Journal of the Minnesota Academy of Science

Volume 25
Number 1 *Vol. 25/26*

Article 20

1957

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The Structure and Development of the Bark of Quaking Aspen[1]

The object of this investigation is to provide more information than is currently available concerning the histological composition of the bark of *Populus tremuloides* Michx. Chang (1954) has made the most comprehensive study of the bark of American pulpwood species. However, he examined relatively few samples of bark and has not given much attention to the development of the different tissues as the age of the tree increases. Aspen bark is now included in certain fiber products. Also, increased attention is being given to the utilization of aspen bark because its removal and disposal are costly. It is important, therefore, that we have a better understanding of the structure, composition, and changes that take place in the development of the bark of this important pulpwood species.

MATERIALS AND METHODS

Several aspen trees, ranging from six to nine inches in diameter at breast height, were cut at different times at the Forest Research Center, Cloquet, Minnesota. Bark samples along with sapwood were taken from each tree at eight-foot intervals starting at breast height. The age at the base of each section was recorded. Twigs of age from one to five years were also collected. Both celloidin and paraffin methods were used to prepare the microscopic sections. Living samples taken from the base of each section were killed and fixed with strong chromic-acetic-acid (Johansen, 1940) followed by ethyl alcohol as the dehydrating agent prior to embedding in celloidin. Similar samples

[1]The authors wish to express their gratitude to Professor E. C. Abbe and Miss A. Hansen of the Department of Botany, University of Minnesota, for their review of this manuscript. This paper is published as Scientific Journal Series Paper No. 3938 of the Minnesota Agriculture Experiment Station, Institute of Agriculture, St. Paul, Minnesota.

destined for paraffin embedding were fixed with Zirkle's reduced chromic fluid (Johansen, 1940) and dehydrated according to Lang's series (1935). The celloidin- and paraffin-embedded material were cut with sliding and rotary microtones, respectively. The sections were stained with haematoxylin and safranin or fast green.

The measurements were made on sections from the celloidin method. The relative amounts of different tissues were measured by the transect method. Cross and radial sections were projected on a screen and then ten equally-spaced radial lines were laid across the central portion of the projected image from the cambial zone to the surface of the bark. The radial extent of each tissue was determined along each of the ten equidistant radii. The total distance from cambium to surface of bark was likewise determined along each of these radii. Therefore, it was possible to obtain the average percentage of the radial distance from cambium to surface occupied by each of the tissues. In measuring the dimensions of perivascular fibers, the macerated bark of one-year-old twigs was used. The dimensions of the secondary phloem fibers were measured from macerated material of older bark.

OBSERVATIONS

The bark of aspen has a persistent periderm with relative smooth surface on young stems (Fig. 1A), but it becomes furrowed on older stems (Fig. 1b) and frequently at the base of young trees. When the bark is smooth, it is greenish-white to cream in color, becoming dark brown or gray on rough bark. Lenticels are found on the smooth bark while the rough bark is fissured.

Aspen bark, depending on the age, consists or varying combinations of epidermis, periderm, cortex, perivascular elements and secondary phloem. The structure and development of each of these tissues are discussed in the following sections:

The epidermis: The epidermis (Fig. 2,E) is a primary tissue and is a single layer of cells in thickness. The outer tangential wall is thicker than the inner tangential wall. There is a thin, continuous, translucent layer of cutin on the outer surface of the epidermal cell (Fig. 2, U). Only immediately adjacent to the terminal bud is the epidermis continuous and unbroken, except for the occasional lenticel. As the

twig increases in diameter with the onset of secondary growth, the epidermal cells do not divide to accommodate to the increase in girth of the stem. By at least the end of the first growing season the epidermis has become broken adhering only in fragments to the subjacent cork cells. It is usually absent in a two-year-old twig. The epidermal cells are tabular in shape and, on the average, are 15.7μ in tangential diameter and 11.00μ in radial diameter as they appear in the cross section of the stem. Fig. 2 shows the broken epidermis of a one-year-old twig immediately after the beginning of growth for the second year. In contrast note the absence of the epidermis in Fig. 3 which shows the complete bark of a two-year-old main stem at the end of the second growing season.

