

FOOD SINKS AND FOOD RESERVES OF TREES IN TEMPERATE CLIMATES

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ABSTRACT

The role of food reserves in tree growth are discussed in relation to a recently completed study with *Pinus banksiana* Lamb. seedlings. Besides carbohydrates, lipids are also important as food reserves. All tissues are important for storage of food reserves but not of equal importance simultaneously. Their importance depends on their relative volume and physiological state. Root and needle volume is greater than that of xylem and bark in young seedlings whereas in mature trees these relations will be different. In seedlings, roots will be more important for storage in early autumn than needles, but needles will be more important during the later part of autumn. Large amounts of photosynthates are used in respiration and wood formation is directly dependent on current photosynthate.

INTRODUCTION

Kramer and Kozlowski (1960) found it regrettable that the topic of food accumulation in trees has received little coverage in plant physiology textbooks, because the accumulation of food reserves each growing season is as essential for tree growth and survival as the use of food in metabolic processes. According to Taylor (1967) food reserves had been studied intensively up to some 30 years ago, but have been neglected until recently. Priestley (1970) also pointed out this apparent lack of interest in the utilisation of the carbohydrate reserves, which he referred to as perhaps the most important field of plant physiology. I suspect that the main reason for this apparent lack of interest is that food reserves are involved to varying degrees in just about every conceivable physiological process and as a result they receive only incidental treatment in most physiological studies.

Trees use food for the production of new tissue and as a source of stored energy. Kramer (1960) incorporated the processes involved under the general term of "metabolism" but they are generally differentiated as assimilation and respiration. The food reserves are those food substances that are not used directly in assimilation and respiration but are stored somewhere in the tree until required. This does not include the diurnally stored photosynthate in leaf parenchyma cells that is caused when photosynthesis produces more carbohydrates during the day, than the phloem can export (Zimmermann and Brown, 1971).

The source-sink concept, which means that the most active sink will receive most of the photosynthate, appears to be well accepted (Beever, 1969). As Larson (1969) pointed out, the distribution of photosynthates within a tree should be viewed as a system of competing metabolic sinks or areas of rapid growth and the metabolic sinks will draw and utilise photosynthate proportional to their degree of activity. Furthermore, the location of these sinks will shift within a tree during the course of a year. It is generally accepted that the reproductive structures, at time of development, draw considerably more photosynthate than do vegetative structures. Reproductive structures can outdraw vegetative ones by as much as 3 to 1 (Dickmann and Kozlowski, 1968).

In hardwoods new developing leaves are initially importers of photosynthate, but when the leaves have nearly completed their development they become photosynthate exporters and contribute to the developing shoot. The time required for a leaf to switch from an importer to an exporter of food substances depends on many interrelated factors. According to Donnelly (1974) the first developing poplar leaves begin to photosynthesise soon after budbreak, but the young leaves continue to utilise stored carbohydrates for about two weeks, because they assimilate and respire more than they produce. On the other hand in conifers, which retain their leaves for several years, old needles (last year's) are at both their maximum photosynthetic efficiency and export of food substances at the time of current needle elongation (Gordon and Larson, 1968). At the end of the period of rapid needle elongation, photosynthetic efficiency of the new needles is maximum, while of the older foliage it has already decreased considerably. Thus, maximum photosynthetic efficiency of foliage in hardwoods is attained in weeks whereas in conifers it takes months.

In general, the concentrations of reserves show a much greater seasonal fluctuation in deciduous species than in evergreen species. In deciduous trees there is a maximum reserve concentration in the autumn, which decreases slightly during the winter and rapidly in the spring with the onset of shoot growth. In evergreens, on the other hand, reserve accumulation can occur during the winter, reaching a maximum in early spring before it decreases with the onset of growth (Kramer and Kozlowski, 1960). For deciduous species in our Canadian climate this food reserve accumulation begins in late summer when growth starts to slow down and continues until leaf fall.

There is an undesirable trend in the literature to equate carbohydrates with food reserves, because many reserves occur as carbohydrates, predominantly in the form of starch and sugars. It is, therefore, desirable to examine the types of food reserves.

