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INCIDENCE AND STRUCTURE OF GELATINOUS FIBERS WITHIN RAPID-GROWING EASTERN COTTONWOOD

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ABSTRACT

An intensive investigation of samples taken within the stems of two 21-year-old *Populus deltoides* Bartr. trees growing rapidly under plantation management revealed that the percentage of gelatinous fibers in the wood ranged from 0.51–97.87. All positions sampled had some gelatinous fibers even though the trees were selected from within the plantation for their dominance, straightness, freedom from lean, and outstanding form. The incidence of gelatinous fibers was particularly high in the upper bole even though the distribution of gelatinous fibers followed no set pattern. In most cases no gelatinous fibers were observed in the last several tangential rows of the latewood cells, but some were associated with vessel elements. Gradations in structure and chemical composition seemed to be related to the position in the tree. Ultrastructurally, the gelatinous fibers were characterized by the absence of an S_3 layer, and a G-layer with a high degree of longitudinal orientation that was loosely attached to the secondary wall. The high incidence of gelatinous fibers in these nonleaning trees suggests that lean may not always be the most important factor in tension wood formation, especially when the whole tree is considered, and that other factors must be involved. It is suggested that the incidence of gelatinous fibers may be of particular importance in the utilization of topwood in cottonwood and in whole trees grown under intensive management.

The gelatinous fibers of tension wood in hardwoods are nothing new to wood scientists; they have been recognized since the late 19th century. The occurrence of gelatinous fibers in many hardwood species and their macroscopic and microscopic anatomy have been reviewed by many authors (Hughes 1965; Onaka 1949; Perem 1964). In addition, there has been much research on the chemical properties (Timell 1969), and ultrastructure of tension wood (Côté and Day 1962; Côté et al. 1969; Mia 1968).

The anatomical, physical, and chemical properties of gelatinous fibers are known to have unfavorable influence on the properties of wood and wood products in which they occur. For example, tension wood is known to be difficult to saw and machine (Wahlgren 1957). In addition, tension wood exhibits excessive longitudinal shrinkage and irreversible collapse during seasoning (Arganbright et al. 1970; Pillow 1953) and is known to have many adverse effects on papers made from its pulp, particularly with respect to their strength properties (Dadswell et al. 1958).

Tension wood, usually characterized by gelatinous fibers, occurs typically on the upper side of leaning and crooked stems and branches (Arganbright and Bensend 1968; Kaeiser and Boyce 1965; Manwiller 1967), although it can occur in straight trees, particularly in *Populus* (Kaeiser 1955).

Also, it has been suggested that tension wood can be associated with rapid growth (Berlyn 1961; White and Robards 1965).

Most researchers, however, have concentrated on either horizontally grown seedlings or on the upper sides of stems and branches of leaning trees. Often, they have restricted their sampling to only one position in the stem. Little research information seems available on the occurrence of tension wood throughout the whole tree and, especially, in straight trees exhibiting rapid growth. Such information seems necessary in light of recent emphasis on complete tree utilization and more intensive management aimed at increasing growth rate.

The objectives of this study were to characterize the within-tree variation of the percentage of gelatinous fibers and to determine their distribution and structure in two straight stems of eastern cottonwood growing rapidly under plantation management.

MATERIALS AND METHODS

Two eastern cottonwood (*Populus deltoides* Bartr.) trees growing rapidly under plantation management were harvested from a Mississippi River floodplain near Ashburn, Missouri. The trees, which were selected from within the stand for their straightness, freedom from lean, and outstanding form, were approximately 16 inches DBH, 21 years old, and 95 feet tall. From each tree, eight cross-sectional discs were cut at approximately 8-ft intervals up the tree, and alternate two-ring samples were cut from pith to bark and stored in 70% alcohol as described by Isebrands (1972). Several 20-μ transverse sections were cut with the sliding microtome from each of the 62 two-ring samples collected from each tree and were stained with phloxin-fast green and chloriodide of zinc.

Percentage of gelatinous fibers

The percentage of gelatinous fibers was determined by projecting the sections onto the attachment screen of an A-O Microstar microscope on which three randomized squares were superimposed. Ten projections of the three squares were observed for each two-ring section. The projections were taken systematically with a ramdom start by using a combination of radial and tangential movements (Isebrands 1972). The percentage of gelatinous fibers was then found by dividing the number of fibers that possessed gelatinous layers by the total number of fibers in the thirty squares and multiplying by one hundred.