The periderm: The first phellogen is formed before the twig is one year old. It completely encircles the twig and is formed from the layer of cortical parenchyma immediately below the epidermis. The phellogen cells (Fig. 2, 3 and 5, N) are tabular and as viewed in transverse section of the stem have their long dimension in the tangential plane. They are filled with dense protoplasm and are thin-walled. As a result of cell division in the phellogen, layers of cork cells are laid down centrifugally while phelloderm is formed centripetally. The thickness of the phelloderm layer is limited to, at most, one layer of cells (Fig. 3 and 5, H). According to Metcalfe and Chalk (1950) layers of lignified phelloderm are usually found in the bark of *Populus*. At least for the smooth bark of quaking aspen such lignified phelloderm is lacking. The first-formed cork cells (Fig. 2, M) are cubical in shape, while the later formed cork cells are more or less flattened radially (Fig. 3 and 5, M). Cork cells produced by the phellogen continue to increase until the layer of cells is about 10 or more in thickness. Table 1 shows that the average number of cells per radial row of cork in aspen twigs increases with age.

TABLE 1—*The average number of cork cell per radial row in cross section of cork of aspen twigs.*

Age of twig, years	1	2	3	4	5
Average number of cells per row[1]	5.1±0.5[2]	6.2±0.5	8.0±0.6	8.8±0.2	10.±0.9

[1]The averages represent 10 rows in five twigs for each of five trees.
[2]Standard deviation computed from the five trees measured.

Smooth bark on the stems five or more years old usually has about ten cells per radial row of cork layers. These cells are rectangular in shape when viewed in cross section and are formed in radial rows which indicates that all cells in a given row are produced by the same phellogen cell. The diameter of the cork cells is 20 to 25μ in the tangential direction and 10 to 20μ in the radial direction. It is obvious that the first-formed cork cells could not continue to keep the cork tissue intact for any extended period of time. The phellogen cells must continue to divide radially in order to provide for the tangential expansion of the cork cambium. The newly formed phellogen cells then function to keep the layer of cork intact, as the stem increases in diameter through the yearly production of xylem and phloem. The old surface cells are gradually sloughed off as new tissues are added beneath. Light scrapings from the surface of aspen bark show numerous cork cells either entirely separate or in small clusters. This accounts for the chalky appearance on the surface of aspen bark and explains why the bark remains smooth over a long period of time. New cork cells are added by the phellogen layer as the old cork cells are sloughed from the surface, this keeps the layer of cork cells fairly constant in thickness. As the tree grows older the bark generally becomes rough at the base. This condition may gradually extend up the tree as it increases in age and size. According to Kaufert (1937) rough bark is an abnormal condition in aspen and is caused by irritation from outside agencies such as lichens, fungi and mechanical injury. Rough bark begins to form when the first-formed periderm ceases to function. Subsequent phellogens are then formed from pre-existing parenchyma cells in the cortex and eventually into the secondary phloem. The period of time during which these later-formed phellogens continue to function is not known. It is probable that each functions for at least one growing season or until a new phellogen is formed beneath it, at which time the older phellogen matures into permanent tissues. The surface of the older bark then becomes fissured. The bottom of each fissure is always sealed by layers of cork cells. The later-formed phellogens are irregular in their formation and perhaps never encircle the stem. As they form deeper in the previously pre-existing permanent tissues, they cut off patches of the old cortex, perivascular fibers, and eventually, secondary phloem which thus become a part of the dead tissues in the rhytidome.

The cork cells from the later-formed phellogens in rough bark are cubical in shape (Fig. 4, M) with an average of 31μ in diameter and comparatively thin-walled with large empty lumens. On the inside of each zone of these cork cells and radially coincident with them occur two to three cells, the inner of which is probably phelloderm (Fig. 4, H) and the one between cork and phelloderm represents matured-off phellogen (Fig. 4, N). The phellogen and phelloderm cells are approximately 28μ in tangential dimension and 8μ in radial dimension. Successive layers of cork cells, phellogen, phelloderm and isolated portions of secondary phloem (Fig. 4, P) are usually found in the rough bark.

The cortex: The cortex is a primary tissue lying between the epidermis or the first-formed periderm and the perivascular region. The cortex is composed mostly of parenchyma irregularly arranged in the young twigs. In addition, there is a collenchymatous region, several cells deep, immediately under the epidermis, subsequently beneath the periderm. In a one-year-old twig the parenchyma cells (Fig. 2, O) are more or less oval in cross-section averaging approximately 22.5μ in the tangential direction and 13.3μ in the radial direction with a radial gradient in size from the outer portion toward inner part of the cortex. There are no fibers in the cortex but sclereids, often in groups of two to four, are present primarily at its periphery (Fig. 2, I).