TYPES OF FOOD RESERVES

In most trees a large amount of the reserves are carbohydrates, and starch is the most abundant form of carbohydrate reserve. However, in some trees lipids in the form of fats and fatty acids are also important as reserves. As early as 1891 A. Fischer classified trees on the basis of the predominant reserves in their wood during the winter as "starch" trees and "fat" trees. This has subsequently been substantiated (Kramer and Kozlowski, 1960). Most coniferous species and the diffuse-porous hardwood species are "fat" trees, while the ring-porous hardwood species are "starch" trees (Ziegler, 1964). These fat reserves occur mainly in the stem and not in the roots, where the predominant form of reserve is starch, regardless of species. The reason for this difference between

roots and stem is not that the roots are biochemically unable to synthesise large amounts of lipids but because the roots are not exposed to the same environmental influences as the stem. It is the temperature fluctuations around the freezing point which cause extensive lipid production (Ziegler, 1964).

In a study with *Pinus banksiana* Lamb. seedlings I also found that a considerable amount of the reserves occurred as carbohydrates in the form of sugars, starch and hemicelluloses (Glerum, 1977; Glerum and Balatinecz, 1980). Furthermore it was observed that as the autumn progressed, an increasing quantity of the total amount of carbon remained in the form of sugars. This is in agreement with Krueger and Trappe (1967) and Little (1970b) who found similar seasonal fluctuations in total sugar concentrations: high sugar concentrations in the winter and low concentrations in the summer.

Although starch is an important form of carbohydrate reserve, I found no great fluctuation in the starch component. This appears to be in agreement with the results of many investigators and suggests that starch is probably a transitory reserve substance particularly during the autumn period. Seasonal fluctuations in starch have been reported (Krueger and Trappe, 1967; Little, 1970a, 1970b, 1974; Loach and Little, 1973) but generally these fluctuations occurred prior to and during the growing season while fluctuations in the autumn tended to be minimal.

In forest trees the hemicelluloses have received little attention as a form of reserves, but my data suggest that this group of polysaccharides could indeed be a form of reserves. This is not a new concept. Hemicelluloses in many seeds are used as food by seedlings during germination. Hemicelluloses in the cell walls of woody tissues of some trees such as apple trees serve as reserve food, which is utilised when growth of the stem resumes in the spring (Meyer *et al.*, 1960). Similar observations have been reported by Priestley (1962).

According to Kramer and Kozlowski (1960) there is some debate concerning the extent to which hemicelluloses found in the cell walls of wood structures are used as reserves. They think it unlikely that the hemicelluloses found in the vegetative structures of trees are important food reserves and that possibly the hemicelluloses never function as reserves. Wood technologists believe that the role of hemicelluloses has not been elucidated as yet (Timell, 1967; Panshin and De Zeeuw, 1970; Page, 1976). However, there is no reason to assume that hemicelluloses cannot fulfil both functions, that of structure and that of food reserve. As Meyer *et al.* (1960) pointed out, compounds of this type, although cell wall constituents, serve as reserve foods in herbaceous plants. This is probably applicable to woody plants as well. It is certain that we will have to pay more attention to the hemicelluloses and their role as reserves. This will not be an easy task, because they are an extremely heterogenous group of polysaccharides.

Several investigators have found little seasonal fluctuations in the crude lipids and stated that lipids, in comparison with sugar and starch, are not a significant storage form of reserves in conifers (Little, 1970b; Krueger and Trappe, 1967; Ronco, 1972). These observations are in disagreement with Ziegler (1964) and mine. I found an increase in lipids in the autumn, which was mainly restricted to the xylem. Ziegler (1964) pointed out that the accumulation of lipids was restricted to the xylem of the stem and branches. On the other hand, Little (1970b) used only the needles of balsam fir (*Abies balsamea* (L.) Miller). Krueger and Trappe (1967) used the tops and roots of

Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco), and Ronco (1972) used the entire Engelmann spruce (*Picea engelmanni* (Parry) Engelm.). In my study the seedlings were subdivided into four tissues, needles, bark, xylem and roots. The increase in crude lipid was found to occur only in the xylem, although there was also a slight increase in the bark. However, when all the tissues were combined the lipid trend of the individual tissues became masked, because at the seedling stage the volume of the xylem is considerably smaller than that of the needles and roots.

