969. Ecological and physiological studies on the vegetation of Mt. Shimagre. VII. Analysis of production processes of young *Abies* stand based on carbohydrate economy. Bot. Mag. (Tokyo), **82**: 6-19.

KIRA, T. 1975. Primary productivity of forests. *In* Photosynthesis and productivity in different environments. *Edited by* J. P. Cooper. Cambridge University Press, New York, NY. pp. 5-41.

KOZLOWSKI, T. T., and T. KELLER. 1966. Food relations of woody plants. Bot. Rev. **32**: 294-381.

KRAMER, P. J., and T. T. KOZLOWSKI. 1960. Physiology of forest trees. McGraw-Hill, New York, NY.

——— 1979. Physiology of woody plants. Academic Press, New York, NY.

MARKS, P. L. 1975. On the relation between extension growth and successional status of deciduous trees of the northeastern United States. Bull. Torrey Bot. Club, **102**: 172-177.

MCLAUGHLIN, S. B., N. T. EDWARDS, and J. J. BEAUCHAMP. 1977. Spatial and temporal patterns in transport and respiratory allocation of [^{14}]sucrose by white oak (*Quercus alba*) roots. Can. J. Bot. **55**: 2971-2980.

MCLAUGHLIN, S. B., and R. K. MCCONATHY. 1979. Temporal and spatial patterns of carbon allocation by white oak canopies. Can. J. Bot. **57**: 1407-1413.

MCLAUGHLIN, S. B., R. K. MCCONATHY, and B. BESTE. 1979. Seasonal changes in within-canopy allocation of ^{14}C-photosynthate by white oak (*Quercus alba* L.). For. Sci. **25**: 361-370.

MEYER, M. M., and W. E. SPLITTSTOESSER. 1971. The utilization of carbohydrate and nitrogen reserves by *Taxus* during its spring growth period. Physiol. Plant. **24**: 306-314.

PENNING DE VRIES, F. W. T., A. BRUNSTING, and H. H. VAN LAAR. 1974. Products, requirements and efficiency of biosynthesis, a quantitative approach. J. Theor. Biol. **45**: 339-377.

SABLON, L. DU. 1904. Recherches physiologiques sur matières des réserves des arbres. Rev. Gen. Bot. **16**: 339-368; **16**: 386-401.

——— 1906. Recherches physiologiques sur matières des réserves des arbres. II. Rev. Gen. Bot. **18**: 5-25; **18**: 82-96.

SCHELLENBERG, H. C. 1905. Über Hemicellulosen als Reservestoffe bei unseren Waldbäumen. Ber. Deut. Bot. Ges. **23**: 36-45.

TESKEY, R. O. and T. M. HINCKLEY. 1980. Root growth characteristics of white oak (*Quercus alba* L.). Physiol. Plant. In press.

WARGO, P. M. 1976. Variations in starch content among and within roots of red and white oak trees. For. Sci. **22**: 468-471.

WARING, R., and J. FRANKLIN. 1979. The evergreen forests of the Pacific Northwest. Science, **145**: 120-135.

ZIEGLER, H. 1964. Storage, mobilization and distribution of reserve material in trees. *In* Formation of wood in forest trees. *Edited by* M. H. Zimmermann. Academic Press, New York, NY. pp. 304-320.

ZIMMERMANN, M. H. 1971. Storage, mobilization and circulation of assimilates. *In* Structure and function in trees. *Edited by* M. H. Zimmermann and C. L. Brown. Springer-Verlag, New York, NY. pp. 307-322.