The cortex is quite well defined so long as the bark remains smooth. According to Eames and MacDaniels (1947) it increases in diameter through the radial division of the pre-existing cortical parenchyma. However, the increase in size of cortical cells, especially in their tangential dimensions, also accounts in part for the increase of the girth of the cortex. As the result of radial division and tangential extension, the cortical cells in mature bark show more or less alignment in the tangential direction (Fig. 3 and 5, O). The tangential dimension of the cortical cells continues to increase for a few years. In a two-year-old twig, cortical parenchyma averaged 29.6μ, 41.7μ for a four-year-old twig and 42.9μ for the older bark. The radial dimension also increases slightly from 13.3μ in a one-year-old twig to 23.2μ in the five-year-old or older stems. That there is an increase in the number of cells in the cortex is supported by direct counts of number of cells in girth of axes of different ages. There are approxi-

mately 25 cortical cells in the girth of a one-year-old twig, 332 in a two-year-old twig and 452 in a four-year-old twig. There is no evidence of crushing of the cortical cells with increase in age until new phellogens arise.

The perivascular region: Between the cortex and the secondary phloem is a region in which isolated groups of fibers are frequent. These fibers are referred to here as perivascular fibers following the usage of Van Fleet (1948). The first-formed secondary phloem ray extends practically to these fiber groups. There is no significant difference in the number and dimensions of the groups of perivascular fibers between twigs of different ages. Table 2 shows the results of these measurements:

TABLE 2—*The number and dimensions of perivascular fiber groups of aspen twigs.*[1]

	AGE OF TWIGS IN YEARS				
	1	2	3	4	5
Average number of perivascular fiber groups	18.7	20.7	19.2	24.0	24.8
Tangential dimension of perivascular fiber groups (μ)	168	158	155	110	133
Radical dimension of perivascular fiber groups (μ)	36.0	36.6	33.8	31.9	37.6

As the stem grows in diameter the perivascular fiber groups become further separated by multiplication of the parenchyma cells included within them. Traces of these fibers have been found in bark of an eleven-year-old stem (Fig. 5, G). They may become distorted to such an extent that they appear to be partially oriented in the radial direction. The spaces between the fiber groups are filled with cells resembling those of the cortex and except for these fiber groups of perivascular zone in the older stem loses its identity. It may eventually be lost entirely through deep development of phellogens. According to Chang (1954) the fibers in the "primary phloem" (that is, perivascular fibers) are not so heavily lignified as those in the secondary phloem. Based on color reaction through staining there is very little evidence for this belief. The perivascular fibers from one-

[1]Measurements were made on five twigs of each of the ages from each of five trees.

year-old twigs were found to be 765± 152μ in length and 12± 3μ in diameter. The dimensions of these fibers, both length and diameter, are only about one half those of the secondary phloem fibers.

The secondary phloem: The structure of the secondary phloem is more complex than that of any of the primary tissues. In the secondary phloem are found sieve tubes, companion cells, phloem parenchyma, fibers, sclereids and phloem rays. Near the cambial zone and during the season of growing the sieve tubes are rectangular to polygonal in cross section and 20 to 40μ in diameter (Fig. 3, C). During the second and subsequent years the sieve tubes become flattened radially with an increase in the tangential dimension due to the radial pressure and tangential tensions developed in the bark. In some cases the sieve tubes may be completely collapsed (Fig. 3, S'). Companion cells always accompany sieve tubes. They are variable in shape and are from 10 to 15μ in diameter. Phloem parenchyma cells fill the space between sieve tubes and fibers and sclereid groups. During the first season they are round or oval and 20 to 30μ in cross section. Due to increasing bark pressure these cells later become flattened with the largest dimension oriented tangentially. Secondary phloem fibers are formed in distinct continuous or intermittent tangential bands during the growing season except in the one-year-old twig. It appears that at least one band of phloem fibers is formed each growing season. Fig. 5 shows groups of sclereids formed from parenchyma between the fiber groups within the fiber band. These bands of fiber and sclereids are often continuous for a considerable distance tangentially and are broken only where the phloem rays are present. The fibers are thick-walled, lignified and average about 1,026 ± 55μ in length and 22 ± 17μ in diameter. The secondary phloem fibers are slightly less than twice the linear dimensions as the perivascular fibers. Crystalliferous parenchyma cells are frequently found on the margin of the fiber bands. These often form a more or less continuous sheath around the fiber groups or are scattered as individual cells. These cells have thicker and more intensely lignified walls on the side next to the fibers.