Gelatinous fiber structure

The structure of the gelatinous fibers was investigated by light, electron, and scanning electron microscopy. For light microscopy, small samples of known positions in the tree were stored in 70% alcohol and postfixed with 2% osmium tetraoxide in a 1:1 phosphate buffer (pH 7.4) and embedded in an epon-araldite resin mixture. From these samples 1-μ-thick sections were cut with the ultramicrotome. For electron microscopy other samples were postfixed with Palade's buffered osmium and embedded in a Maraglas resin mixture. Thin sections (700 Å) were cut from these samples with the ultramicrotome and observed with the RCA-EMU 3 electron microscope. For scanning electron microscopy sliding microtome sections 100-μ thick were cut from certain samples and allowed to air dry. These sections were then coated with a 100-Å-thick layer of gold and observed with the Cambridge Stereoscan scanning electron microscope at 20 kv.

RESULTS AND DISCUSSION

The presence of large numbers of gelatinous fibers on the upper side of leaning and horizontally grown hardwood trees has been well documented. Although gelatinous fibers apparently occur in all cottonwood trees, their number can be minimized by selecting for straight trees with good form (Boyce and Kaeiser 1964). In this study the trees sampled were selected from within a plantation for their dominance, straight-

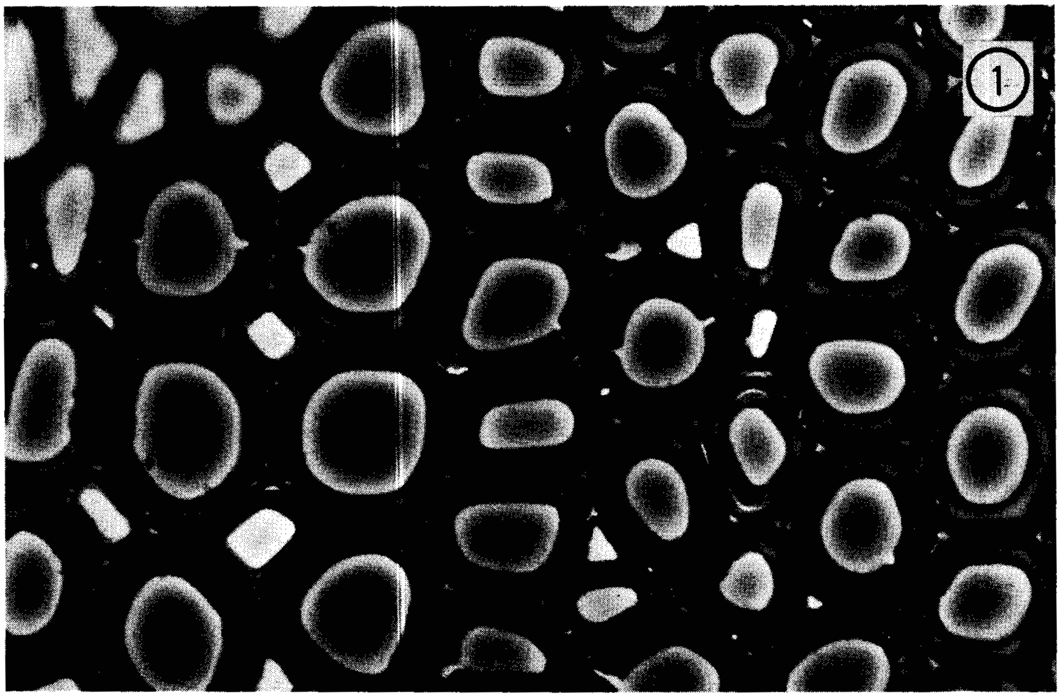


FIG. 1. Transverse section (1μ) taken from the crown showing numerous gelatinous fibers with *G*-layers ($1000\times$).