Nitrogenous compounds also have received little attention as food reserves in forest trees. Kramer and Kozlowski (1960) noted that seasonal fluctuations occur in these compounds, such as proteins and amino acids, but that their highest concentration is in tissues where the cells have a specific physiological function (e.g., meristematic tissues). Storage tissues are not mentioned. Most of the information available on nitrogen storage is based on fruit trees and there is little doubt that nitrogen storage in the autumn is important for subsequent growth (Taylor, 1967; Tromp, 1970). One reason why an increase in total nitrogen during the later part of the growing season is frequently not detected, is because nitrogen concentrations are nearly always expressed on a dry weight basis and the rate of dry matter accumulation exceeds that of nitrogen (Taylor, 1967; Tromp, 1970). Part of the rise in nitrogen level in the stem during the autumn is due to the translocation of nitrogenous compounds from the leaves during senescence. The increase in total nitrogen in the bark is due mainly to protein nitrogen while in the wood it is due mainly to soluble nitrogen such as amino acids and amides (Tromp, 1970). Arginine is the most important amino acid in the dormant period according to Tromp (1970) followed by glutamine and asparagine. He also points out that the nitrogen needed at the beginning of leaf development comes mainly from the mobilised nitrogenous compounds of the bark. It appears that the chief function of the nitrogenous storage is to supply nitrogen for new nitrogenous compounds when growth resumes in the spring.

In my study I did not resolve whether or not amino acids and proteins act as a form of reserve. A negligible amount of carbon-14 was incorporated into the free amino acids or into the amino acids of the proteins. Other investigators have also observed low to negligible carbon-14 incorporation into amino acids, but their period of assimilation varied from 6 hours to 7 days (Rangnekar and Forward, 1969; Shiroya *et al.*, 1962, 1966; Steponkus and Lanphear, 1968). In my study the period of assimilation varied from 50 to 300 days. There was also considerable variability as to morphological development at time of treatment. In spite of all these differences, these observations are still comparable if the suggestion by Rangnekar and Forward (1972) is correct that the spatial distribution pattern of photosynthates is essentially stable after the first three days of carbon assimilation. They suggested that within a few days, assimilates formed in the leaves may reach a semifinal destination but metabolic changes involving labelled substrates will continue. My observations tend to support this suggestion.

Certainly, both carbohydrates and lipids are important as food reserves in forest trees. The lipids are more prominent in the xylem and to a lesser extent in the bark than in the needles and roots. Carbohydrates, on the other hand, are prominent in all tissue components, but particularly in the needles. However, it should be remembered that as the tree grows the volumes of the various tissues change in relation to each

other. For instance, in a mature tree the xylem will occupy a considerable part of the total volume, which should enhance the importance of the lipids as a reserve.

LOCATION OF FOOD RESERVES

The storage of reserves occurs in living cells only, and these cells must remain in contact with each other to maintain the assimilate-translocation system (Ziegler, 1964). Most living parenchymatous cells in the tree can function for storage of food substances. The only living cells which do not have a storage function are the specialised cells where an accumulation of reserves would interfere with their physiological functions (Ziegler, 1964). Examples of specialised cells are the sieve elements and companion cells in hardwoods and sieve cells and albuminous cells in conifers and all meristematic cells. In the xylem, the storage tissue consists of vertical and ray parenchyma cells of the sapwood. The pith cells are also able to store reserves and frequently they remain alive for a long time in many tree species. Pith cells probably are important for storage purposes, particularly during the seedling stage because at that time the proportion of living pith cells in relation to the total xylem is relatively large. In the bark, the storage tissue consists mostly of ray and vertical parenchyma cells that are located in the living phloem between the periderm and the conducting phloem. In all cases these living storage cells must remain in contact with each other as well as with the conducting phloem in order to survive (Ziegler, 1964; Zimmermann and Brown, 1971).