During the first season after formation the phloem rays are strictly uniseriate and straight radially. These ray cells, in cross sectional view, vary from 60 to 100μ in the radial direction and 10 to 20μ in the tangential direction. In the tangential sections the ray cells are

more or less circular in outline and about 10 to 20μ in tangential diameter. During the second and subsequent season after formation the rays become distorted and the individual ray cells are somewhat compressed radially. Moreover the ray cells may begin to divide in radial plane so that the rays become biseriate or multiseriate (Fig. 6). After division the daughter cells enlarge tangentially so that they become 20 to 45μ in length in the radial direction and 50 to 60μ in the tangential direction. As might be expected there is little or no change in the vertical dimension of the ray cells. Development in this way is in response to the radial pressure within the bark and to consequent tangential increase in the extent of secondary phloem as the tree continued to grow in circumference. Ray parenchyma cells between the phloem fiber groups frequently develop into sclereids. The increase in tangential diameter of secondary phloem rays along with the enlargement of very young sclereids provides almost entirely for the tangential increase of the secondary phloem. Also in the older phloem these rays blend in with the parenchyma of the pericyclic region and the cortex to such extent that it becomes difficult to delimit one from the other with precision. So long as the bark remains smooth, however, isolated groups of perivascular fibers can often be distinguished and the approximate inner limit of the cortex can be determined in this way. The tangential enlargement of the phloem rays tends to distort all other remaining secondary phloem tissues separating them into patches or groups. Sclereids are frequently formed abundantly in the outer portion of the secondary phloem. Most of these sclereid groups arise from the phloem rays. The individual cells are generally very irregular in shape, thick-walled and with simple pits (Fig. 7, T) and frequently with crystal deposits within the cell lumen. Fig. 8 shows a radial section of the inner portion of aspen mature bark.

The relative proportion of tissue elements in aspen bark changes with the roughness of bark and the age of bole from which the bark is taken. Structurally, the mature aspen bark may be divided into three distinct layers. The outer layer is phellem or cork. It is brown in color, thin and fairly easy to peel off when the bark is smooth. The second layer includes the phelloderm, cortex and perivascular region. The outer part of this layer is green in color due to the presence of the chloroplasts in the cortical cells (Chang, 1954). The inner layer is

secondary phloem. The relative proportion of the above three layers in smooth bark averages as follows:

TABLE 3—*Average relative proportions of different tissues in smooth aspen bark.*[1]

Layer	Tissues	Relative proportion (%)
Outer	Phellem	2.06±1.39
Second	Phelloderm, cortex and perivascular region	24.39±4.88
Inner	Secondary phloem	72.56±5.42

The fibers and sclereids make up 8.54 ± 2.24 and 13.88 ± 4.00 percent of volume of mature aspen bark respectively. When the bark is young as in the one or two-year-old twigs, it is composed of about 10 percent of phellem, 30 percent of cortex, 15 percent of perivascular region and 45 percent of secondary phloem. It is obvious that the secondary phloem continues to increase in amount as the tree grows and thus the other tissues will decrease in relative proportion. However, the relative proportion of phellem in the older bark shows a wide variation. In general, the bark of old trees or the bark at the base of the tree tends to have high percentage of phellem (Fig. 9 and 10). The phelloderm, cortex and perivascular region as well as the secondary phloem do not change significantly in relative proportion after the tree is over ten years old. This is due to wide variation in relative proportion of such tissues even though the bark is of same age. The fiber content in aspen bark does increase with the age of the bole from which the bark is taken (Fig. 10).

SUMMARY

Bark structure and development of quaking aspen have been studied histogenetically. Epidermis is present only in one-year-old twigs. Periderm starts to develop in the first growing season. Periderm develops from the outer portion of cortex and continues to function so long as the bark remains smooth. In the rough bark, phellogens may develop from the inner portion of cortex or even from the secondary phloem parenchyma. The increase in girth of cortex in response to the diameter increase of the stem is through the radial division of the pre-existing cortical parenchyma and the tangential extension of the

[1]The averages were obtained from five sections of each of five trees. Each average is followed by its standard deviation computed from five trees. The ages of these trees range from 20 to 35 years.

cortical elements. The perivascular region is easy to identify in the young twigs by locating the perivascular fiber groups. As the tree grows old, the perivascular region merges with cortex and secondary phloem parenchyma and ray cells. The scattered perivascular fiber groups are the only traces of the perivascular region in the old bark. Secondary phloem is composed of fibers, sclereids, phloem rays, sieve tubes, companion cells and parenchyma. The fibers often form tangential bands. Sclereids develop more abundantly in the outer part of the secondary phloem. Sieve tubes function only in first one or two growing seasons. They gradually collapse due to the pressure resulting from the growth of stem. The increase in girth of secondary phloem is through the radial division of ray cells and tangential extension of all parenchymatous elements. The change in dimensions and relative proportion of different tissues and tissue elements with the age have also been observed.

