The Seasonal Changes in Starch and Fat Reserves of Some Woody Plants

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Introduction

The seasonal change of the food reserves in woody plants has received the attention of numerous investigators in the past and still claims the interest of many. Researches hitherto done, however, concern chiefly the aerial portions of deciduous trees. For the evergreen trees only a few data are available on this subject. This is likewise true concerning the roots. Our present knowledge may be summarized briefly as follows:

For the deciduous trees it seems established beyond all doubt that the starch reserves in the aerial parts show a maximum at leaf-fall and a secondary maximum at early spring, and that each of the maxima is followed by a minimum occurring at dormancy and when the tree is in growth respectively. The previous data on some evergreen trees seem to indicate that there are also two maxima and minima of starch in the stems. Some workers have reported the existence of two maxima and minima of starch in the root as in the stems; whilst others showed the absence of winter minimum, or one maximum and minimum only.

It is well known that FISCHER (1891) attempted to classify a number of trees into two groups, the starch trees and the fat trees, based upon the behaviours of their starch and fat reserves during winter. This classification, however, has been found by such workers as SCHMIDT (1909), SINNOTT (1918), etc., to be untenable for all trees. It has also been supposed that at the seasonal changes starch is converted directly into fat or fat directly into starch. On the other hand, NIKLEWSKI (1905) and others seem to show that changes in these two types of reserve food occur independently of each other. It is, however, generally accepted that branches and trunk are apparently richer in fat during winter than at any other seasons, while roots are very poor in fat even in mid-winter.

The cause of the chemical changes occurring in woody tissues during the rest period has been the subject of much discussion, but at the present moment there is no theory of their cause which can command general acceptance.

The starch changes during the growth period have been studied fairly accurately for the hard-woods, but the fat changes in the same season are still far too little known. All the authors so far cited in this paper are in agreement that in the aerial parts of trees the starch disappearance in spring begins in the twigs and thence proceeds basipetally, but they are not agreed as to the order of starch deposition in summer. Some of them show that the order of accumulation is basipetal in sequence, while others claim that it is basifugal. A few of them have also pointed out that in the roots the starch depletion in spring takes place from the distal ends proximally, and the appearance in summer occurs in the reverse manner.

The forgoing brief reference to the literature shows clearly that our present knowledge on this subject is far from being complete and further investigation is necessary, before the relation of the changes in these reserves to other physiological or physical phenomena becomes at all clear.

The object of the present paper is, therefore, to determine exactly the distribution of starch and fat in woody plants and its change from season to season. It contains the results of three years' observations on five deciduous and two evergreen trees. In each case both aerial and underground parts were examined.

My grateful thanks are due to Prof. Dr. K. KORIBA, under whose direction this investigation was carried out, for his constant helpful suggestions and criticisms in regard to the problem.

Meteorological Notes

Investigations into the subject in question have been made hitherto in various regions of the northern hemisphere including Russia, Germany, Canada, America and France. In other words, they have been carried out under more or less differing climatic conditions which suggest that some of the conflicting opinions may be the result of differences in environmental conditions, as well as differences in the materials used, the methods of sampling and of food estimation.

In view of this, a brief record of the meteorological conditions in Kyoto district may serve for reference, as the temperature has been emphasized by many workers for its importance in connection with the food fluctuations in plants. That the winter season extends to March is characteristic of the district, though March weather is quite variable, periods of cold being frequently followed by warmer spells. The first frost comes by the end of October or the beginning of November, and the last by the end of April. The snowfall is slight, occurring from early or mid-December to late March. The precipitation is lowest in winter, averaging from 55 to 66 mm.; the highest, 232-198 mm., comes in June and July respectively. The following records of annual temperatures are those supplied by the "Monthly Weather Reports" of the Kyoto Meteorological office.

Mean, mean of daily maximum and minimum, and mean of monthly max. and min. temperatures (C.), 1886 to 1931; at Kyoto.

Month	Mean	Daily max.	Daily min.	Monthly max.	Monthly min.
January	2.6	8.7	−2.1	14.4	−6.8
February	3.1	9.3	−1.8	16.1	−6.8
March	6.3	12.9	0.6	20.8	−5.1
April	12.3	19.0	5.9	25.7	−1.5
May	16.6	23.2	10.3	29.1	3.0
June	21.1	26.7	16.0	31.6	8.8
July	25.2	30.7	20.8	34.6	15.5
August	26.2	32.2	21.5	35.4	17.0
September	22.2	28.1	17.7	33.3	10.6
October	15.7	22.4	10.3	27.4	3.3
November	9.8	16.7	4.1	22.7	−1.5
December	4.7	11.2	−0.5	17.5	−5.4

Mean monthly temperatures (C.) of the soil in winter, 1931 to 1933.

Depth (m.)	December	January	February	March
0.0	5.6	3.8	4.2	7.6
0.1	6.5	4.5	4.4	7.1
0.2	6.9	4.8	4.6	7.0
0.3	7.6	5.4	5.0	7.1

Materials and Methods

The following woody plants were employed as materials for study: *Castanea pubinervis*, SCHNEID., *Alnus japonica*, SIEB. et ZUCC., *Robinia pseudoacacia*, L., *Tilia miqueliana*, MAXIM., *Populus nigra*, L., *Quercus glauca*, THUMB., and *Pinus densiflora*, SIEB. et ZUCC.. These trees are all vigorously growing in the plantation and grounds of the University. The age, height, and number of trees of each species used are as follows:

Species	Age	Height (m.)	Number
Castanea pubinervis	10–13	3.5–5	25
Alnus japonica	11–14	4–5.5	7
Robinia pseudoacacia	4–8–10	3–6–8	30
Tilia miqueliana	9–11	3.5–4.5	7
Populus nigra	4–8	4–12–15	40
Quercus glauca	10–13	3–4	30
Pinus densiflora	10–12	3.5–5	30

In each species, samples were gathered at intervals of from one to two weeks during the period January, 1931 to May, 1934, while in 1931–32 the attention was paid mainly to the branches and small roots. For comparison of materials from one date to the another, the following procedure of sampling was adopted and found to give satisfactory results.

In each case, three trees were selected in respect to the uniformity of their growth conditions, and then collections were made on each of two individuals respectively, the other one being left in situ till the next gathering as a check. On the day following collection, samples were taken from this check tree and one other comparable tree. Again a further check tree was chosen for the next sampling. In the cases of *Alnus* and *Tilia* two similar trees were selected every time and one of them was used for sampling. In *Tilia*, too, all the trees were ramified into several uniform main branches at or near the base, so that these branchings were often employed as an individual tree, especially in the case of felling.

Branches: One or two of 5–6-year-old branches were cut off from the each of the selected trees, with particular attention paid to uniformity of length, size, and position on the tree. From each of the branches samples, pieces of 2–4 cm. in length, were taken from the basal parts of every year's growth along its main axis, and in so far as possible, from other parts also. The shoot and bud of the current year have also been kept under observations.

Trunks: Small cuttings including the whole bark and 1–2 woody rings, were removed by means of a sharp knife from the trunks of these trees. Trunk samples were mainly taken from the basal portion, but also at suitable intervals along the whole length. These were not always from the same side of the trunk, while control samples were taken also on other faces. No remarkable difference with regard to the distribution and amount of starch or fat was however noted in these control samples, north or south, west

Roots: One or two healthy surface roots were removed from each of the trees. In all cases, the roots were first carefully excavated and followed out to their slender parts of about 1–1.5 mm. in diameter. Root samples (2–4 cm. long) including the whole woody rings, were collected at intervals of from 3 to 10 dm. along the length of the root (in major cases, the secondary roots have not been examined). Generally, the root system of a mature tree shows a thickened basal part adjacent to the trunk 3–7 dm. in length. It then tapers off to the root system proper. This portion was also taken for observations in the same way as in the case of the trunk, though samples here were taken from the upper surface only.

During the periods of March to May and November to December, just when environmental changes bring about pronounced physiological changes within the tree, more detailed observations were made than in other seasons of the year.

At proper times, particularly during the periods just mentioned, one or two trees were felled and samples were taken at close intervals along representative branches, from the trunk downwards, and along at least three roots (except *Alnus* which was not cut down). In the cases of *Populus* and *Robinia* only the young trees (3- to 5-year-old) were employed for felling. The felled trees were always examined in detail to check any deficiency which might arise from observations only upon definite points of the trees.

Each of the samples was kept in a mixture of equal parts of alcohol and glycerin and the position of each samples on the tree was recorded. Sections, transversal and longitudinal, were cut with a razor by free hand. These sections were all treated with iodine and Suddan III to bring out respectively the starch and the fat content present.

The determination of fat was carried out at less frequent intervals than that of starch, as the fat changes proceed at a slower rate. As far as possible, for the fat tests sections were obtained from fresh or nearly fresh materials. These sections were stained in an excess of a standard concentrated solution of Suddan III, in a mixture consisting of pure plopyl alcohol (GROSS, 1930) and glycerin in equal parts, and mounted in glycerin. This solution was found to be more favourable than the usual Suddan III solution in ethyl alcohol and glycerin.

Both starch and fat were determined by the temporary mounts so obtained, and too, a large number of semi-permanent preparations were preserved as a constant check. Each material was examined as quickly as possible in the order of its collection. Also in order to prevent any personal bias creeping in, it was examined in duplicate when a complete collection had been made for every season. (This latter procedure was found possible only for the determination of starch.)

For fat, the criterion was mainly the colour reaction of the Suddan III mentioned above. Some other fat stains, osmic acid and alcannin solution, were also applied when the results seemed doubtful.

Attempts to distinguish fats from other staining substances, like resins and volatile oils, were made on the sections, particularly in the case of *Pinus* which contains abundantly such contaminating substances. Sections were treated with such solvents as alcohol, chloralhydrate solution, and acetic acid which have been used by many (see especially the text book of histology, MOLISH, and TUNMANN-ROSENTALER). Unfortunately, no one of these solubility tests was found to be satisfactory. Only on *Pinus* they were employed with limited value.

The heating of sections on the slide to about 130°C., has been found useful as a means of removing of volatile oils (MOLISH). However using this method on the twigs of *Pinus*, *Tilia*, and *Populus*, no reliable results could be obtained in any case, though in some cases the intensity of colour reaction diminished after heating.

The original intention was to determine the fluctuations in sugars which have been proved to be significant in connection with the starch changes. Some of the materials were tested for sugars by means of MEYER's and FLUCKIGER's reactions, but a detailed determination of sugars could not be expected by such methods; and in the absence of a satisfactory microchemical test, the work was not continued.

For both starch and fat it is difficult to determine the actual amounts present. This is especially true with fat, but constant practice enables an observer to decide fairly rapidly as to their relative contents. In each case, the amount present in every tissue was indicated by the numbers 0, 1, 2, 3, 4, 5, 6; each of the numbers representing in sequence total absence, very small amount, small amount, fair amount, fair abundance, abundance, and great abundance. The total amount present in any definite point on the tree was assigned by the sum of such numbers which were estimated for every tissue of that point. To designate the graduation of decrease: no decrease, 6; very slight decrease, 5; slight decrease, 4; fair decrease, 3; marked decrease, 2; very marked decrease, 1; and total disappearance, 0.

From the figures so obtained the seasonal fluctuations in both starch and fat were plotted, as will be seen in the following pages. All of the points on the curve represent the average of many values of the observations. It is emphasised, however, that the graphs have no significant quantitative value, but merely indicate the relative value and the fluctuations from season to season.

In the following record of observations, for each species, the starch curves, unless stated otherwise, represent in (A) the base of the one-year-old twig (tw), the five-year-old branch (br), and the base of the trunk (tr); in (B) the current season's shoot (sh) and the vegetative bud (bd); in (C) the tissues in the twig, namely the pith (p), wood (wd), and bark (bk) of the one-year twig (the graphs are drawn with double scale); in (D) the basal (rb), middle (rm), and distal portions (rd) of the root.

The basal part of the root here mentioned is the region about 5-6 dm. or so from the ground-level and the distal portion is the fine root a short distance behind the growing point, with a diameter of some 2-1.5 mm..