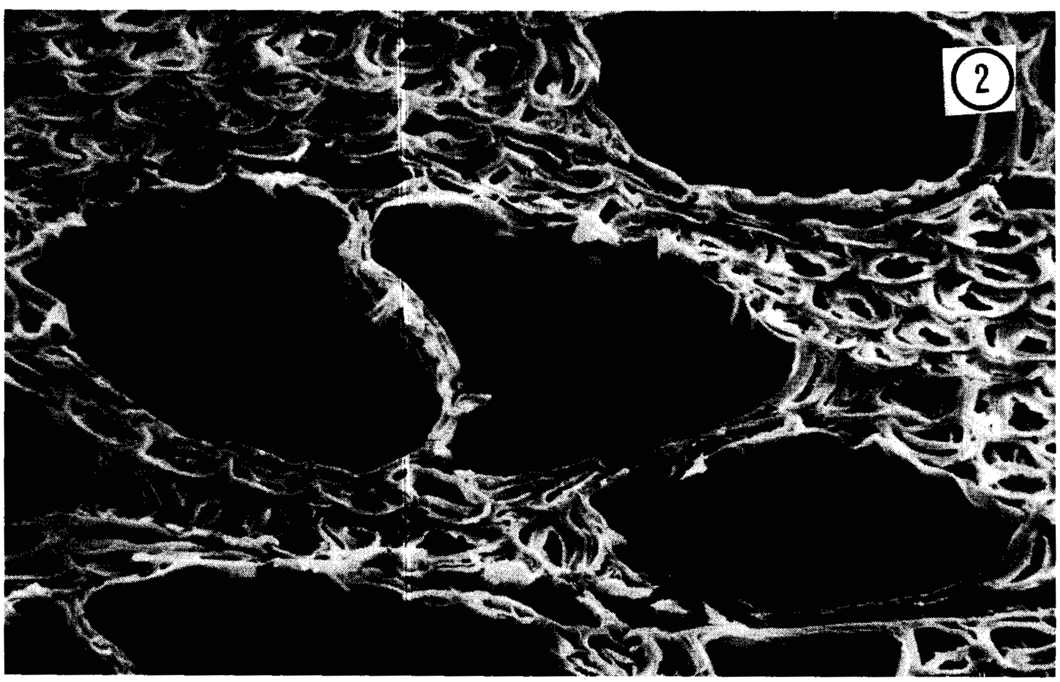
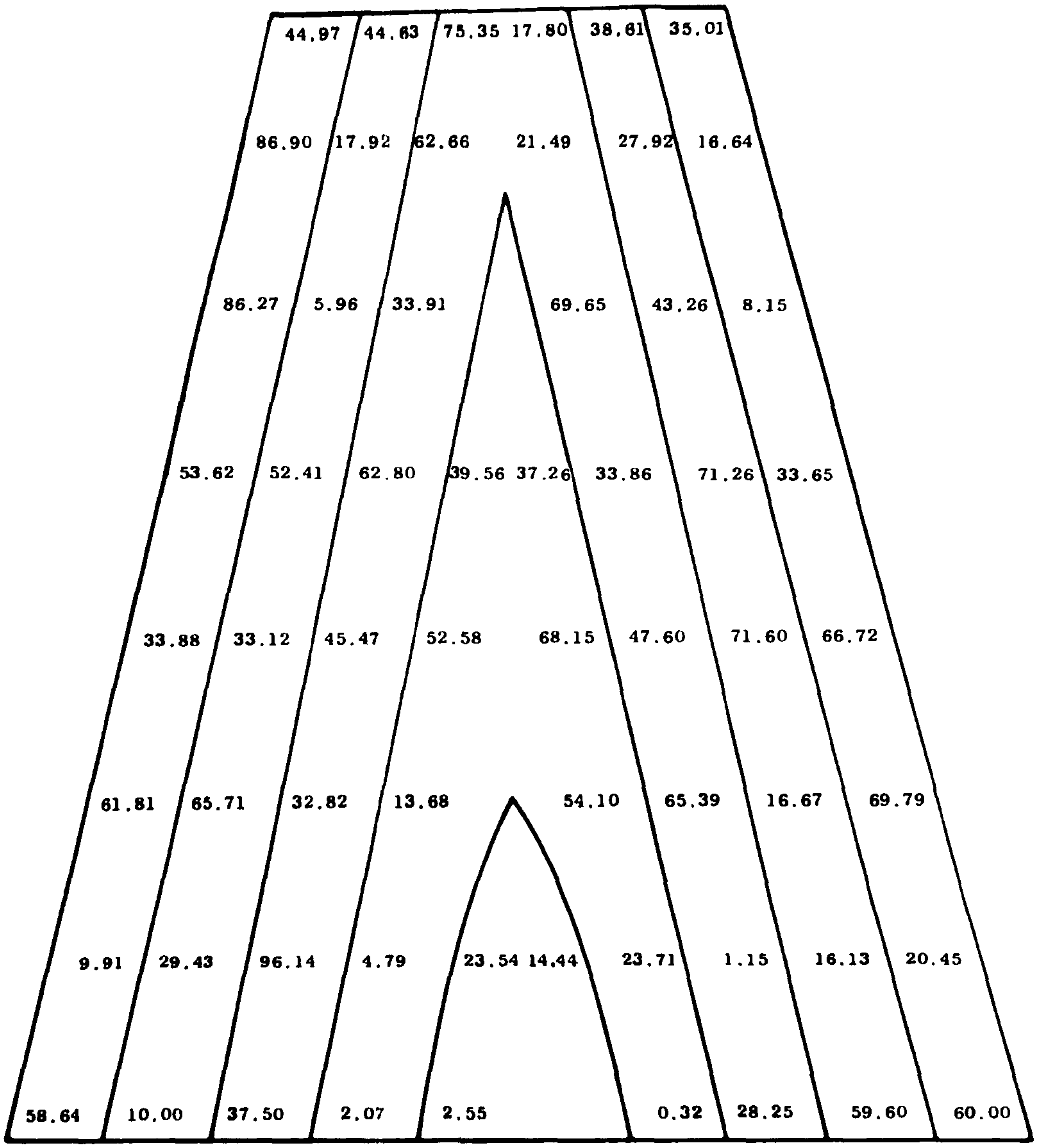