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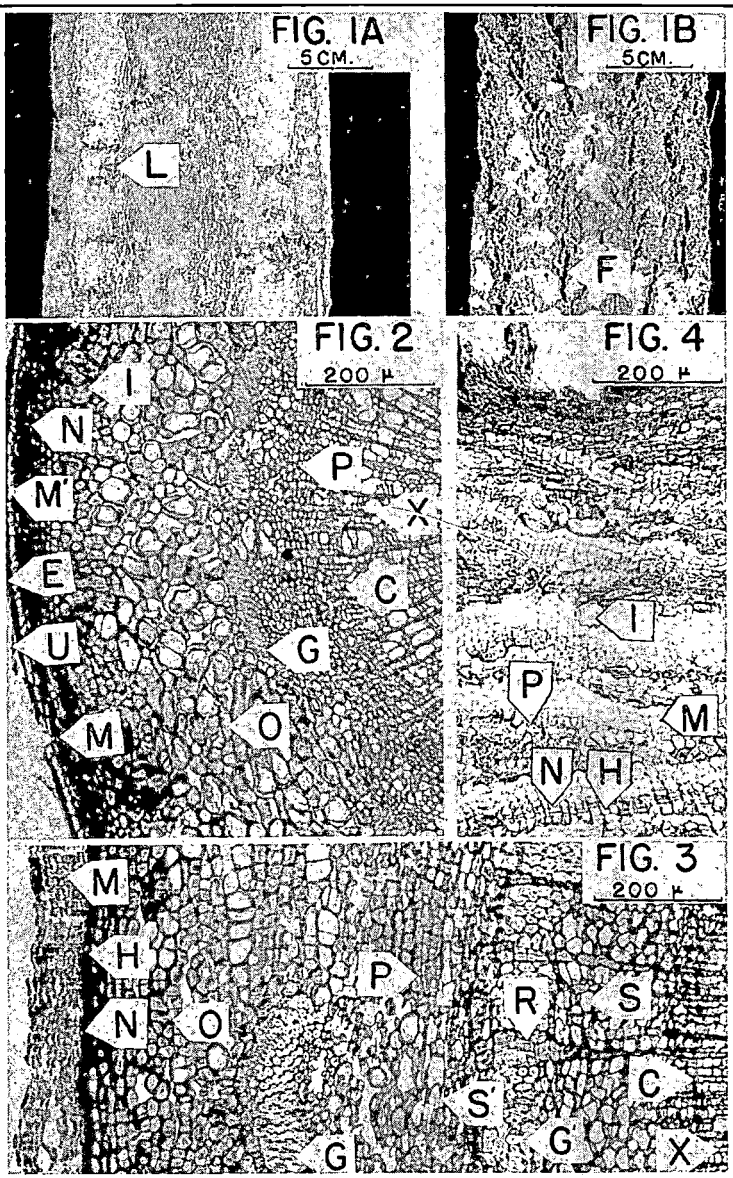

Fig. 1A Aspen smooth bark.
Fig. 1B Aspen rough bark.
Fig. 2 Cross section of one-year-old aspen twig immediately after the initiation of growth for the second season.
Fig. 3 Cross section of the bark of a rapid growing two-year-old main stem.
Fig. 4 Cross section of a rough aspen bark.