Results

(1). The starch reserves

The general features of starch fluctuation in the whole aerial portion and root will be seen by a glance at the graphs in A, B, and D. They show also the differences in several regions of the tree in various seasons. In graph C is shown the same fluctuation in twig tissues.

(A). The deciduous trees

Castanea pubinervis, SCHNEID.

Castanea may be regarded as a tree representative of all the deciduous species examined, in so far as the starch change is concerned; therefore it will be treated here in more detail than the others.

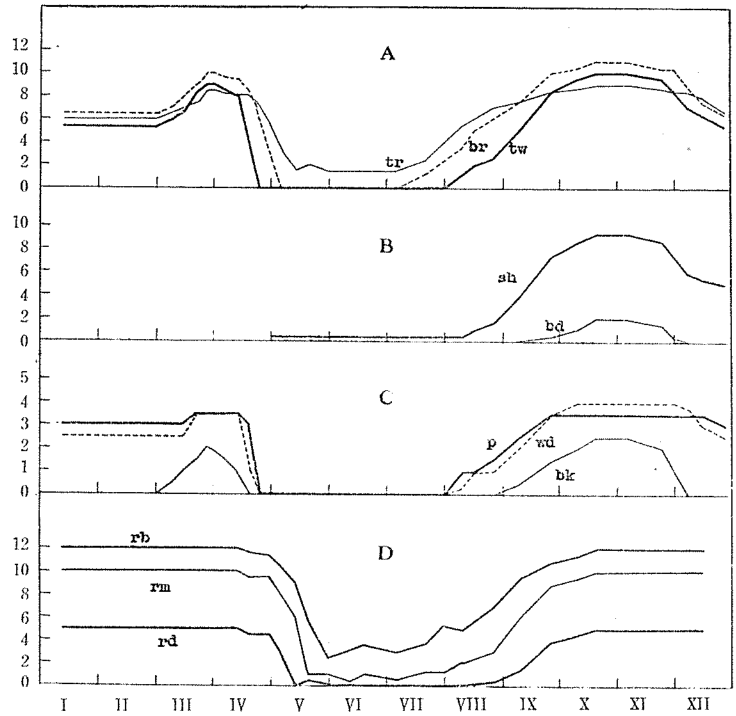

Fig. 1. *Castanea pubinervis.* Seasonal starch distribution. The ordinates are based on an empirical qualitative scale as described in the text. The abbreviations are employed throughout.
A–B. Stem parts: tw, one-year-old twig; br, five-year-old branch; tr, trunk; sh, current year shoot; bd, vegetative bud (To avoid piling up the curves sh and bd are separated in B).
C. Twig tissues: p, pith; wd, wood; bk, bark (phloem-cortex).
D. Roots: rb, basal portion; rm, middle portion; rd, distal portion.

The aerial parts

From winter to spring. During January and February the starch content is at a minimum all through the aerial portion. The extent of starch change varies greatly from part to part of the tree, and from tissue to tissue in the same part. Starch disappears totally from the bud and the terminal region of the twig, and to a considerable extent from the young branches; the main stem shows, however, a comparatively slight drop which occurs only in the cortical tissues.

Such longitudinal and radial gradient of starch disappearance is shown in Table 1. The disappearance is seen to be very pronounced in the phloem-cortex, but slight in the wood and pith, growing less so towards the center.

Table 1 (*Castanea*)

The starch distribution in the aerial parts at mid-winter.

Part of tree	Phloem-cortex	Outer wood	Inner wood	Pith
Bud	absent			
Tip of 1-year-old twig	absent	absent	absent	absent
Base of 1-year-old twig	absent	marked decrease	slight decrease	very slight decrease
Base of 2-year-old twig	absent	marked decr.	very sli. decr.	no decr.
Base of 3-year-old branch	absent	fair decr.	no decr.	no decr.
Base of 5-year-old branch	almost absent	very sli. decr. ?	no decr.	no decr.
Base of 7-year-old branch	small amount	no decr.	no decr.	no decr.
Trunk at 50 cm. above ground (middle part of trunk)	small amount	no decr.	no decr.	no decr.
Base of trunk	fair amount	no decr.	no decr.	no decr.

In early March starch begins to regenerate, this process going on fairly rapidly to a spring maximum at the end of March. In all the branches, as well as in the trunk, starch increases first in the inner phloem, and, so far as could be determined, evenly along the whole length of the tree at about the same time. In the twigs and small branches the regeneration spreads rapidly all over the bark, while on the wood side it occurs somewhat later and proceeds to a less degree. The older parts show a similar behaviour but it is less regular.

At the end of March the distribution of starch is similar to that found in the preceding late autumn, while the amount is a little less, especially in the bark. The spring maximum is maintained only for a short duration, at most for several days.

The maximum is followed again by a decrease which begins with the bud swelling. The decrease is very slow up to mid-April, when most of the buds begin to expand. After this there occurs a sudden drop to a minimum at mid-May, accompanied by a rapid growth in leaves and shoots.

Once the starch begins to disappear, the process spreads rapidly.

It becomes apparent throughout the tree during the first week of April when the foliage buds are protruding through the separated scales. They are then entirely free from starch. In the branches and trunk, however, the change is noticeable only in the cambial layer or in the adjoining phloem cells. Otherwise the distribution of starch is unchanged.

A fortnight or so later, about April 20th, when the vegetative buds are mostly opening, starch has totally disappeared from the bark and wood of the distal region of the youngest twigs, though some is retained in the pith. It has also been depleted from the whole bark of the basal half of the twigs, but from the two-year-old one downwards it is present in all the tissues and increases gradually towards the trunk, where the mobilization is still limited to the cambial region.

The evidence is thus clear that the loss of starch due to the bud growth is only small, no significant amount being withdrawn from the lower portions as it expands in spring.

Opening of the buds is followed, however, by a rapid drop from all the stem tissues, which first reaches " minimum point " in the uppermost twig, spreading thence basipetally down the tree. Generally, in the 5-year-old branch the minimum point is about two weeks later than in the youngest twig, and a week or so earlier than in the base of the trunk (see the graphs in A).

As shown in the curves in C, complete mobilization of starch is seen first in the bark, then in the wood and finally in the pith. In the bark it proceeds centrifugally, whilst in the wood centripetally.

By mid-May the starch content has reached its spring minimum throughout the tree. It has disappeared entirely above the five-year-old branches, but is present in increasing amounts towards the base of the tree. The pith and inner wood of the main stem contain less starch. The quantity in them shows smaller fluctuations as they grow older.

From summer to winter. The spring minimum continues until the beginning of July, when starch begins to reappear slowly. At first the rate of accumulation is slow, then it increases steadily until late October, when the autumn maximum is attained over the entire tree.

The most vigorous growth takes place from late April to the end of June, then growth activity slows down. Early in August the longitudinal growth is over, though the radial growth continues for longer. It will thus be seen that the period of starch minimum coincides with that of most vigorous growth, and that starch does not sensibly increase in amount till the growth is slackening off.

The first accumulation of starch is noted in the third week of July, when the trunk shows a slight gain in the woody portions but not in the unlignified areas, although the small branches are still entirely free from it. After that it reappears in the upper portions successively, and in the second week of August the accumulation becomes general in all parts except the current season's growth. The amount is always definitely in a rising gradient from the twig to the trunk, a basifugal progress of starch deposition being clearly indicated.

In the shoots of the current year starch appears as early as May, though it is only visible in the starch sheath. This state persists till mid-August, followed by a parallel increase in the young twig. The accumulation is initiated finally in the bud, where it goes on slowly from late September to late October.

Generally, starch is accumulated much earlier in the pith and wood and attains its maximum more rapidly than in the bark. In the pith and wood the storage takes place from the center to the outer rings, while in the bark it proceeds from the outside towards the innermost phloem which is the last to be stored with starch.

From late October to early November the starch reserves show the autumn maximum. In late November, when the leaves have died or fallen, a slight drop is perceived in the cortical tissue, and more especially towards the upper portions. After this there is a gradual fall to the winter minimum in all parts. The decline is more rapid in the young branches than in the older ones, and conspicuously slow in the trunk where it is only slight till mid-December, when starch has totally gone from the bark of the upper branches.

Without exception starch remains unaltered for a longer time on the wood side than in the bark. In the former it diminishes centripetally, while in the latter almost evenly.

The roots

From winter to spring. In all of the roots the starch is found to be practically unreduced in amount during the winter months (Fig. 1 D). All the root tissues are quite full of starch, especially in the bark, the amount and distribution being as that found in the preceding autumn maximum.

An exception to the condition of this general statement takes place in the trunk under the ground level and in the thickened basal part of the root, where a slight winter reduction occurs in the bark. Further downwards a definite increasing gradient of starch is noticed. Several successive samples taken at suitable intervals in this region show that the extent of reduction lessens with the increasing distance from the stump, and does not extend beyond a distance of about 65 cm. from the ground surface (Table 2).

Table 2 (*Castanea*)

Starch distribution in the bark of the stems and roots near the ground-level at mid-winter (except the wood which shows no change).

Part of tree	Starch in the bark
Trunk at 5 cm. above ground	fair amount
Trunk at 5 cm. below ground	fair abundance (slight decrease)
About 15 cm. below ground (the region common to trunk and root)	fair abundance (slight decrease)
About 40 cm. from the ground (the thickened foot of the root)	abundance (very slight decrease)
About 65 cm. from the ground (the part suddenly tapering off to the root proper)	great abundance (almost no decrease)
Beyond 65 cm. (normal root)	no decrease

It is thus seen that there is a remarkable contrast between stem and root in the distribution of starch at winter dormancy, and the subterranean portion of the trunk represents a transition with a striking rise towards the root system. Similar circumstances are also noted with other species (except *Alnus*, from which no reliable data were obtained on this point). This fact is of interest from the standpoint of starch behaviour in the tree during the rest period (see the later pages).

The winter status of the starch distribution in the root is maintained till about mid-March, followed by a regeneration in the regions which have exhibited the winter reduction. The rise here must have taken place as in the stems, though it is difficult to say when the change was began, owing to individual differences and also to the slightness of the change. So far as examined, the regeneration becomes apparent in late March and continues till its original maximum is reached in early April. The regions near the ground-level have thus a periodicity of their own, upon which the stem fluctuations are presumably imposed.

In the early half of April all roots are filled with their maximum amount of starch. There follows then a marked drop to a minimum at the end of May.

The first disappearance in the root occurs about three weeks later than it does in the twig (except the root-crown, which shows similar indications about a week before this). It is at first barely discernible in the cambial region, but is more noticeable in the basal and distal parts than in the intervening region. Further change is very slow up to the end of April and hardly comparable with that obtained in the earliest state of disappearance in the stems.

By the beginning of May all the roots examined shows, however, a sudden spurt of decrease along their whole length, i. e., a fairly marked dissolution occurring in the inner bark and some outer bark cells, progressively outwards from the cambial zone, while no change is yet to be seen on the wood side.

After this starch disappears rapidly from all the root tissues, reaching its minimum at the end of May. The disappearance occurs most rapidly in the slender parts, whence it proceeds at a slower rate irregularly towards the root-crown. Accordingly, there is a clear basipetal (upward) propagation of starch minimum from the distal end towards the proximal foot (graphs in D).

The depletion, too, is always less rapid in the wood than in the cortical tissues. In the bark it takes place from the inside outwards, whilst in the wood it progresses in a reversed direction. At the minimum, starch is completely gone from the fine roots, but is present in greater amounts towards the base.

To sum up the available data. In the roots, excluding the region common to trunk and root, and perhaps the proximal foot of the root proper, the beginning of starch disappearance in spring is some weeks later than in the stem, its minimum being attained proportionately late.

From summer to winter. From June to early July the starch content is at its minimum throughout the roots. It is, however, still present in the large roots, especially in the inner wood. Generally, in the inner woods of the thicker and more proximal regions the reserve starch seems to remain nearly unaltered throughout the seasons, as in the case of the trunk. During this period it is also at its minimum in the aerial portion.

By the end of July starch is still absent in the thin roots, while in the thicker ones it has already begun to rise in the wood. The deposition is particularly evident in the root-crown and grows less so downwards to the thicker part, beyond which, however, the amount still remains at the minimum. After that starch appears and increases gradually up to its maximum in late autumn.