FIG. 2. Scanning electron micrograph showing vessels surrounded by gelatinous fibers ($825\times$).

TABLE 1. *Sampling positions and the percentage of gelatinous fibers within the two trees.* (A) *Tree 1* (B) *Tree 2*

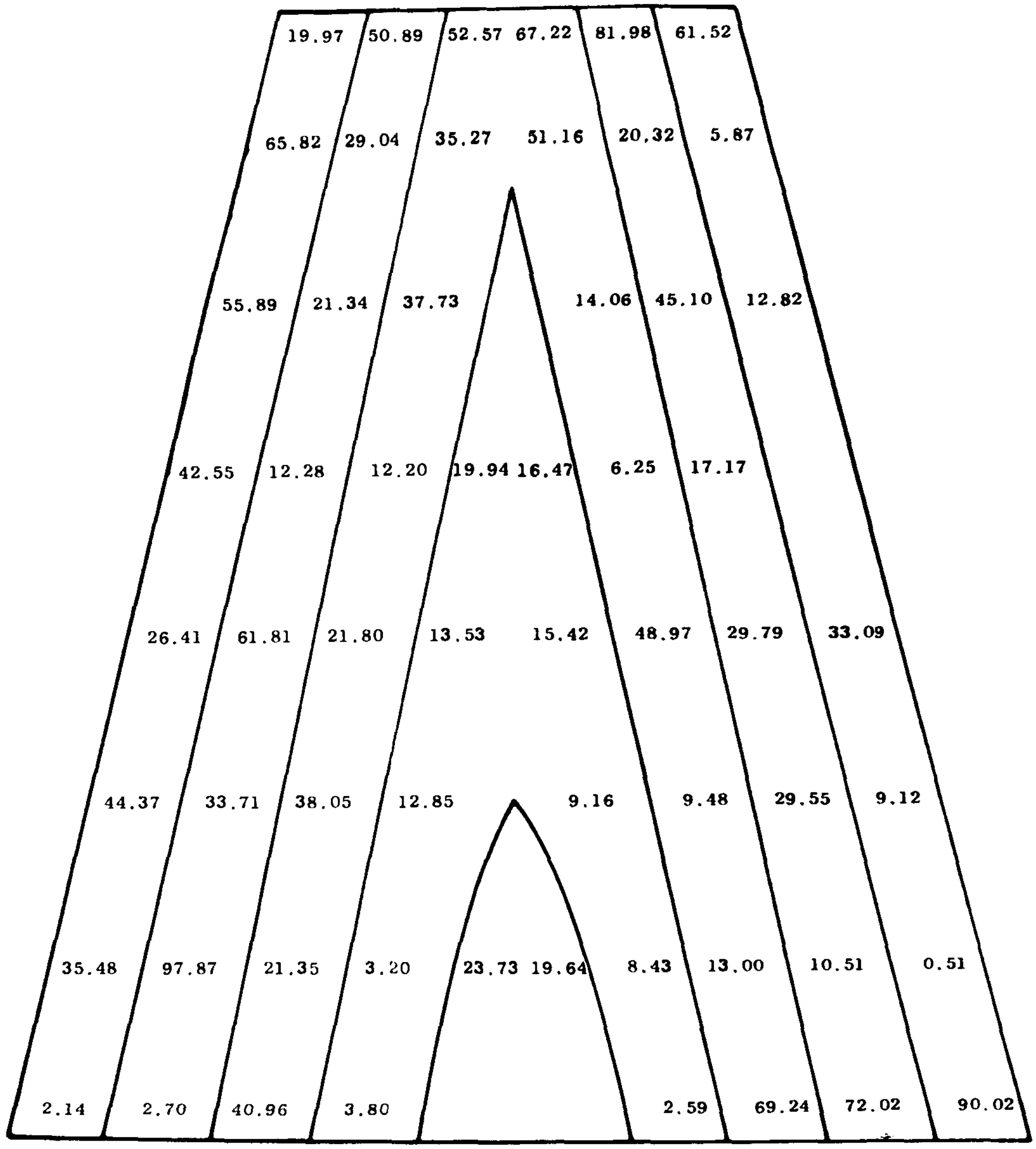


ness, freedom from lean, and outstanding form.