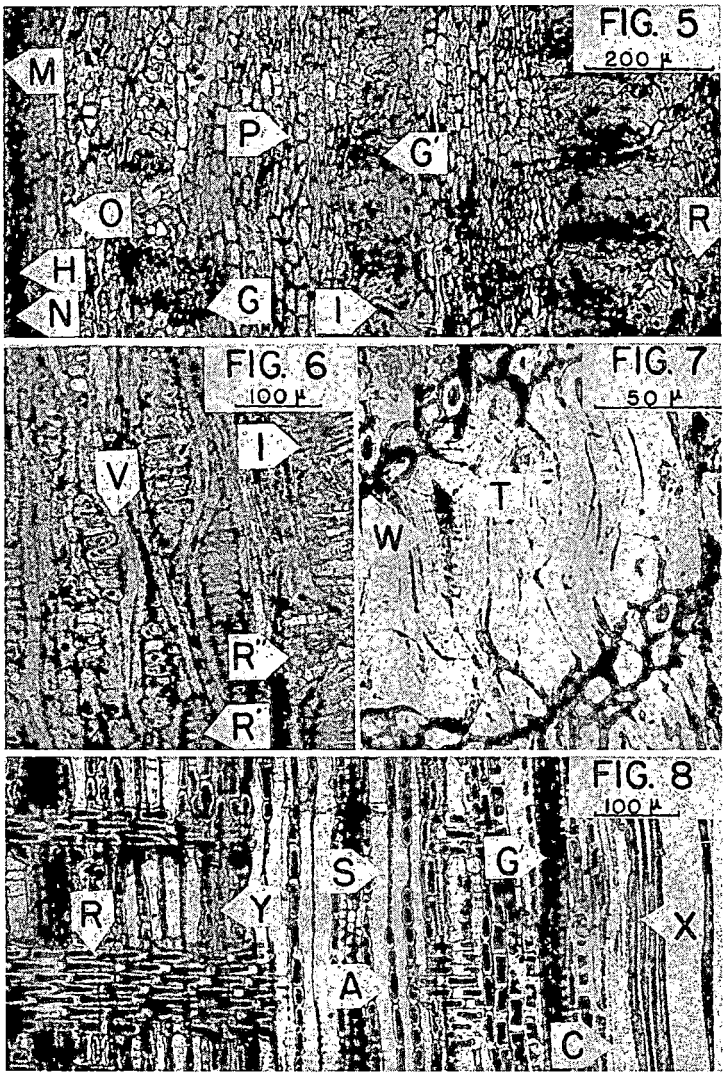

Fig. 5 Cross section of the outer portion of an old smooth aspen bark.
Fig. 6 Tangential section of the older portion of secondary phloem.
Fig. 7 Cross section of sclereid group in the secondary phloem.
Fig. 8 Radial section through inner phloem.

A, companion cell; C, cambium; E, epidermis; F, fissure; G, perivascular fiber group; G', secondary phloem fiber strand; H, phelloderm; I, sclereids; L, lenticel; M, phellem or cork cell; M' first-formed phellem; N, phellogen; O, cortex;

P, secondary phloem; R, phloem ray; R', uniseriate phloem ray; R'', multiseriate phloem ray; S, sieve tubes; S', flattened sieve tube formed during the first growing season; T, single pit; U, cuticle layer; V, intervening tissues pushed out of alignment and even broken by the enlarging phloem rays; W, thick cell wall of sclereids with many layers of secondary thickening, X, secondary xylem; and Y, phloem parenchyma.

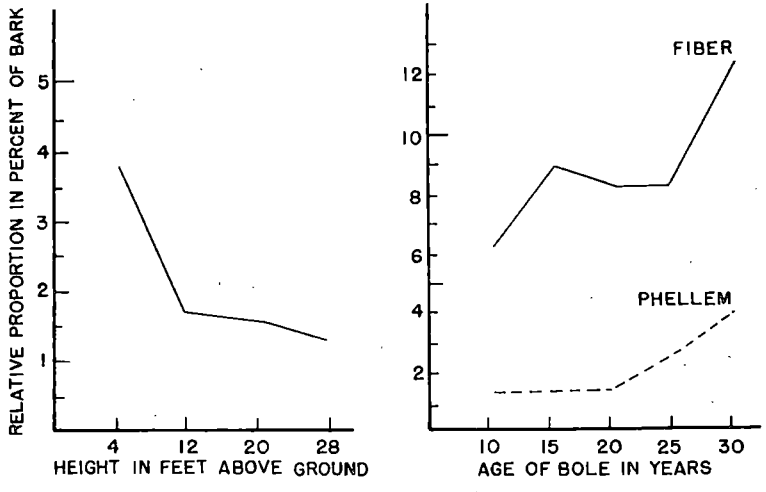

Fig. 9 Relative proportion of phellem in aspen bark taken at different heights of tree.

Fig. 10 Relative proportion of phellem and fibers in aspen bark taken from boles of different ages.