In the second week of August the accumulation extends to the middle region, but beyond this the amount falls off rapidly towards the slender part, where it does not occur until the end of August or the beginning of September. At this phase the thicker part attains nearly its maximum. In all cases the deposition goes on more rapidly in the wood than in the bark, and ends finally in the innermost phloem.

The data given above seem to be conclusive in showing that in the root the accumulation of starch commences in the base and thence works distally along its length.

In late October all the roots are filled densely with starch and no further indication of changes is noticed until the following spring, except the slight winter drop in the root-crown from late December till mid-March. At the maximum there is always a greater abundance of starch than in the aerial portion.

The winter fall in the root-crown seems to start later than in the trunk above ground, though with some irregularity. Most certainly an impulse to starch reduction seems to be sent down from the stem to the roots, in which it tends gradually to appear further and further away from the base till mid-winter.

Comparing the data presented in figs. A, B, and D, it will be seen that the starch storage in the roots commences at or shortly after the time it does in the stems, but goes on more slowly than in the latter. This is probably related to the conditions of growth in the roots, for their growth persists for a much longer period than in the aerial parts. The smaller rate of storage seems to be quite natural. Similar features are also noted with the other trees examined.

Alnus japonica, Sieb. et Zucc.

The aerial parts

From winter to spring. As is shown in Fig. 2 A–C, there are two maxima and minima of starch in the aerial parts. As *Castanea*, the winter reduction of starch is most marked in the twigs, less so in the older branches and least of all in the trunk where it is strictly limited to the bark. Especially, in the terminal region of the twig starch is completely nil.

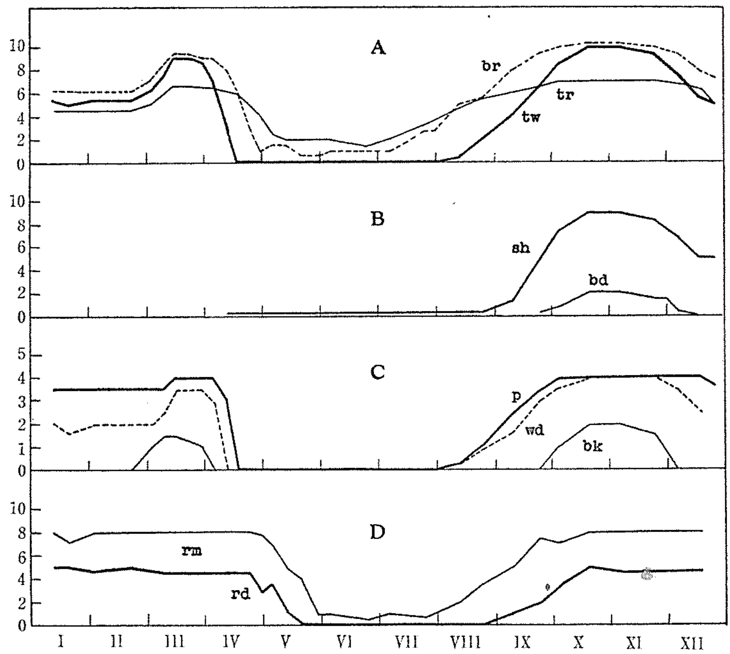

Fig. 2. *Alnus japonica.* Seasonal starch distribution.
A–B. Stem parts. C. Twig tissues. D. Roots.

By the end of February starch begins to regenerate, rising up to the spring maximum at mid-March. The regeneration occurs first in the inner phloem, then in the outer bark and wood side. The beginning of it seems to be uniform all through the tree.

In late March, with the commencement of bud growth, there occurs a slow decrease, followed after bursting by a rapid fall to the spring minimum at mid-May. Here again, as in *Castanea*, the minimum is reached first in the uppermost twig, whence it is propagated basipetally down the tree. The disappearance proceeds also in a definite order in the tissues : it commences in the inner phloem, and is followed by the outer bark, wood, and pith, in the order named.

From summer to winter. The spring minimum persists till early July, with a total absence in the upper branches. In the latter part of July, when growth slows down, starch is again rising and continues to rise until the autumn maximum. The starch accumulation begins at the base of the trunk and thence proceeds upwards with great regularity, as has been found with *Castanea.*

The current year shoots are starch-free, except in the starch sheath, until the end of August or the beginning of September, when their growth has just ceased. After that they are filled with starch fairly rapidly. Starch appears lastly in the buds, though the amount is small even at its maximum. The sequence of starch accumulation in the tissues is very regular and just inverse to that of the spring disappearance (graphs in C).

The autumn maximum is seen from late October to early November. In late November the leaves are almost entirely fallen, and the winter depletion of starch is just commencing. Here also starch disappears most rapidly from the twig and further down the axis it persists progressively longer. In all cases the depletion starts in the bark, spreading slowly and inconspicuously to the wood and pith.

The roots

In the root curves (Fig. 2 D) only the changes in the middle and distal portions are represented, for the data from the basal part are not sufficient to construct the graph. It may be said, however, that starch develops poorly in the basal portion and its amount differs greatly according to individuals.

As the curves indicate, the winter reduction of starch is not seen. All of the roots contain their maximum starch equal to that found in the late autumn. This winter status persists until the end of April, then it slowly begins to fall until it reaches the minimum between the end of May and July. The disappearance is therefore later than in the stem and progresses in a basipetal manner, just as in *Castanea.*

In the large roots starch is accumulated after August, whilst in the fine ones it does not appear till early or mid-September, when the former attains nearly its winter level. The evidence seems thus clear that the order of deposition is from the base towards the apices, as in *Castanea.* The deposition is apparently slower than in the aerial parts.

Robinia pseudoacacia, L.

The aerial parts

The starch shows a somewhat different distribution : it is mainly stored in the bark and the young wood, the pith being generally free except in the young twigs. The bud is also negligible as a storage seat of starch or fat.

From winter to spring. The starch curves (Fig. 3 A–C) are seen to be essentially similar to those for *Castanea* and *Alnus*, showing two maxima and minima. The winter minimum is not so conspicuous, the reduction being restricted to the bark except in the one- to two-year-old twigs.

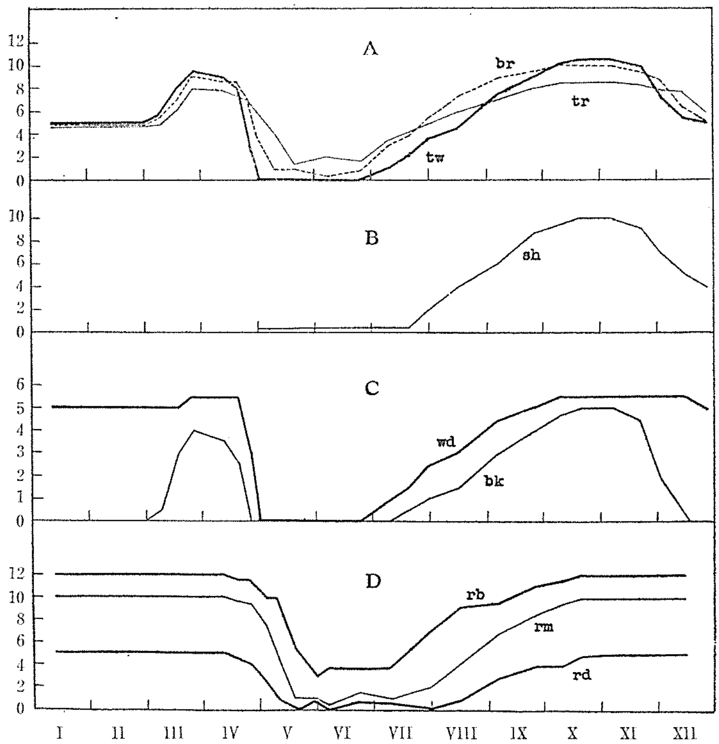

Fig. 3. *Robinia pseudoacacia.* Seasonal starch distribution. A–B. Stem parts. C. Twig tissues : wd, wood and pith ; bk, bark. D. Roots.

By the beginning of April starch is at the spring maximum, with a prelusive regeneration in March. The vegetative buds burst out in the latter part of April. After the bursting of buds the starch content rapidly drops off to the spring minimum in the latter part of May, when the trees are through blooming and vigorous growth is in progress. Here again the minimum occurs first in the twigs, and finds its way basipetally down the tree.

From summer to winter. The spring minimum is maintained until the end of June, when starch begins again to appear together with the slackening of growth. As seen from the graphs, no definite time differences of starch reappearance are found in the aerial portion except in the new shoot; it merely rises at greater rates in the older and more basal parts, an upward deposition being suggested.

In the current year shoot starch accumulation begins some weeks later than elsewhere. Occasionally, especially in the young trees, "Johannis triebe" are formed in late July, leading a sudden but slight drop followed again by a rapid rise of starch. Such a transitory minimum takes place, however, only in the upper branches and tends to appear less often below, while in the trunk starch rises independently.

Starch is at the autumn maximum during late October to early November. Late in November the trees are generally destitute of leaves and enter upon the winter reduction of starch. Particularly in the twigs it disappears after that rapidly, while in the trunk it remains almost unaltered till mid-December.

The roots

During the winter the starch content of the root is unreduced (Fig. 3 D). Only in the root-crown, as well as in the trunk below ground, it disappears slightly from the bark and appears again in late March, just as in *Castanea*.

In early April the whole subterranean portion is filled with starch approximating that of the autumn maximum. In the thicker roots there is usually a marked decrease in starch towards the center, as in the trunk. During May it shows a rapid fall, with a preliminary slight reduction in late April. It is at the spring minimum until the early part of July, rising again to the maximum in late autumn.

From the graphs it is seen that in the root the seasonal changes in the growth period occur some weeks later than those in the aerial portion, as in the case of *Castanea* and *Alnus*. *Robinia,* too, is in good agreement with them as starch disappearance in spring goes on in a basipetal direction, and in summer its reappearance proceeds in the reverse manner.

Tilia miqueliana, MAXIM.

The aerial parts

Although the general features of starch changes are similar to those in other trees, there are yet some differences found in *Tilia*; so that it is designated a fat tree.

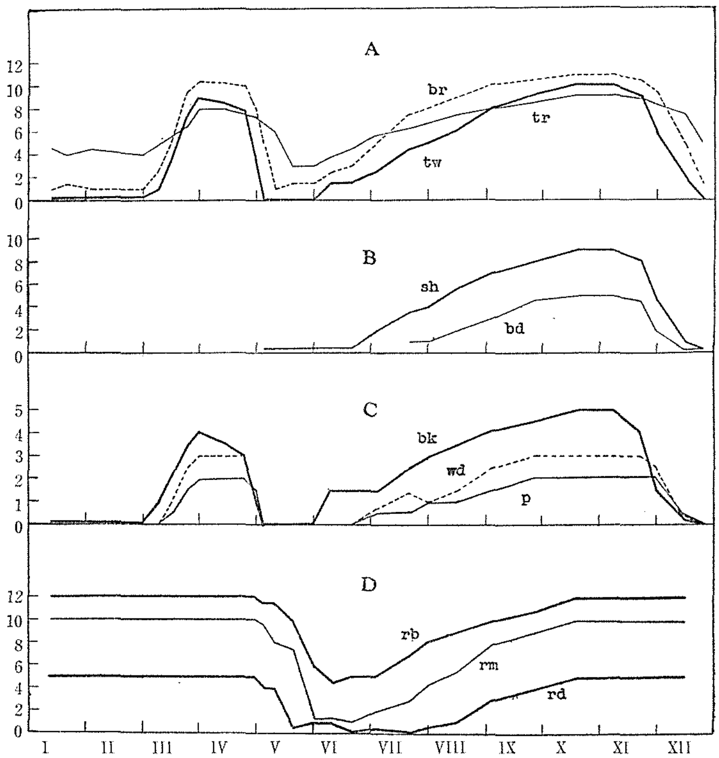

Fig. 4. *Tilia miqueliana.* Seasonal starch distribution.
A–B. Stem parts. C. Twig tissues. D. Roots.