Despite these selection criteria, the incidence of gelatinous fibers within the trees was high and extremely variable. The percentage of gelatinous fibers ranged from 0.51 to 97.87, and every position sampled within the trees had some gelatinous fibers (Tables 1 and 2). Their number was so striking that many positions were remeasured on matched sections as a check, and the results were comparable each time.

It is evident that the incidence of gelatinous fibers in these trees followed no regular pattern. Often, at a given height, one side of the annual ring had a high

TABLE 1. Continued



percentage of gelatinous fibers and the other side a low percentage; whereas at the next sampling height, the same annual ring showed the opposite circumstance. Occasionally, both sides of the annual ring had a high percentage of gelatinous fibers (Tables 1 and 2), while in some instances, the whole annual ring was made up of gelatinous fibers. Although some gelatinous fibers occurred singly, others could often be recognized on the circumference tangential to them. In addition, tangential bands of gelatinous fibers were common.

Gelatinous fibers were particularly abundant in the section of the tree bole formed in the crown (Fig. 1). In contrast, fewer gelatinous fibers were present in the wood formed while the tree was young, even in

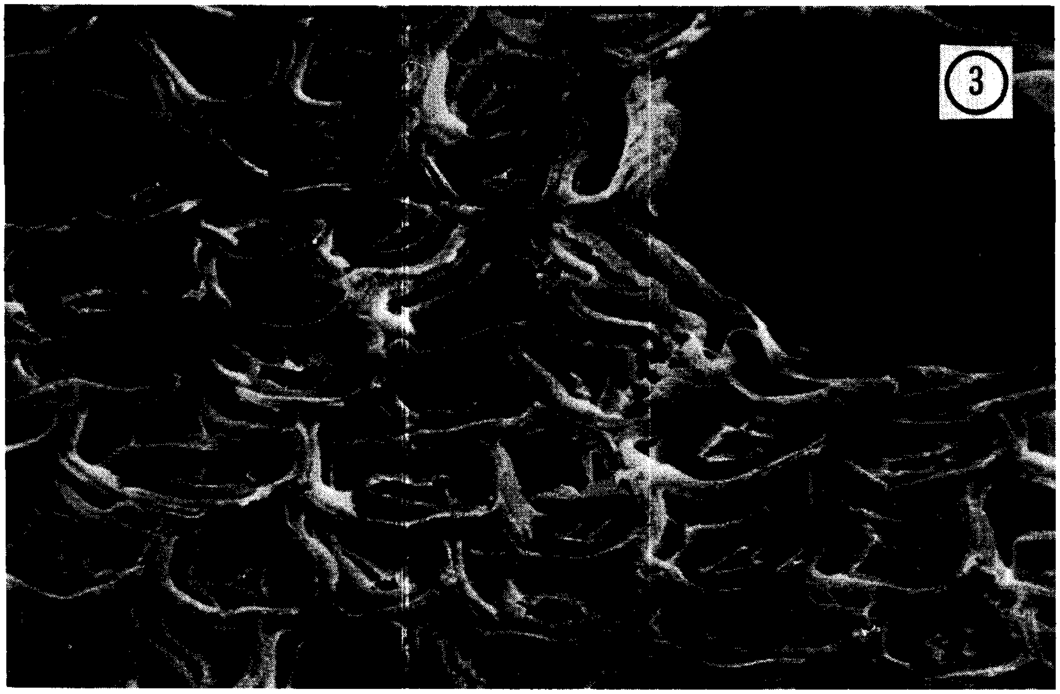


FIG. 3. Scanning electron micrograph taken from an upper crown position showing gelatinous fibers with thick *G*-layers (1650 ×).