It has been stated that the source of the photosynthate, the needles, is also the strongest sink (Webb, 1975). In my study the needles retained a significant amount of labelled photosynthate which is also in agreement with Schier (1970). I found that a considerable portion of the photosynthate occurred in non-structural components, which suggests that the needles are important for storage of reserves. It should be emphasised that this is particularly applicable to seedlings, where the foliage volume is still considerable in relation to the other tissues.

All tissues appear to play an important role for storage purposes at one time or another depending on such factors as time of year and age of tree. For instance, the needles and roots in my study were the biggest carbon-14 sinks of the tree, but this is attributable to their volume, which was considerably larger than that of the other two tissue components. The roots stored more photosynthate in August and part of September than the needles, but after mid-September the needles became increasingly more important in storing photosynthate than the roots. This also suggests that there is an increasing reduction in translocation of photosynthates from needles to roots as the autumn progresses. Webb (1977) had similar findings.

The concentration of reserves is believed to be higher in the roots than in the stem (Kramer and Kozlowski, 1960). However, in most forest trees the tops contain more total reserves than the roots because of the larger volume of the tops. The ratio of top to root can be as high as 16:1 in mature forest trees according to Kramer and Kozlowski (1960). Since the roots do not constitute a sufficiently large fraction of the tree it follows that they cannot store the major part of the reserves. However, this is not applicable during the seedling stage when the roots constitute a large part of the tree.

UTILISATION OF FOOD RESERVES

Food reserves are utilised when the demand arises. This occurs regularly in the spring with budbreak, but it can occur also in emergencies such as when a tree is defoliated by insects. The food reserves in hardwoods are generally not completely used during leaf flush and shoot elongation. Enough remains for a second flush of leaves if the first is lost through frost or insect attack (Büsgen and Münch, 1931). Hardwoods generally cannot withstand a second defoliation. Conifers are generally more sensitive than hardwoods to such adversities as defoliation, but this appears to be more due to the lack of dormant and adventitious buds in conifers than due to the lack of reserves. Under natural conditions, the reserves are mobilised in the spring by being converted into sugars, mainly sucrose, which is by far the most common of the translocation sugars and as such, is translocated to the sites of utilisation (Beevers, 1969; Zimmermann and Brown, 1971).

There is little doubt that food reserves play an important role in the life of a tree. Seed production depends heavily on reserves. In deciduous trees the maintenance of life during winter and the growth resumption in the spring are entirely dependent on food that accumulated during the previous growing season. In deciduous trees the building materials for shoot development come almost completely from the reserves whereas in evergreens a large part of the building material is supplied by current photosynthesis of the mature foliage (Büsgen and Münch, 1931; Ziegler, 1964). However, the extent of this dependency of shoot and cambial growth on reserves is not precisely known. According to Kozłowski and Keller (1966) the generalisation often made in the literature is that shoot growth primarily utilises reserves whereas cambial growth depends mostly on current photosynthates. They suggest that the differences in shoot growth patterns between and within species, among age classes and even among different shoots on the same tree indicate that various degrees of utilisation of reserve and currently produced photosynthates occur. Although the role of reserves in growth is not fully understood there seems to be a consensus that their most important use is in maintaining respiration during absence of photosynthesis (Kramer and Kozłowski, 1960; Kozłowski and Keller, 1966).

In my study large carbon-14 losses, from 70% and up, were observed (Fig. 1). These losses, which were due to respiration, increased from the first to the last feeding date. More and more current photosynthate was used as autumn progressed, which is in agreement with several other investigators. Ursino and Paul (1973) working with white pine (*Pinus strobus* L.) found that the major loss of carbon-14 occurred through respiration. Steponkus and Lanphear (1968) observed that during autumn most of the current photosynthate in *Hedera helix* L. was used in respiration. Gordon and Larson (1970) working with red pine (*Pinus resinosa* Ait.), concluded that photosynthate produced late in the growing season contributed quantitatively much more to respiration than to storage and structure.