From winter to spring. The winter minimum is very pronounced: starch is almost entirely absent from the branches, though the trunk retains still a fairly considerable amount especially in the wood, and increasing towards its base. This indicates that the classification of trees into two groups, the starch trees and the fat trees, is by no means so rigid as advanced by FISCHER (1891) and others.

Following this minimum there is a marked rise to the spring maximum at the beginning of April. The regeneration of starch begins in the inner phloem, whence it spreads suddenly but irregularly, both outward and inward. Such activity seems to be uniform along the entire length of the tree.

The spring maximum again drops off to the minimum at mid-May, falling nearly to the same level as in mid-winter. When the buds open, about April 25th, the decrease proceeds rapidly, though in a basipetal manner. The high rate of disappearance compared with other trees is due to the exceedingly rapid extension of growth in that period. This growth is about half completed in early May.

From summer to winter. It is noticeable that the spring maximum is of very short duration, followed by the deposition after two weeks at most. Early in June the extension of growth is over, and the starch storage goes on all over the plant except in the current growth where it begins some weeks later. Unlike other plants, the earliest accumulation takes place in the medullary rays of the phloem, but here also the innermost phloem is the last to be stored with starch.

It is difficult to determine exactly in which part the accumulation begins, as even at the spring minimum the main parts retain some starch in the medullary rays of the phloem. The rate of deposition is, however, apparently more rapid in the older and more basal regions, suggesting a tendency toward upward progress.

For about three weeks before the leaf falls the starch maximum is seen, after that the winter reduction follows. In all parts starch disappears rapidly from the bark, while it persists longer in the wood and longest in the pith. It, too, remains longer in the lower parts of the tree.

The roots

Here again no winter reduction of starch can be seen in the roots, except a slight drop in the region near the ground-level, which is slightly more marked than in the case of other trees.

In late March starch begins to regenerate in the root-crown and early in April it attains the autumn level. After May all roots lose their starch rapidly and show a minimum amount during June, followed again by a rise to the autumn level. The depletion in spring is basipetal along the root, while the storage in summer is inverse, as has been described for all other species.

Comparing the graphs for stem and root, there is seen to be a fairly wide interval between them in the beginning of starch deposition. The unlikeness of their growth conditions is suggested as a possible cause for this. As mentioned before, the elongation of growth in the shoot is over in May, followed by a period of radial growth. On the other hand, in the root the growth is most vigorous in June, persisting for a more extended period than in the case of the aerial part, even though slowly.

Populus nigra, L.

The aerial parts

General features of the curves (Fig. 5 A–C) are in accordance with those found with all other deciduous species:

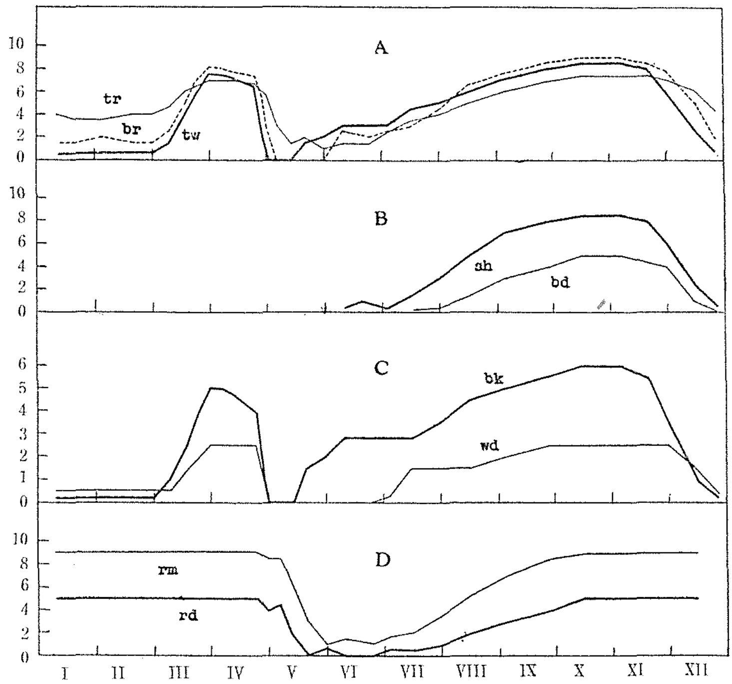

Fig. 5. *Populus nigra*. Seasonal starch distribution.
A–B. Stem parts. C. Twig tissues: wd, wood and pith; bk, bark.
D. Roots.

From winter to spring. The winter depletion of starch is very conspicuous, being comparable with *Tilia* in its degree. Though also a fat tree, it is noteworthy that *Populus* shows a fair amount of starch in the trunk even at mid-winter.

In early March starch begins to regenerate all through the phloem, reaching the spring maximum just before bud swelling. As in the case of *Tilia*, the regeneration occurs suddenly and irregularly all over the plant except in the bark which is the first to show it.

As the buds unfold, the starch content suddenly falls off to the spring minimum at mid-May. Evidently the starch disappearance proceeds basipetally, though it is so sudden that the minimum points are found in the first week of May throughout the branches, and almost simultaneously for the tissues (graphs in A and C).

The particular suddenness of this disappearance, is, as in *Tilia*, associated with the rapidity of growth extension in that period. But here the initial want of reserve starch may also be suggested as a possible cause, for in *Populus* starch is poor except in the bark.

From summer to winter. Like *Tilia*, the spring minimum passes rapidly, followed by a period of starch storage, which however, begins during the period of vigorous elongation of growth. The elongation of growth does not slow down until early July.

The most notable fact is that the starch deposition occurs in the twigs earlier than in the branches and probably also earlier in the main branches than in the trunk. The first deposition of starch was noted in the latter part of May, when a small amount had been deposited in the outer bark of the one- to two-year-old twigs, though in the older branches it was still absent and the trunk was found just at its minimum. About three weeks later, in the second week of June, the accumulation had reached the lowest branch, but from here downwards there was still no change. In each tree the increase is less apparent towards the base, where it does not occur till about six weeks after it has started in the uppermost twig.

There is thus a tendency for a basipetal progress of starch deposition, but this tendency is maintained for only a short period, about the month of June. After July all parts are uniformly and gradually filling up with starch, and by mid-October the autumn maximum is attained.

The basipetal progress mentioned above does not hold, however, for the new shoot, where starch begins to rise still later than in the older portions. In all cases the earliest and greatest deposition takes place in the bark, and finally in the innermost phloem.

From mid-October to early November starch is at the autumn maximum, declining to the winter level. The starch disappearance is comparatively rapid in the small branches, while slow in the trunk.

The roots

Generally, in the roots of young trees starch is distributed evenly along their length, whilst in large trees the thicker roots show often great irregularity in starch content. The root curves are shown therefore for the middle and distal parts only (Fig. 5 D).

In the root the starch is unchanged in winter and remains constant until late April. Young trees retain also their maximum root starch during the same period, with the exception of a slight winter drop in the proximal foot.

The starch content falls slowly in the early part of May, then rapidly to the minimum during June. Afterwards it is again rising up to the maximum in late autumn.

As seen from the graphs, the seasonal phases also occur in this case later than in stem. The decrease is basipetal while the increase is basifugal, as in the cases of all other deciduous trees.

(B). The evergreen trees

Evergreen trees are especially instructive in respect to the seasonal change of reserves as compared with deciduous trees. Particular attention was paid to *Quercus glauca* and *Pinus densiflora* as representatives of the evergreens. The former bears its leaves during winter, though these are entirely displaced by new ones in mid-May, while the latter retains its leaves for several years.

Quercus glauca, THUMB.

The aerial parts

The starch curves for the stems (Fig. 6 A–C) agree generally with those for the deciduous trees; i. e., they show two maxima and minima.

From winter to spring. The winter minimum comes in late December and is confined generally to the bark, where however the starch content is rather poor even at its maximum, so that the reduction itself is also comparatively slight. Here also, however, as in the deciduous trees, the greatest reduction is in the uppermost twig, and the least in the trunk, though the difference is trifling.

The minimum period ends by the end of February, when starch begins to regenerate all through the inner phloem. By mid-March the starch content reaches a level approximating that of the preceding late autumn, but a further increase is recognized until late March, when the spring maximum is attained in all portions.

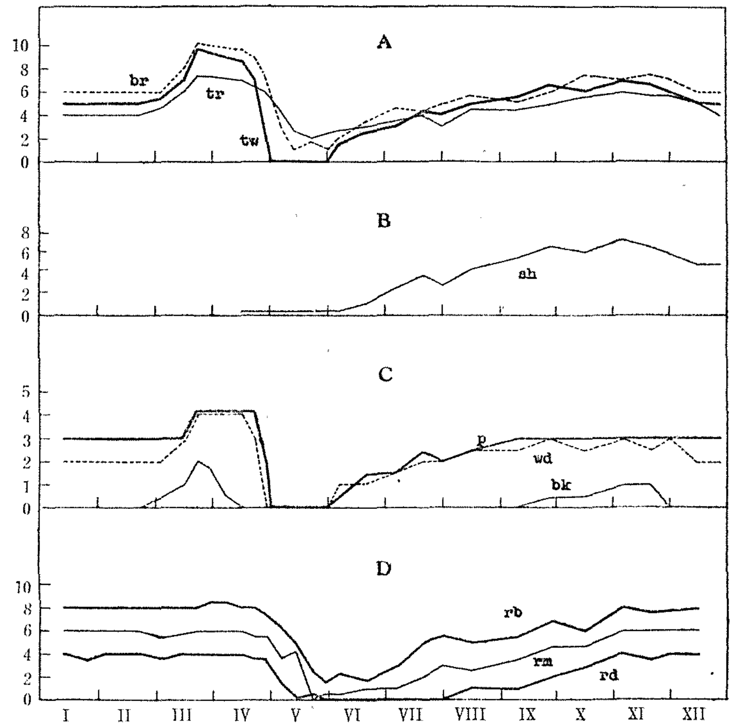

Fig. 6. *Quercus glauca.* Seasonal starch distribution.
A–B. Stem parts. C. Twig tissues. D. Roots.

Unlike the deciduous trees, the starch content in *Quercus* is thus the highest just before the bud swelling throughout the year. In all parts starch develops largely in the wood and pith, but only poorly in the bark.

After the awakening of growth all stem parts lose their starch slowly until the last week of April, then rapidly until the spring minimum is reached in mid-May. The decrease occurs basipetally along the axis: in the trunk the minimum is attained some three weeks later than in the uppermost twig (graphs in A). It is also seen that the starch dissolution is complete only in the upper portions, while in the main stems it is far from complete. In all cases, starch disappears in the following sequence; the inner bark, outer bark, outer wood, inner wood, and finally the pith.

The general features of starch depletion in spring are thus quite similar to those which have been described for the deciduous species. In those cases, the slow drop of starch in spring is related to the slow growth in the same period, and the subsequent rapid drop is caused by a sudden burst of active growth ; but the same does not hold for *Quercus* at all.

In *Quercus*, even at the beginning of the marked growth, the dislocation of starch is still slow. The rapid decrease is first seen when most of the new leaves have completely opened and the new shoot has generally developed more than half of its full length. In the period of the slow decrease, however, the old leaves are still on the tree and the rapid drop begins about the time when the old leaves are commencing to fall. By mid-May, when the starch reaches its minimum, the old leaves have been wholly displaced by the new ones, and it is at this phase that elongation of growth is over.

The data given above appear to be conclusive in showing that the slow decrease is due to a net gain from the synthesis in the old leaves, and the subsequent rapid decrease to a rapid utilization of the reserve starch for the growth at the time of defoliation, when the synthetic ability is already fading.

From summer to winter. The spring minimum lasts for about two weeks. Early in June starch accumulation sets in generally except in the season's growth: starch increases then gradually, reaching its maximum in late autumn. In the current year shoot starch does not actively increase till late June or early July, during a period of increase elsewhere in the tree above ground. In the bud it appears much later, in late October, and the amount is negligible even at its maximum.

The order of starch deposition is not easily determined, as the distribution and amount is rather irregular in the early period of accumulation. So far as the writer made examinations, however, there is no distinct evidence that it proceeds in any definite direction, i. e., in upward or downward sequence.