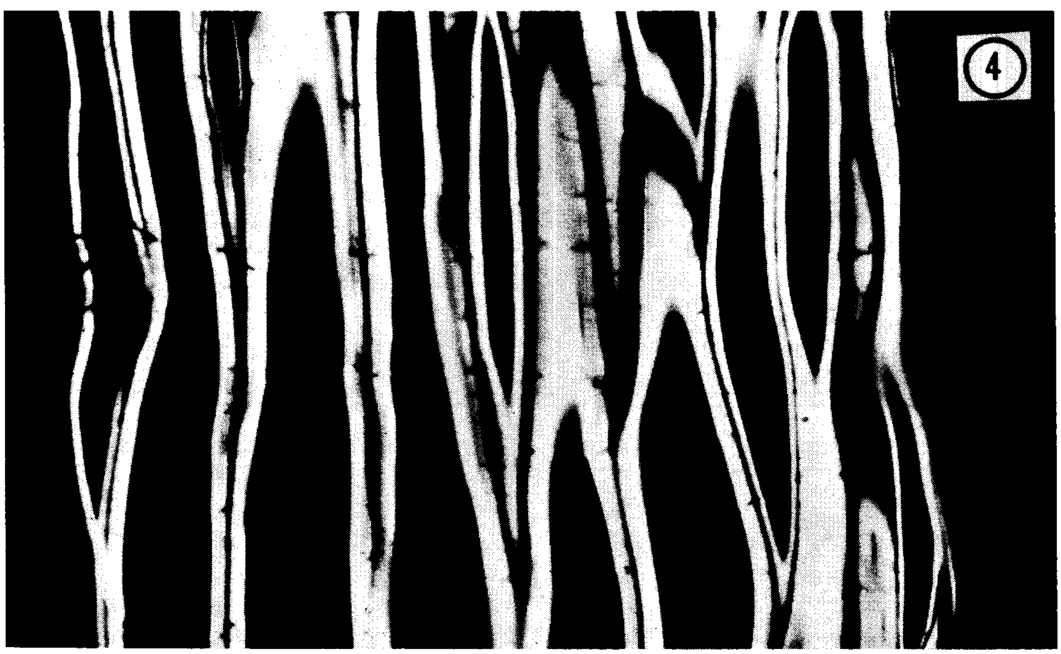


FIG. 4. Radial section of gelatinous fibers with *G*-layers in the cell ends and numerous slip planes (640 ×).

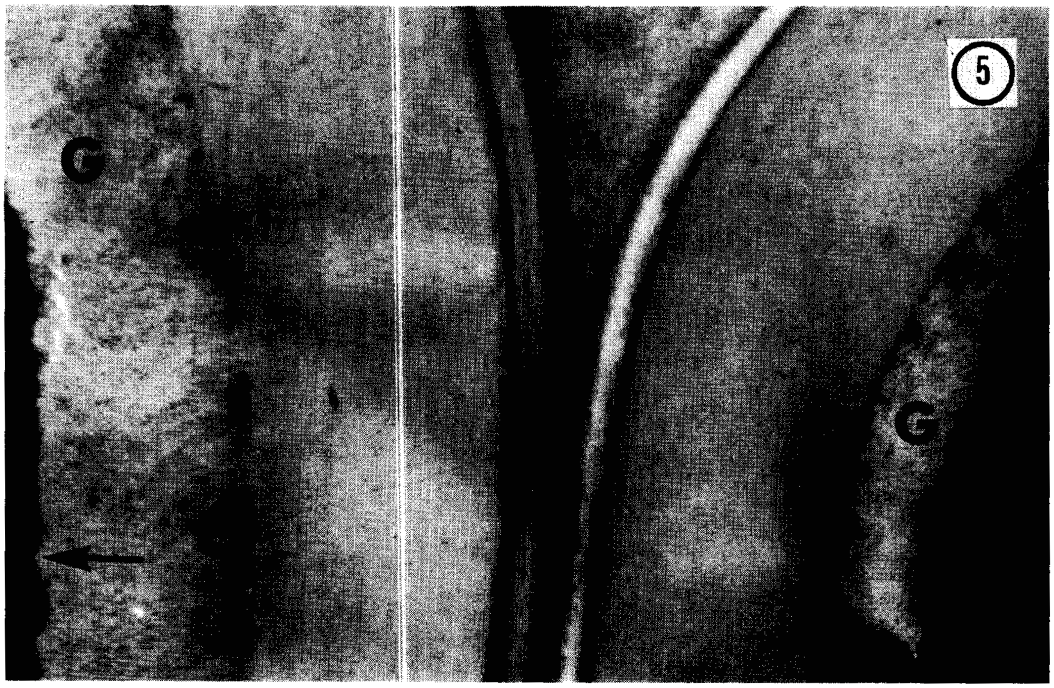


FIG. 5. Transmission electron micrograph showing porous G-layer (G) attached to the S_2 layer of the cell wall and warty layer (arrow) (40,500 ×).