Only small amounts of labelled photosynthate were translocated into the new shoots (approximately 3.5%). This is in general agreement with other long term investigations such as those by Gordon and Larson (1970), Schier (1970), Ursino and Paul (1973) and Ursino *et al.* (1968). The major part of the reserves was mobilised and used in respiration with the resumption of growth and only a small part of the reserves was translocated and utilised by the new growth. This leads to the conclusion that the

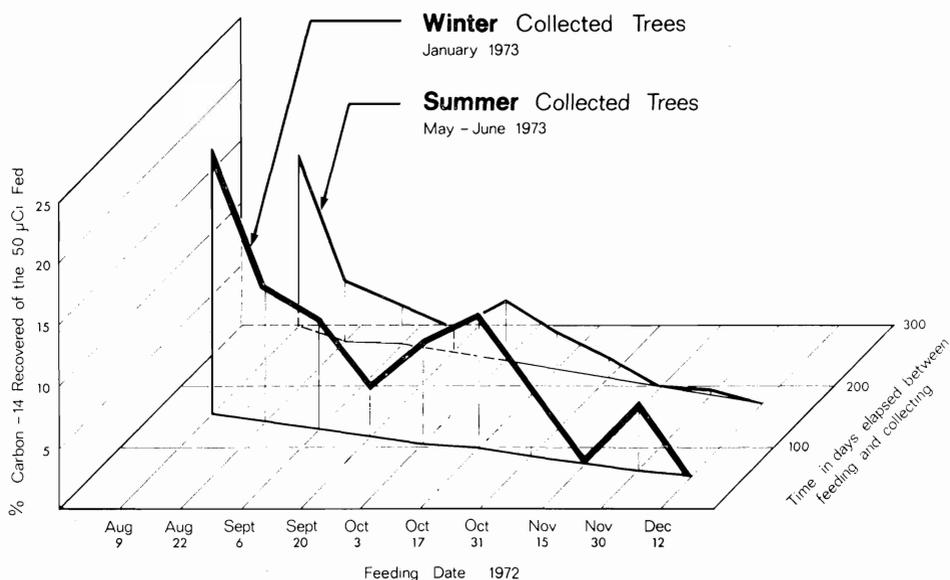


FIG. 1—The amount of carbon-14 recovered from the jack pine seedlings expressed in percent of the amount of carbon-14 initially used ($50 \mu\text{Ci}/\text{tree}$). The amount recovered in relation to the time elapsed between feeding and sampling is also shown. The winter collection is an average based on 3 trees while the summer collection is an average based on 2 trees per feeding date.

reserves play a major role in respiration to supply the tree with the necessary energy to resume growth. It is in accordance with the fact that when growth resumes in the spring cellular metabolism is shifted from a lower to a higher level of activity, which requires much energy, as does the process of mobilisation of reserves (Kramer and Kozlowski, 1960; Zimmermann and Brown, 1971).

The amount of carbon-14 found in the new growth xylem was small, and suggests to me that the reserves do not play a direct role in wood formation. It could be argued that during the initial stages of growth resumption the xylem forms only a small part of the total new shoot volume and as a result the reserves are used up by the other tissue components before the xylem starts to augment its volume. However, the new xylem formed by the secondary meristem all along the stem contained no carbon-14 (Fig. 2), whereas there were carbon-14 containing compounds in soluble form at the time of its formation. It seems reasonable to assume, therefore, that if no reserves are needed for wood formation along the stem, they will not be needed for wood formation in the new shoot.