The beginning of starch deposition is thus irregular, but after July all parts except the bud show a relatively uniform distribution of it and no appreciable difference in the rate of accumulation. Its order in the tissues is inverse to that of the spring disappearance, but less regular.

The starch content is at the autumn maximum in early November. In the latter part of the month a slight decrease is evident in the bark, particularly towards the young twigs. Further changes, however, are only slight in all portions.

The roots

From winter to spring. In the roots (Fig. 6 D) there is no reduction of starch during winter, the distribution and amount being similar to that of the preceding late autumn. The wood possesses always more starch than the bark as is the case in the stem, while the distribution is more dense than in the stem part.

As in the cases of deciduous trees, a slight reduction is found in the bark of the thickened basal part, though it is not so marked. Then it remains unchanged till about mid-March, followed by a regeneration occurring in the root-crown in late March, and early in April, when all parts show their maximum starch.

Roots examined in the last ten days of April show always the inception of starch depletion. However it is slight and only visible in the innermost phloem up to the beginning of May. Afterwards all parts lose rapidly their starch until the spring minimum at the end of May.

The depletion of starch proceeds from the apices backwards, hence there is a definite basipetal sequence of its minimum (graphs in D). The depletion is rapid in the bark, while slower in the wood, in which, too, starch persists progressively longer towards the center. Usually, it remains almost unchanged in and near the center of the thicker and more basal regions.

Although the first sign of starch dissolution fluctuates more or less according to individual roots, even in the same tree, there is a distinct indication that it begins a week or so later than in the trunk. Accordingly, the minimum comes in the root about ten days late.

It is interesting to note here that in the root-crown the starch maximum in spring is slightly higher than it is initially in the preceding late autumn. A corresponding but smaller increase is also noted towards the thicker part, whilst there is no change in the remaining portions. It seems, then, likely that the small gain of starch may result from the assimilated material being transferred from the leaves downwards. The data, too, seem significant in suggesting the basifugal deposition of starch in the root (see later pages).

From summer to winter. The minimum persists during June, after which a steady increase takes place up to the maximum at early November. In all parts, the starch storage occurs, first in the wood and finally in the inner bark.

The commencement of deposition varies in different individuals. But, all the roots examined during the accumulating period show always a gradually falling amount of starch towards the growing points, suggesting that the deposition is basifugal along their length. Generally, in the root-crown it is visible early in July, whilst in the slender region it does not occur until about mid-August, approximately five weeks later.

From the figures it is also seen that on the whole the starch storage comes later in the roots and is slower than it is in the aerial portion. This may be explained partially by the longer maintenance of growth activity in the root, as has been already stated for the deciduous trees.

Pinus densiflora, SIEB. et ZUCC.

The aerial parts

The starch curves for the stem are given in Fig. 7 D. Here the graphs represent chiefly the fluctuation in the bark, as the starch reserves are mainly stored in this tissue. Others are poor in it.

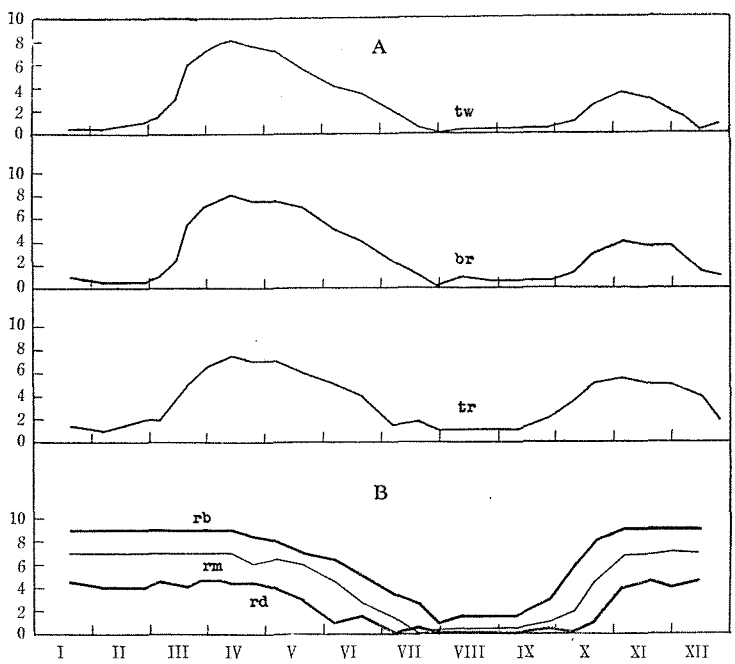

Fig. 7. *Pinus densiflora*. Seasonal starch distribution.
A. Stem parts. B Roots.

From winter to summer. As seen from the figures, there is a conspicuous winter minimum of starch occurring from January to the end of February. During this period all of the twigs and branches are almost entirely free from starch. Even in the base of the trunk, the least decreasing portion, the amount is only small in the wood.

Pinus shows thus the most marked winter depletion of starch among the species examined and undoubtedly belongs to the typical fat tree. Like others, however, there is a rising gradient in starch towards the base of the tree, though it is less regular.

In the early part of March starch is slowly regenerating in the bark. Towards the beginning of April all the stem tissues suddenly fill with starch and by mid-April the spring maximum is attained. The regeneration seems to be uniform along the whole length of the tree.

The spring maximum is the highest throughout the year, and the starch is evenly distributed from the twig to ground-level. The phloem and cortex are very full of starch up to the phellogen, while the wood and pith contain only small amounts in the rays and parenchyma.

From mid-April the starch content slowly drops off to the minimum in August, approximating that of mid-winter. The decrease occurs first in the innermost phloem, whence it spreads slowly outwards and more slowly inwards as the season advances.

The buds are entirely starch-free during winter dormancy, but by mid-April they are densely filled with this material, except in the terminal region where it is entirely absent. The starch then decreases in the buds along with the decrease in the rest of the tree, reaching its minimum by the end of July. Thus in *Pinus*, unlike other species, the spring decrease of starch progresses evenly all over the tree; hence the minimum is reached simultaneously along its length.

It is worthwhile to note that there is no such intimate relation between the mobilization of starch reserves and the mode of growth activity in *Pinus*, as has been found in the deciduous trees. At first the bud (the new shoot) grows slowly from late March to mid-April, then a vigorous growth occurs until mid-May and by the end of May or the beginning of June growth in length is generally over. It will thus be seen that the rapid rise in starch occurs just at the period when slow growth is in progress, and that the major part of extension growth takes place while starch is present in very large quantities all through the tree above ground.

In conclusion it seems clear that in the early period of growth the synthesis of carbohydrate in the old leaves takes place at such a rate that more is formed than is used in metabolism, and that the photosynthetic activity is probably at its maximum from mid- to late spring, slowing down gradually towards the summer months. In other words, the starch curves during the growth period are closely governed by the fluctuations of photosynthetic activity in that period, especially by those in the old leaves.

From summer to winter. Starch is at its minimum in August, being almost totally absent from the young branches and only small in amount even in the main parts. After September it again rises slowly, and early in November it reaches the autumn maximum throughout the tree.

As is shown in the figures, the autumn maximum is much lower than that of spring. Also the difference is less in the trunk when compared with the differences found in the branches. In the trunk, too, there is in the autumn a marked increase in starch towards its base.

The evidence seems to be clear that the order of starch deposition is from the base of the tree upwards. In the tissues, however, no definite order can be detected, the only obvious fact being that starch appears last in the innermost phloem and is often absent in this tissue even at the autumn maximum.

The autumn maximum is again followed by a gradual fall to the winter level. The disappearance of starch commences rather irregularly in various tissues. The reduction, however, proceeds apparently at a greater rate in the branches than in the trunk, so that the latter does not appreciably lose its starch until mid-December, when the upper branches are showing a marked drop.

The roots

From winter to summer. As in all other species, the starch in the roots is practically unreduced in winter except in the proximal part (Fig. 7 D). The bark is very rich in starch, whilst the wood has a much smaller amount.

The trunk below ground and the thickened basal part of the root show a slight reduction in the bark. This is more marked in the trunk just below the ground-level ; above it there is a striking drop in all the stem tissues. The line between the starch-free and the starch-containing parts of the trunk is particularly sharp and coincides exactly with the line of the ground surface.

In early March the starch distribution is in the winter state. Late in the same month it has regenerated in the regions which had shown the winter decrease and the amount is approximately at its autumn level in all parts. In such regions the starch content continues further to rise until early April, when they show a greater abundance of starch than in late autumn. This change is much less conspicuous however than in the aerial portions. The increase is especially evident in the bark of the trunk just below ground where it is about the same as in the aerial stem part. The thickened basal part of the root shows a corresponding but smaller gain, but there is no appreciable change in the remaining parts.

As in the case of *Quercus*, the small gain of starch just mentioned presumably takes place as a result of downward transference of carbohydrate from the leaves. This brings about also the marked rise in the stems in the same period. The fact, too, seems to add support to the view that in the roots the order of starch deposition is from the base towards the apices (see later pages).

From mid-April the starch maximum slowly drops off to the minimum which is attained by the end of July and lasts till about the beginning of September. The disappearance begins in the innermost phloem and from whence spreads gradually both outward and inward.

As shown in the graphs, the decrease goes on generally along with that in the stems, but in the roots it proceeds in a basipetal manner, just as is found with all other species. As a result, the minimum is found, first in the distal region and finally in the thickened foot.

The similarity between the curves for stem and root during the growing period can only be accounted for by the presence of a continuous food supply from the leaves during that period. No measure of assimilation during the period under observation has been obtained, however.

From summer to winter. During the summer minimum starch is nil in all except the thicker portions which retain some in the outer bark and the inner wood. By the end of September starch accumulation has obviously commenced, especially in the thicker and more proximal portions. Afterwards there is a steady gain until early in November, when the maximum is attained all through the root.

The order of starch deposition is regular as compared with that in the aerial portion. It commences in the root-crown and thence proceeds distally (see the graphs). The earliest and greatest accumulation occurs in the bark, and the last in the innermost phloem.

The first deposition in the root-crown takes place about the same time as in the trunk above ground. The subsequent rise, however, is much more marked in the root; hence the starch maximum in the roots is the same as that in spring. Moreover, in the trunk there is now a definite rise in starch towards its base and this basal part is the only place where the amount approaches its spring level.

It is, therefore, safe to say that the accumulation begins simultaneously in the base of the stem and root and works towards both extremities, but the starch produced in autumn is mainly stored in the roots.

(2). **The fat reserves**

The preceding section shows clearly that on the one hand the well known fat trees, like *Tilia* and *Populus*, retain a fairly considerable amount of starch in the trunk throughout the winter, but on the other hand a so-called starch tree, like *Castanea*, loses its starch in the wood as well as in the bark. In other words, the classification into starch and fat trees, as done by FISCHER (1891), is by no means rigid. At least three groups can be distinguished in regard to the fat distribution in the stem tissues at mid-winter.

(1). *Tilia, Populus,* and *Pinus* are those in which fat is present in abundance all through the stem tissues, constituting the main visible reserve during winter.

(2). *Castanea, Robinia,* and *Quercus* are those in which fat is almost confined to the bark.

(3). *Alnus* is intermediate in character between the first and second types. It possesses both fat and starch in the wood, though starch predominates.

General tendency of fat fluctuations is found to be rather similar in all the species studied, though with differences in its distribution and amount. For the sake of brevity, therefore, the data presented here in detail concern only *Castanea* and *Tilia*; the former represents the first group and the latter is typical of the second group. In these two cases the fat curves are constructed for several fixed points on the tree, viz. (A) the one-year-old twig (tw), the five-year-old branch (br), and the trunk (tr), and (B) the new shoot (sh) and the bud (bd). For other species, they are plotted only from the data obtained with the one-year-old twig and the current season's growth, which show the most marked changes. Those for the remaining parts will be assumed from those for *Castanea* and *Tilia*. No graphs are given for the fat in the root, as its amount and changes are not significant.

Castanea pubinervis, SCHNEID.

The aerial parts

The results are given graphically in Fig. 8. In all the branches and trunk the fat is at its maximum from January to March. From the beginning or middle of April it slowly drops off to a minimum in July. Afterwards it rises gradually until mid-winter, when the winter-level is again reached.