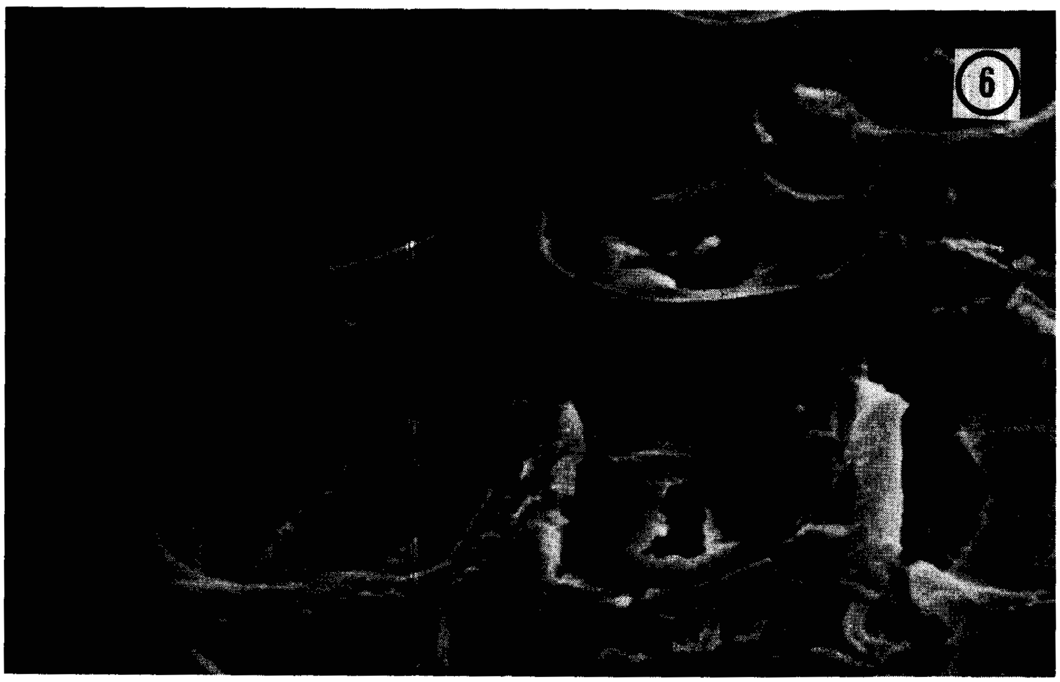


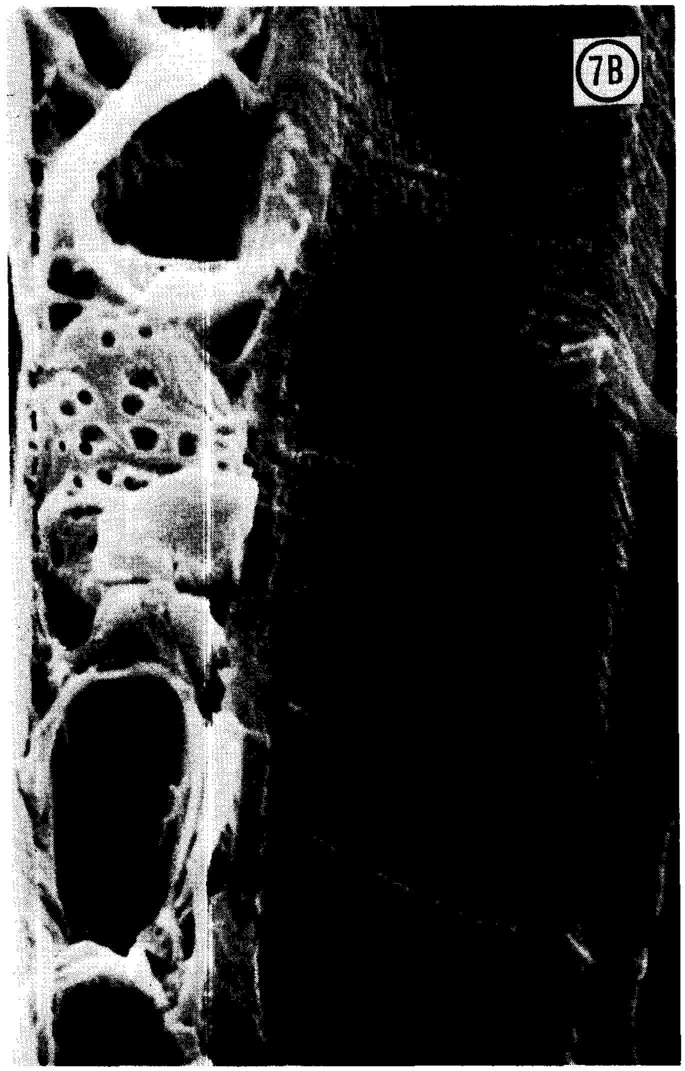
FIG. 6. Scanning electron micrograph showing G-layers loosely attached to the secondary wall due to mechanical damage caused by sectioning (3300 ×).