Another point to consider is the manner in which the carbon-14 is incorporated by the xylem when it is introduced during a period of active wood formation. For instance, when the carbon-14 incorporation from the first feeding date was compared with that from the third feeding date, it was found that there were more radioactive tracheids from the first feeding date than from the third and its radioactivity was also more intense than that from the third. Furthermore, radioactive tracheids from the first

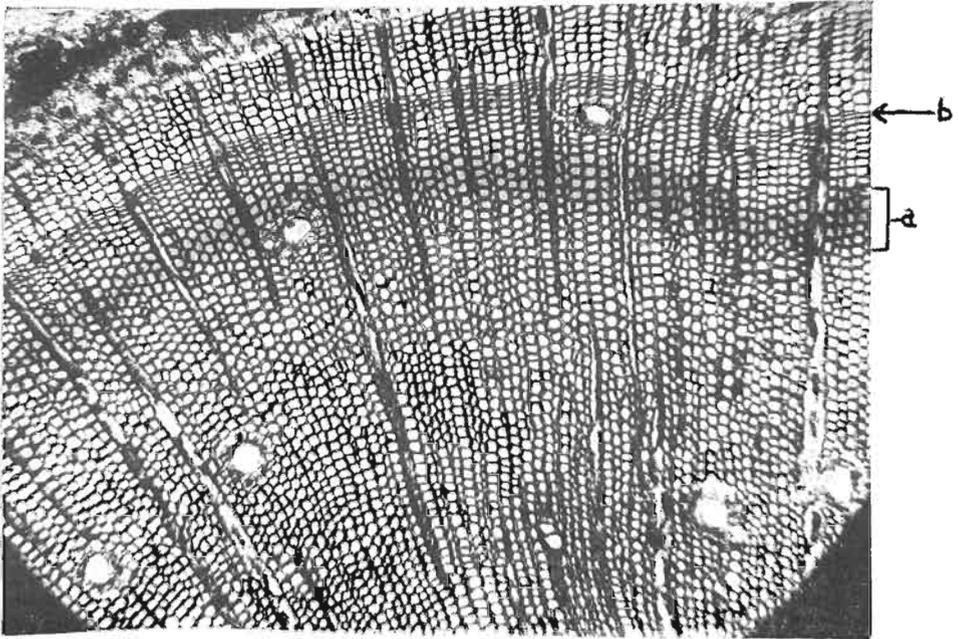


FIG. 2.—Autograph of a 10 μm thick section of a summer collected tree fed on August 9. The band of radioactive tracheids (a) is visible and is several tracheids away from the end of the annual layer (b). There is no radioactivity in the annual layer of the new growth (55 \times).

feeding date formed a distinct band and the subsequent tracheids were not radioactive. These nonradioactive tracheids were formed when still large amounts of carbon-14 labelled compounds were available in soluble form. This also supports Ursino's suggestion that some form of compartmentalisation in the cells exist. Similar results have been obtained by Balatinecz *et al.* (1966), Rangnekar and Forward (1969) and Rangnekar *et al.* (1969).

The observations reported in the last two paragraphs suggest to me that the link between the photosynthetic pathway and wood formation is a direct one. This implies that wood formation is dependent on current photosynthate and that under normal circumstances one- or two-week-old photosynthate will not be incorporated into the xylem.

Olofinboba and Kozlowski (1973) noted that appreciable shoot growth occurred even when currently produced carbohydrates were not available. It is likely that this included xylem formation as well, because the bark was not separated from the xylem in their investigation. They prevented translocation of currently produced photosynthate by girdling the phloem at the base of the terminal leader and defoliating that leader well before shoot elongation commenced. Since they still obtained considerable shoot elongation they concluded that this occurred at the expense of the reserves in the terminal above the girdles. However, I believe that those reserves were used because of the girdling treatment and most likely at the expense of other processes while under

normal conditions (i.e., no girdling) these same reserves probably would have been used in those processes. It makes only evolutionary sense that vital processes in particular, are not dependent on one pathway but that they have several other pathways at their disposal to enable them to survive periods of stress.

Thus under normal conditions the wood formation process is dependent on current photosynthate, while the food reserves play only an indirect role in this process. Preliminary results from two other conifer species suggest that this finding is probably applicable to all coniferous species. The extent to which it is applicable to deciduous species still remains to be determined.

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