It is clearly seen that no corresponding decrease in fat occurs in March when there is a marked regeneration of starch, and no particular increase takes place in the period of starch disappearance in December.

From winter to summer. During the winter maximum all of the branches and trunk contain considerable amounts of fat in the bark especially in the cambial zone and adjacent phloem, whilst none or very little fat is found in the wood and pith. The main stems are relatively richer in fat than the young ones.

Also in the twigs it is noticeable that in spite of the marked

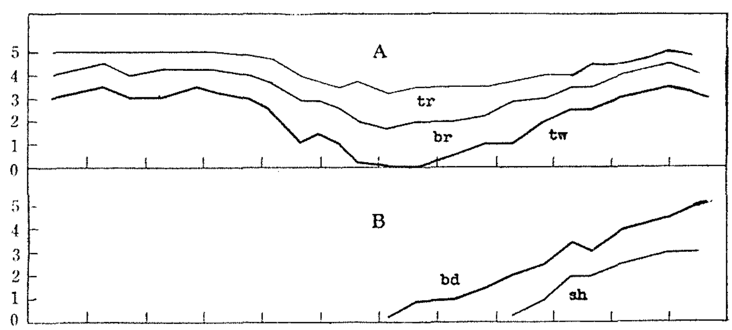

Fig. 8. *Castanea pubinervis.* Seasonal fat distribution in the aerial parts.
A: tw, one-year-old twig; br, five-year-old branch; tr, trunk.
B: sh, current year shoot; bd, bud.

depletion of starch no fat appears correspondingly on the side of the wood. This at once indicates that the starch which disappears at dormancy, at least that in the wood and pith, has been transformed into some soluble substances other than fat. The buds are very rich in fat, while quite free from starch.

The disappearance of fat seems to begin at the awakening of vegetation. By the beginning of April it has gone from the distal portion of the growing bud, but is present in large amount towards the base. In branches and trunk there is yet no sign of disappearance.

When the buds unfold they totally lose their fat. By this time the initiation of disappearance becomes apparent in the cambial cells all through the tree, but otherwise the distribution is unchanged. It is more marked in the region just below the bud on the shoot than elsewhere, and only discernible in the main stems.

After active growth commences all the parts show a slow diminution occurring in the cambial region and in the cells of the bark from the inside outwards progressively. As a result, fat remains longer in the outer phloem than in the inner phloem, and much longer in the cortex than in the outer phloem.

From summer to winter. At the summer minimum fat is quite absent from the last year's twig and almost completely from the two-year-old one. But it is still present from this point downwards and increases in amount gradually towards the base of the tree. The trunk still retains a fair amount and shows only a slight drop occurring mainly in the inner bark.

In the early part of August fat can be always detected in the bark of the young twigs. Though only small in amount, it shows that its accumulation has obviously set in. The accumulation is at first most marked in the young twigs, while in the main stems it becomes discernible after September. There is no order of deposition in various tissues, though apparently it takes place some weeks later in the cambial cells than elsewhere in the bark.

In the new shoot the first appearance of fat occurs in early September, when a very small amount is just visible in the cells near the starch sheath and more particularly towards its base. Afterwards it appears gradually in the whole bark, rising slowly until the maximum is attained in January. In the buds it appears early in July, increasing up to its winter level. The fat accumulation in the bud commences in the distal half and spreads in the basal direction.

It is interesting to note that in the bud the appearance of fat proceeds some two months before that of starch, suggesting clearly that fat is formed independently of starch.

The roots

In the roots the amount of fat is only small even at mid-winter and shows no appreciable changes throughout the year. The greatest amount is in the thickened basal part, beyond which it diminishes gradually towards the distal end where fat is nil. The trunk below ground contains more fat than the roots, though the amount is far less when compared with that in the trunk above ground. Only in this part a slight fall is noticed in summer.

There is thus a striking difference between stem and root in their ability to produce fat, the trunk drawing a boundary between them.

Robinia pseudoacacia, L.

The aerial parts

As in the case of *Castanea*, there is a winter maximum and a summer minimum of fat (Fig. 9). The maximum is maintained from winter to the awakening of growth, independent of the starch regeneration in March. The minimum occurs in early July.

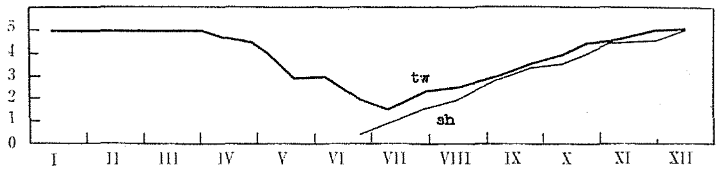

Fig. 9. *Robinia pseudoacacia*. Seasonal fat distribution in the young aerial parts.

During the maximum period all parts show a large amount of fat in the bark. Often, too, very little fat is present in the rays or parenchyma of the young woods. In the bark of the trunk it fades towards the phellogen.

The disappearance starts from the cambial cells and proceeds slowly but regularly outwards; hence in summer there remains a relatively greater amount of fat towards the cortex.

Unlike *Castanea*, fat is never totally absent in summer even in the youngest twig which shows the greatest drop, and increases gradually towards the trunk where it is still present in fair amounts.

By the end of July fat begins to accumulate, more especially in the upper parts. The accumulation seems to occur first in the outer phloem, spreading then slowly into the whole bark.

In the current season's shoot fat appears in late June first in the cells adjacent to the starch sheath of the basal portion. After that it appears in like manner in successively upper regions of the shoot and becomes general by mid- or late August. The deposition spreads from the starch sheath both outward and inward, and finally in the cambial zone.

The roots

The root is very poor in fat throughout the year. The largest amount is in the proximal part, but this is negligible compared with that in the stem.

Quercus glauca, THUMB.

The aerial parts

The whole tree above ground is richest in fat from January to March, and is poorest during July and August (Fig. 10).

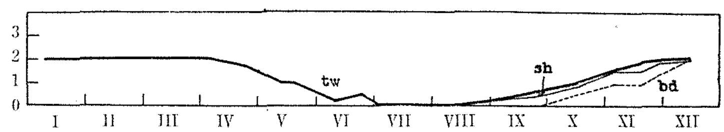

Fig. 10. *Quercus glauca*. Seasonal fat distribution in the young aerial parts.

Quercus may belong to the typical starch tree so-called by FISCHER. Even in winter there is only a small amount of fat in the inner bark. The bud contains a small amount at dormancy; this disappears with its elongation in early April.

During the summer minimum the small branches are entirely fat-free and only traces or very small amount are present in the outer bark of the main stems.

In early September a slight reaction toward fat gain is noticeable in the phloem of the new shoots. The older parts show also the beginning of a steady increase toward the winter level. In the bud it appears in mid-October, rising slowly to its winter level.

The fact that in the bud fat is stored but almost no starch is accumulated towards the dormant period seems to strengthen the theory that the development of fat has no direct connection with the existence or non-existence of starch.

The roots

The roots are usually fat-free except for a minute amount in the proximal portion.

Tilia miqueliana, MAXIM.

The aerial parts

The fat curves (Fig. 11) are similar to those for the trees belonging to the first group. The trend is: a winter maximum which begins in January and lasts till the awakening of growth; a subsequent slow decline to a minimum in July; finally a gradual rise to the winter level. The curves do not reveal any interdependence of fat and starch.

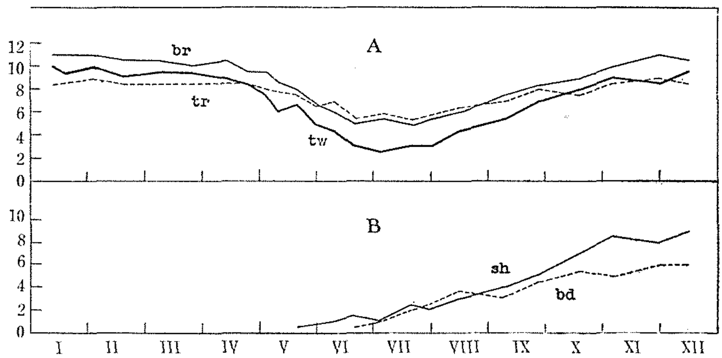

Fig. 11. *Tilia miqueliana.* Seasonal fat distribution in the aerial parts.

From winter to summer. Just before the initiation of growth, fat is found in abundance all through the stem tissues, especially in the inner bark and the young wood, the distribution and amount being the same as that in mid-winter. The vegetative buds are packed with dense fat during dormancy: this begins to disappear with their growth and is totally gone at about the time they open.

The inception of disappearance in the bud is followed by that in the young twigs, whence it seems to be propagated basipetally down the branches to the trunk. Generally, in the trunk there is no change until the beginning of May.

In all parts fat disappears first from the cambial zone, subsequently from the phloem adjoining the cambium. The diminution progresses, however, at a very slow rate in the remaining tissues, especially in the inner wood and pith. It is the slowest and the least marked in the pith, where the amount is the least, too.

From summer to winter. The greatest drop occurs in the youngest twigs but even they retain a small amount in the wood and pith. Further downward, the amount of fat increases gradually until the trunk is reached. This is still rich in the wood and outer bark.

By mid-August a slight rise is evident in the young parts. A corresponding but smaller increase is also noticeable in the older ones. No distinct order of fat appearance was traced however in various tissues.

In the new shoot and the bud fat appearance takes place in the later part of May and of June respectively, followed by a steady gain to the maximum in winter. In the new shoot it begins in the ray cells of the wood, then appears irregularly in all other tissues. It, too, occurs first in the basal region, and thence spreads upwards. In the buds it goes from the tip to the base.

In both of the current shoot and bud the initiation of fat deposition is nearly coincident with that of starch accumulation, but the two progress independently of each other. Especially in the bud it is noteworthy that fat is stored at a greater rate than starch.

The roots

In the subterranean parts, the fat is much less in amount than in the stem. It is greatest in the stem portion, where a fair amount is noted in the bark and the wood. From this downwards it diminishes gradually to the least in the fine roots.

Both in the subterranean stem and the proximal region of the root the amount is slightly high during the winter dormancy compared with that in the summer months, but in the remaining parts there is no appreciable change throughout the year.

Populus nigra, L.

The aerial parts

The fat graph for the twig (Fig. 12) shows a maximum in winter and a minimum during late June to July. Here also there is no evidence showing any direct relation between fat and starch.

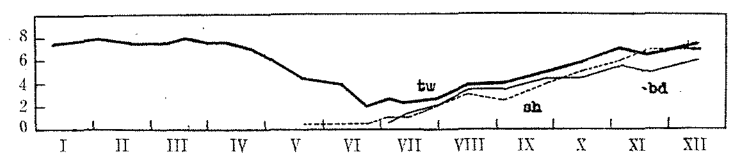

Fig. 12. *Populus nigra.* Seasonal fat distribution in the young aerial parts.

From winter to summer. During the rest period the bark and the woody rays are rich in fat, while the pith is free except in the young twigs. The branches contain more fat than the trunk. In the latter there are minor amounts towards its base.

The inception of fat reduction becomes apparent first in the bud, which possesses a large amount at dormancy, but loses it by its unfolding. The process spreads then further and further away from the bud, until it reaches the trunk where it takes place probably only after the bursting of active growth. In every part fat is resolved first from the cambial tissues, then the disappearance spreads but slowly, particularly in the wood.

From summer to winter. Fat is by no means absent at its summer minimum. Even the youngest twig, the portion of the greatest drop, retains small amounts of fat in the woody rays and the cortex. From this point downward there are less variations as the age of the stem increases. In this it is like in *Tilia*.

By mid-August a tendency to storage is evident in the bark except in the cambial region, and more especially towards the young twigs. After this, all of the branches and trunk become gradually richer in fat until the maximum is attained in January.

The fat appearance in the new shoot occurs in the latter part of May, when the basal portion shows some gain in the woody rays, but none is found in the other tissues. Then it extends to higher regions on the shoot. While it is only slight until the end of active growth, there is afterwards a steady gain to a winter level, leading to fat appearance in all the tissues. In the bud fat appears some weeks before the time of starch appearance and increases at a greater rate than the latter.