FIG. 7. Scanning electron micrograph of a tangential view of gelatinous fibers showing slip planes and minute compression failures. (A). 750 × (B) 3000 ×

crown formed wood (Table 1). This suggests that the crown may influence gelatinous fiber formation as the tree ages.

It is generally accepted that, in certain hardwood species, gelatinous fibers are not present adjacent to vessel elements (Côté et al. 1969). In this study, however, vessels were often completely surrounded by gelatinous fibers (Fig. 2). In addition, very few gelatinous fibers were present in the last 5–6 tangential rows of cells in the latewood portion of the annual ring as shown by Berlyn (1961).

Preliminary information suggested that there was no close relationship between the percentage of gelatinous fibers and radial, tangential, and longitudinal shrinkage (Isebrands, unpublished), which was contrary to the findings of Arganbright et al. (1970). These data led to a more detailed investigation of the variation in G-fiber structure. We felt the lack of correlation of these physical properties with the per cent of gelatinous fibers could have been caused by gradations in structure and chemical composition as well as by the distribution



of gelatinous fibers (Kaeiser and Boyce 1965).

Gradations in structure of the gelatinous fiber seemed to be related to position in the tree, and the structure of the gelatinous fibers formed in the crown seemed to be different from those formed in the rest of the tree. The gelatinous layer (G-layer) was thickest in the tension wood of the upper crown (Fig. 3). In addition, at a given height, the G-layers usually were thicker in the more recently formed wood near the bark. This implies that the structure of the gelatinous fiber varies with age of the tree. Also, the G-layer was often thick and well developed at the cell ends (Fig. 4).

Microtome sections removed from 70% ethyl alcohol were placed on slides and treated with two drops of chloriodide-of-zinc. The cover glasses were applied and sealed with beeswax.

After 10 to 15 minutes the reaction of chloriodide-of-zinc also indicated gradations in the chemical composition of the G-layers, which were related to the position in the tree. G-layers found in the upper crown were most heavily stained. The gradations in structure and chemical composition observed in these trees may be related to the proximity of a segment of a given growth increment to available hormones and photosynthates produced in the crown.

The ultrastructure of the gelatinous fibers observed was characterized by the absence of the S_3 layer of the secondary wall, a *G*-layer with a high degree of longitudinal orientation, and a warty layer (Fig. 5). The *G*-layers resembled those shown in aspen by Mia (1968) and in beech by Côté et al. (1969) and, in some instances, had a porous texture (Scurfield 1967). The *G*-layer was loosely attached to the secondary wall and was particularly susceptible to the mechanical damage caused by sectioning (Fig. 6). Côté, et al. (1969) also have shown similar damage. This damage is evident by the groups of microfibrils that extended from the gelatinous layer to the remaining secondary wall (Fig. 6). The gelatinous layer also exhibited many slip planes (Fig. 4) and minute compression failures (Fig. 7A,B), which agrees with the work of others (Wardrop and Dadswell 1948; 1955). These failures represent areas of the cell wall that have folded under stress.

Although gelatinous fibers have been identified in straight *Populus* trees, their abundance has been largely associated with lean. The extremely high incidence of gelatinous fibers in these trees and the variability with which they occurred suggest that lean is not always the most important factor involved in tension wood formation, especially when the whole tree is considered. It is the experience of the authors after observing trees grown under growth chamber, nursery and field conditions, that the incidence of gelatinous fibers in straight cottonwood trees is common and can no longer be regarded as an exception. The cottonwood cambium appears to be very sensitive to the stimulus involved in the initiation of tension wood, which is widespread in some annual rings and localized in others.

The high incidence of gelatinous fibers in these trees seems especially important in light of the current trends of complete tree utilization, intensive management, and tree improvement. Large volumes of gelatinous fibers would undoubtedly influence the utilization potential of topwood. It also seems that gelatinous fiber formation may be influenced by growth acceleration. Intensive management practices aimed at increasing growth rate, therefore, may result in a higher percentage of gelatinous fibers. In addition, the percentage of gelatinous fibers in *Populus* may be genetically controlled (Schönbach 1956) and should, therefore, be considered in a tree improvement program of cottonwood.

In conclusion, the incidence of gelatinous fibers should be a primary consideration in evaluating the complete tree wood quality of cottonwood trees exhibiting rapid growth.

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