The roots

Only large roots show the presence of fat in the cambial region or in the woody rays, although the amount is very poor and nearly unchanged from season to season.

Alnus japonica, SIEB. et ZUCC.

The aerial parts

The fat curve (Fig. 13) agrees essentially with those of all other trees examined, showing a winter maximum and a summer minimum.

All of the branches and trunk possess in winter a fair amount

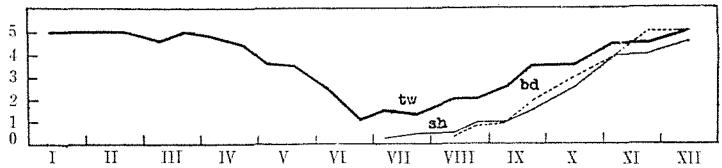

Fig. 13. *Alnus japonica*. Seasonal fat distribution in the young aerial parts.

of fat both in the bark and the wood. Fat is most densely located in the cambial region and diminishes from there both outwards and inwards, the pith being usually free from it. During the winter dormancy the young branches contain relatively more fat than the main ones, but the trunk has less.

As was mentioned previously, nearly all starch disappears in winter from the terminal region of the twig, but no corresponding increase of fat can be detected at all. This indicates clearly an independence of starch depletion from the amount of fat in winter.

During the growth period all parts lose their fats slowly. This is most marked in the twig, though the loss is not complete. Loss is slower in the older branches and slowest of all in the trunk.

The new shoot shows a gain of fat in the woody rays in early July, though the amount is very small and limited to its basal region. Further gain is also small until the cessation of growth, then a steady gain takes place until mid-winter. In the vegetative buds fat is accumulated from late summer to mid-winter, its appearance preceding by several weeks the appearance of starch.

The roots

In the roots fat develops very poorly; only the large ones show its presence in the cambial cells or woody rays, especially in winter.

Pinus densiflora, SIEB. et ZUCC.

The aerial parts

As is shown in Fig. 14, there is a winter maximum and a summer minimum of fat. The maximum is not affected by the starch regeneration occurring in March.

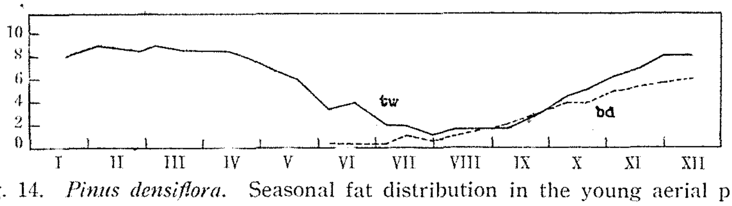

Fig. 14. *Pinus densiflora*. Seasonal fat distribution in the young aerial parts.

During the dormant period all of the branches and the trunk possess very large quantities of fat. Usually, the branches show a greater abundance than the trunk. The winter bud is also packed with dense fat.

At the awakening of vegetation mobilization of fat is always noticeable in the apex of the bud. Correspondingly, the fat in the stems slowly begins to diminish, reaching its minimum in August.

The bud loses its fat comparatively rapidly, while it still retains some throughout the growing season. In branches and trunk fat disappears early from the cambial zone, but persists longer in the outer bark and longest on the side of the wood.

Unlike other fat trees, there is a relatively enormous decrease: hence at the minimum all parts contain only small amounts especially in the wood and pith. The largest variation is in the twigs and the least in the trunk, though the difference is slight.

By the end of September all portions show a slight gain, more especially the upper ones. The appearance of fat occurs rather irregularly in the tissues, but apparently starts later in the cambial cells than elsewhere.

The parallelism between the period of fat disappearance and of starch disappearance seems to be purely coincidental, as there is no evidence showing any special relationship between the two reserves.

The roots

The subterranean parts show a much lower content than the stem. The largest is in the trunk below ground, whence downwards the amount diminishes gradually to the least in the fine roots. The only discernible change occurs in the region shortly below the ground, where it is slightly higher in winter than in summer.

Discussion

The seasonal starch changes in trees

All the deciduous trees studied show that in the branches and trunk there is a distinct starch fluctuation with two maxima and minima, the maxima occurring at leaf fall and just before the bud break; the minima at mid-winter and at the time of active growth. This is essentially in agreement with the results of FISCHER (1891), SWARBRICK (1927), TRAUB (1927), and many others.

Contrary to this idea, and to many data already known, there is GARDNER's observation (1929). He followed the starch changes in Bartlett pear trees throughout the dormant season, using macrochemical methods, and claimed an absence of the second maximum in spring. Up till now, however, no definite case is on record in which a tree under natural conditions has begun to grow without showing a second increase in starch. Furthermore, CAMERON (1923), using microchemical methods, has reported this spring maximum in the same pear tree to take place in February just before the beginning of growth. It is thus clear that GARDNER's statement has little significance when no further data are given. His observations require reexamination.

Both *Quercus* and *Pinus* show also an existence of two maxima and minima for the starch in the stems. Here it is very noticeable that the spring maximum is higher than that of the autumn, and that in *Pinus* the spring maximum slowly drops off to a minimum in August which corresponds to the spring minimum in the case of deciduous trees.

From his researches on the reserve food of trees DU SABLON (1904, '06) concluded that in evergreen trees the gain due to the assimilation compensates the loss due to the formation of new organs, so that the starch minimum is attained later than in the deciduous trees. RAMANN and BAUER (1912) stated that in *Conifers* the dry weight of branches falls more slowly than in deciduous trees. Recently, PREISTING (1930), working with *Ilex*, *Hedera*, and *Pinus*, found that in these evergreens the photosynthetic activity is at its maximum during May and June, and the chief assimilation product is starch.

In the light of these facts, it seems clear that in both cases of *Quercus* and *Pinus* the high spring maximum originates from the active synthesis in the old leaves, and that the slow drop of starch in *Pinus* is ascribable to the adequate food supplies of the leaves.

The roots show, on the contrary, only one maximum and minimum of starch: the maximum persists throughout the rest period and the minimum occurs in the growth period. Only in the transitional region of the stem and root for a short distance below ground, does the starch show a slight winter drop followed by a rise in early spring.

WEBER (1908) found that the starch reserves in the root of *Tilia* persists unaltered during winter. Similar results have been reported by PRESTON and PHILLIPS (1911) for both hard and soft wood trees. On the other hand, WIGHT (1933) showed a winter minimum of starch in the root of *Pinus*, but the figure he gives shows such irregular fluctuations that the existence of the minimum cannot be regarded as established. COCKERHAM (1930) has also asserted it for *Acer*. His paper indicates that both in the root and trunk a winter minimum occurs in late October, whilst in the upper branches it is reached in January, during a period of increase elsewhere in the tree. He shows also that in the trunk and root the fall to the minimum is closely accompanied by a renewed phloem differentiation, which brings the winter minimum. Differentiation of the phloem perhaps may be proportional to the depletion of starch in the case of *Acer*, but it is not usually considered that the phloem differentiation is causally connected with the starch reduction in winter in one way or another. At least, the results of COCKERHAM cannot be said to show the general features of starch changes in the tree under normal conditions.

(a). Starch changes during the rest-period

The starch decreases after the autumn maximum, but not to the same extent in each species. The greatest drop occurs in the so-called fat trees, and the least in the so-called starch trees. The classification, starch and fat trees, however, is of limited significance (see p. 2).

That temperature is of importance in producing the starch changes in winter has long been known by the fact that starch regeneration may be induced even in winter by bringing twigs from an open into a warm place. It has also been shown that exposure to low temperature at dormancy causes a transformation of starch into sugars in woody tissues (NIKOLEWSKI, 1905; GARDNER, 1929; etc.).

On the other hand, the following authors asserted that the starch behaviours in dormancy cannot be explained solely upon the basis of temperature. WEBER (1908) found that the characteristic winter changes of starch cannot be brought about in summer by lowering the temperature, and that starch regeneration occurs in early spring even though the branch of *Tilia* remains under a low temperature (0° C.). He showed also that in the roots the starch is not affected by low temperatures from 2° to −15°C. even at mid-winter. SINNOTT (1918) indicated that the winter changes of starch occur not only in trees growing where the northern temperature is low, but also in trees growing in the frostless region of the Gulf of Mexico. LEWIS and TUTTLE (1923) showed that in leaf cells of *Picea* the first appearance of starch took place on April 5, 1920, even at temperatures below the freezing-point. This occurred after a period of six days, during which the maximum temperature remained below 32° F. and the minimum was −14°C..

In fact, in Kyoto, the starch regeneration in early spring occurs with lower temperatures than those in November when the winter reduction begins to take place. In other words, the former occurred in early March when a minimum temperature of 0.6°C. was recorded and when the maximum was 12.9°C, whilst the reduction commenced at a temperature ranging from 4.1°C. (minimum) to 16.7°C. (maximum).

Further data have shown that in the subterranean portions the starch variations during dormancy are only slight and strictly confined to the regions near the ground-level. This suggests also that some factors other than such external ones as temperature might be responsible for initiating the food changes. The conditions of soil temperature in March when starch regenerates are almost comparable with those found in December when it begins to dissolve, the difference between corresponding levels being less than 1°C., except at the ground surface (see p. 4).

The evidence is thus clear that change of temperature alone is not sufficient to account for the seasonal change in food reserves, though it evidently acts as an accelerator.

Some workers have showed a close correlation between the changes of starch and the activity of enzymes. BUTKEWITSCH (1908) demonstrated an amylotic enzyme in the bark of some woody plants, *Sophora*, *Robinia*, *Caragana*, and *Populus*, and concluded that the starch stored in the stem tissues is transformed into glucose in winter. COVILLE (1920) explained the starch-sugar transformation in plants on exposure to low temperature as an increased permiability of the starch grain to enzymes, thus allowing the hydrolytic catalyst to come in contact with the starch. However he does not explain the regeneration of starch with the increase in temperature. SINNOTT (1918) believed that the character of the food reserve in any cell depends primarily upon the ease with which water, or enzymes carried by water, have access to the storage cell.

These enzyme concepts may explain partially some results reported in this paper, though the evidence does not prove it conclusively ; e. g., in all the trees studied, the starch reduction in winter and its regeneration in spring occur first in the bark and proceed more rapidly in this tissue than elsewhere.

Reasons are not clear as to why the change is more marked in twigs than in the older branches or trunk, nor why in the roots the starch should remain unaltered throughout the period of winter dormancy.

The starch changes at dormancy appear, therefore, not only to be bound up either with mean annual temperature relation or the variation in quantity or quality of the enzymes. In all probability, other inner factors might be suggested as playing some part in the chemical processes of reserve starch.

(b) Starch changes during the growth period

The preceding pages point clearly to the fact that in all except *Pinus*, the spring minimum is attained first in the bud and subsequently in successively lower regions of the stems. This basipetal propagation of the starch minimum seems to show that the starch is transported in wave-like movement from lower and lower portions successively to the actively growing regions during the progress of vegetation.

The order of starch disappearance in the stem has already been discussed for the hardwoods. PFEFFER (1899) quotes T. HARTIG, in the statement that the starch of stems diminishes from above downwards. WOTCZAL (1890) says that in spring the starch transformation occurs basipetally from the tip. Similar results are also obtained by such workers as CAMERON (1923), GARDNER (1925), SWARBRICK (1927), and COCKERHAM (1930). So far as the writer is aware, there is as yet no real evidence of any upward progress of starch reduction in the trees. It seems, therefore, to be conclusive that the order of starch diminution in spring, at least in the deciduous trees, is from the tip downwards.

It is interesting to note in connection with this fact that in the root starch decrease occurs some weeks later than in the stem, and proceeds from the apices backwards. The basipetal progress of starch disappearance in the roots has also been reported by WOTCZAL (1890) and recently by COCKERHAM (1930).

It seems thus likely that in the root the starch is transmitted from the base distally to the growing apices, where it is used up as material for new roots. All the trees, too, show that starch is never totally gone in spring from the large roots nor in the main stem, and the residue is found in increasing amounts towards the root crown. Moreover, at the time when the starch minimum is reached in the young aerial parts the leaves are generally well developed, and are presumably able to provide somewhat for requirements elsewhere. In view of these facts it seems conceivable that the starch reserves in the roots are, at least at first, transported chiefly towards the root spices than upwards to the twigs where it is used up to their growth.

The accumulation of starch is dependent upon, and is correlated with the activity of synthesis and the progress of growth. These two conditions are entirely characteristic through all species, though the accumulation begins at different times in different species, even if they are growing under similar climatic and soil conditions.

As regards the order of starch deposition in the stems the only justifiable conclusion is that starch deposition takes place in various directions and ways according to species, and that it commences later in the season's growth than in the older parts.

HARTIG (1892) and WOTCZAL (1890), who worked on the starch relation in each tree as a whole, showed that starch deposition begins in the base of the tree and proceeds upwards, reaching the terminal twigs last. A similar result has been reported by COCKERHAM (1930) for *Acer*. On the other hand, GARDNER (1925) and SWARBRICK (1927) made observations on one-year-old twigs of Bartlett pear and five-year-old branches of apple respectively, and came to the conclusion that starch accumulation was basipetal in sequence. It is possible that GARDNER and SWARBRICK in making a detailed examination of the younger stems neglected the general features of starch deposition in the trees as a whole.

SWARBRICK is certainly in error in supposing that the downward propagation of starch deposition is closely associated with the basipetal spread of the cessation of radial growth. So far as the writer made examinations, in all cases the cambial activity ceases first in the new shoot and then in successively lower regions on the tree; but starch accumulation begins evidently later in the current season's growth and proceeds at a slower rate than in the remaining parts. (The seasonal activity of the cambium will be fully considered in a later paper).

Analysis of the data reveals that in the roots a wave of starch deposition progresses from the base to the distal end. On the whole it comes later in the roots and is slower than in the stems. WOTCZAL (1890) pointed out that starch accumulation begins in the stump and thence proceeds distally. A similar fact has also been recorded by COCKERHAM (1930) for the root of *Acer*.

Unfortunately, no definite evidence is available to explain the later and slower accumulation of starch in the root system, but this seems to be related with the conditions of growth in the root. It is a generally accepted view that growth activity is apparent in the roots for a much more extended period than in the aerial portions (see PRIESTLEY, 1930). In fact, no one of the trees examined fails to give the same evidence to a greater or less degree.

The seasonal fat changes in trees

All the trees tested have a maximum fat content in winter and a minimum in summer. That fat is most abundant in winter is entirely in agreement with the results of most previous workers.

The work of FABRICIUS (1905) seems to indicate that in the large trunk of *Picea* conditions may be different from those in small trunks, branches, and twigs, and that starch there may have its maximum in winter and fat its maximum in summer. WEBER (1908) also reports that in both *Picea* and *Abies* fat is at its maximum in summer. These findings of FABRICIUS and WEBER seem to be special cases, since the latter shows on the other hand a winter maximum for the fat in the stems of several kinds of deciduous and evergreen trees, and the *Picea* was the only species examined by the first-named author.

As was noted before, some workers (FISCHER, 1891; ANTEVS, 1915; TUTTLE 1919, '21) thought that at the seasonal changes starch is converted directly into fat or fat directly into starch, and that temperature changes produce this effect. These authors have not doubted but that there is a corresponding rise or drop in fat according to the increase or decrease of starch which occur in early spring and early winter respectively. Apparently, however, there is nothing to indicate such a close relationship between the changes in starch and temperature, to the changes in fat. The evidence for the independence of the two former from the latter will be seen from the following facts: (1) The starch regeneration in early spring occurs without causing any appreciable reduction of fat. (2) The starch decrease in early winter does not bring about any corresponding rise in fat. (3) Such trees as *Castanea* and *Alnus* show a marked winter reduction of starch in the wood and pith of the twigs, but not a corresponding rise in fat, to suggest that the starch is transformed into sugars. (4) The accumulation of fat is by no means confined to the cold seasons, but occurs also in summer with high temperatures. (5) In the new shoot and the bud of some species fat appears in late spring or early summer, often before the time that starch appears in them.

WEBER (1908) concluded from his study that fat fluctuations in woody tissues are independent of those in starch, and bear no relation to temperature, but depend upon season. NIKLEWSKI (1905), with cutting branches of *Tilia*, *Prunus*, and *Betula*, quantitatively determined the amount of fats present in the branches before and after exposure to various temperatures from 1° to 22°C.. He could not find any effect from such temperatures on the fat contents in them at dormancy. A similar result was obtained by GARDNER (1929) for pear trees. POJARKOVA (1924) found an inversion of starch into sugar, but reports complete absence of fats in the species investigated, *Berberis*, *Lonicera*, *Amelanchir*, *Acer*, and *Corylus*.

Certainly, therefore, the fat content in trees cannot be connected directly with the changes of temperature (mean annual temperature), nor does it appear to be related to the fluctuations of starch reserves. The annual changes in the two types of reserve food are two distinct seasonal cycles.

SINNOTT (1918) called attention to the existence of a transitory substance from starch to fat, occurring in winter in the bark as well as in the wood, in the cells which had been filled with starch. Similar facts have also been reported by TUTTLE (1921) and previously by SUROZ (1891). In fact, the majority of the plants examined showed the presence of some storage material which did not react positively to the tests for both starch and fat. It is evident chiefly in the early winter and spring, occurring frequently in the cells of the phloem, but is entirely absent during the period of active growth. Various tests were applied, but the identity of the substance was found impossible to determine microscopically. Both starch and fat appear to be accumulated separately, and so far as could be determined, there is no obvious reason to suppose the direct conversion of starch into fat. In all probability, the transitory substance mentioned by SINNOTT is not a stage in the transition from starch to fat, but a transition product from starch into sugars, probably a dextrin-like substance.

All of the trees examined showed that fat disappearance begins upon the awakening of vegetation, and is less marked with increasing distance from the growing points.

KOSTYSCHEW (1926) quotes I. IWANOFF, in the statement that in spring in the bark of various kinds of trees there is a consumption of fat, which is analogous to that occurring in the germinating seeds. Generally, the winter buds contain large amounts of fat at dormancy, but this rapidly disappears as growth commences. Correspondingly, all the stems show the initiation of fat disappearance occurring in the meristematic layer which has resumed its activity. These data seem to lend some support to the KOSTYSCHEW's view that fat is transformed into some soluble substances in spring and utilized in growth.

On the other hand, however, the relation between the major movement of fat and the progress of growth activity is undoubtedly less intimate than the relation of the starch changes to the growth activity. In all cases, the minimum fat content is attained in early or mid-summer, when most of the growth is already over. Moreover, in major instances, fat is never totally gone even from the young twigs, in which the decrease is the most marked, and is still present fairly abundantly in the trunk of such trees as *Tilia, Populus, Robinia,* and *Castanea.*

As a result, it seems preferable to suppose that the fat stored in woody tissues, especially that of the main stems, does not play so intimate a role in plant metabolism as starch, but its changes are associated with the growth cycle, since the amount present falls in the growing season and rises again toward the time of winter dormancy.

In the roots, without exception, the fat is only small in amount, and its fluctuation is so slight that the changes cannot be traced in most cases. WEBER (1908) pointed ont that the root of *Tilia* contains only small amounts of fat which remain constant throughout the year. SINNOTT (1918) has also said that fat is very poorly developed in the roots of woody plants even in winter.

Concerning the underlying causes which determine the difference between stem and root in their ability to produce fat there is nothing to say from our present knowledge.

Summary

A study has been made of the distribution and seasonal changes of both starch and fat reserves of trees in Kyoto. The observations were carried out upon five deciduous and two evergreen species (*Castanea pubinervis,* SCHNEID.; *Alnus japonica,* SIEB. et ZUCC.; *Robinia pseudoacacia,* L.; *Tilia miqueliana,* MAXIM.; *Populus nigra,*

L.; *Quercus glauca*, THUMB.; *Pinus densiflora*, SIEB. et ZUCC.). In every case, both aerial and underground portions were investigated. The following results, unless stated otherwise, hold for all of the species studied.

The starch reserves

1. In all of the deciduous trees, the starch curve, for all aerial parts, shows a maximum when the leaves are falling or a little before it and a secondary maximum at the time just before the bud break. Minima occur at mid-winter and when the leaf growth is vigorous.

2. The starch reserves in the roots of deciduous trees show a maximum at leaf fall which is maintained during the rest period, and a minimum in the growing season. In the trunk below ground, and in the proximal foot of the root proper, however, there is a slight winter drop followed again by a regeneration in early spring.

3. The starch curves for *Quercus*, both for stem and root, agree fairly closely with those for the deciduous trees, except that the spring maximum in the stems is higher than that in late autumn.

4. *Pinus* shows starch fluctuations of its own, which have two maxima and two minima in the aerial parts and one maximum and one minimum in the roots. In this case, however, the spring maximum in the stems occurs at the time when growth is in progress, and is very much higher than that of autumn. The following minimum is reached by the end of July, when the starch in the roots is also just at its minimum.

(a) The aerial parts

5. The winter depletion of starch occurs first and most rapidly in the phloem-cortex. It tends to become slower and lesser in degree as the ages of branches and trunk increase.

6. The starch regeneration begins in the inner phloem, and as far as could be determined, begins uniformly throughout the tree above ground, at the end of February or the beginning of March.

7. The spring disappearance of starch commences also in the innermost phloem and thence spreads outwards, then inwards.

8. The spring minimum of starch is attained first in the buds and then successively in lower regions of the twigs, branches, and trunk. In the case of *Pinus* the minimum is reached simultaneously in all parts.

9. The disappearance is complete in young branches but incomplete in main branches and trunk.

10. The deposition of starch occurs at very different times and in different ways according to the species. The order of deposition in various tissues is as follows: for *Castanea*, *Alnus*, *Robinia*, and *Quercus*......pith, wood, cortex, phloem; for *Tilia* and *Populus*...... cortex and outer phloem, wood, pith, and inner phloem in the order named. *Pinus* shows no definite order of deposition. In all cases the innermost phloem is the last to be stored with starch.

11. The order of starch deposition along the length of the tree is as follows: in *Castanea, Alnus, Robinia, Tilia,* and *Pinus* the order is from the base of the tree upwards. The upward propagation of deposition is especially shown clearly by *Alnus, Castanea,* and *Pinus.* In *Populus* the deposition takes place at first in a basipetal sequence, then uniformly along its whole length. No obvious order can be detected in the case of *Quercus.*

12. All the trees except *Pinus* show that starch is accumulated later in the current season's growth than in the rest of the tree above ground.

(b) The roots

13. In general, the roots are some weeks later both in the commencement of starch decrease and in the attainment of its minimum in spring, than is the case with the aerial portion. In the root of *Pinus,* however, the starch decreases in amount generally along with that in the stems.

14. The depletion of starch proceeds in a wave-like movements from the apices backwards.

15. The accumulation of starch begins in the root-crown, at or shortly after the time it begins in the base of the trunk, and thence works on distally. On the whole, however, the accumulation comes later in the roots and is slower than in the aerial portion.

16. The order of both starch decrease in spring and of its increase in summer in the root tissues is similar to the order found in the stem tissues, but it is less regular.

The fat reserves

17. The fat content in the aerial parts is at its maximum from mid-winter to the time of the awakening of vegetation, and at its minimum in the summer months.

18. The changes in the fat seem to be independent of the changes in the starch.

19. The disappearance of fat seems to begin upon the awakening of growth in spring. It is most marked in twigs, less so in older branches and least of all in the trunk. It is, too, more marked in the inner bark than anywhere else and in other tissues.

20. The majority of the species examined show the presence of a fair amount of fat even in the summer minimum, although a few species contain only a small amount of it. The amount is fairly considerable in the trunk of such trees as *Tilia*, *Populus*, *Robinia*, and *Castanea*.

21. The accumulation of fat is never confined to late autumn or early winter, but begins in summer with its high temperature. This is particularly evident in the shoot and bud of the current year.

22. The fat content in the root is small and the amount decreases with increasing distance from the thickened basal part which contains the greatest quantity.

23. In the root the amount of fat remains almost constant throughout the year. The only appreciable variation is noted in the cases of *Pinus* and *Tilia*, which showing a slight summer fall in the root-crown.

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