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Cellulose structure and biosynthesis*

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Abstract: Carbohydrate researchers may think it is reasonable to believe that the synthesis and structure of a crystalline β-1,4 glucan would be quite straightforward; however, this is not the case. The pitfalls and detours of research have been counterbalanced by exciting new discoveries in cellulose structure, biosynthesis, and molecular biology. Cellulose exists in crystalline and noncrystalline states, with the metastable cellulose I allomorph being the most abundant native crystalline form. Two stages of cellulose I crystallization will be described as well as a new form of ordered, noncrystalline cellulose known as quasi-tactic cellulose. The biosynthesis of cellulose is exceedingly complex, involving many genes and enzymes. Ordered membrane complexes (TCs) control the polymerization and crystallization to form cellulose microfibrils. Biochemical investigations have proven to be very difficult; however, recent breakthroughs on *in vitro* cellulose I assembly lend confidence that this part of cellulose research will soon yield great advances. The greatest success has come from molecular genetics research where the genes for cellulose biosynthesis from *Acetobacter* have been identified, cloned, mutated, and expressed in other systems. The multidomain architecture of β-glycosyl transferases has led to a better understanding of glucan chain polymerization leading to the twofold screw axis in cellulose as well as finding similar domains hypothesized to function in higher plant cellulose biosynthesis. The recent flurry of activity in this field promises to give even more clues to the developmental regulation of cellulose biosynthesis among plants, including the major textile and forest crops.

INTRODUCTION

This review will highlight developments in cellulose structure and biosynthesis. In addition, I will offer suggestions as to the status of the field and where it should move in the near future.

STRUCTURE

Recent advances have given us new insight into the structure of cellulose. Cellulose can exist in a crystalline or non-crystalline state. Crystalline cellulose has at least two distinct allomorphs, cellulose I and cellulose II. Both are found naturally synthesized in nature; however, cellulose I is by far the most prevalent. No eukaryotic cells are known to abundantly synthesize cellulose II *in vivo*.

Cellulose II

Cellulose II is the most thermodynamically stable allomorph of cellulose [1]. Glucan chain orientation within cellulose II is antiparallel. The chains may or may not be folded; however, there is strong evidence that chain folding is present in bacterial cellulose which is synthesized by aberrant cultures or cells which have undergone mutation [2]. Cellulose which has undergone solubilization, then re-precipitation (e.g. mercerization) is cellulose II; however, chain folding has not been demonstrated in this type of cellulose II. It is argued that the chains are antiparallel by virtue of chain exchange from microfibrils which may

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have been antiparallel to each other at the time of solvation. Understanding the structure of cellulose II derived from mercerized products is one of the last remaining areas of cellulose structure to be elucidated.

Cellulose I

To date, we know the following about cellulose I. The glucan chain orientation is exclusively parallel. This has been re-affirmed by several independent approaches using electron diffraction, enzymatic degradation, and silver labeling of the reducing ends [3,4]. The cellulose I allomorph is the thermodynamically metastable form of cellulose [1]. Cellulose I can be converted directly to cellulose II; however, cellulose II cannot be directly converted to cellulose I.

There are two known suballomorphs of cellulose I first discovered by Atalla & VanderHart in 1984 [5] using NMR and later confirmed by Wada *et al*. [6] using electron diffraction (cellulose Iα and cellulose Iβ). Of these two forms, cellulose Iβ is the most stable thermodynamically. Usually these two suballomorphs coexist together within a given microfibril; however, only one group of organisms appears to synthesize almost exclusively cellulose Iβ. This group includes the tunicates which assemble animal cellulose (7). Cellulose Iα has a triclinic unit cell, and cellulose Iβ has a monoclinic unit cell.

Computational modeling suggests two assembly stages of cellulose I crystallization

Using computational analysis, Cousins and Brown have shown that during the biogenesis of cellulose I, the most favorable initial ordered aggregation of glucan chains is through hydrophobic interactions to first assemble a monomolecular glucan sheet [8]. This is supported by experimental evidence where the *in vivo* assembly of cellulose can be interrupted by the addition of an optical brightener, Tinopal LPW. This dye has a preferential affinity for H-bonding to the glucan sheets, thus preventing the induction of the second stage of cellulose crystallization to form the cellulose I microfibril [9]. Thus, in the crystallization sequence, glucan chains associate to form a monomolecular layer glucan chain sheet by van der Waals forces. This sheet normally is short lived and immediately associates with adjacent sheets via H-bonding to produce the mini-crystal. Mini-crystals associate to produce the crystalline microfibril. The size and shape and degree of crystalline perfection is largely due to the geometrical positioning of the catalytic sites within the enzyme complex (to be described below).

Quasi-tactic cellulose: a recently discovered new form of cellulose

Dr Tetsuo Kondo of the Forestry and Forest Products Research Institute in Tsukuba, Japan, visited our laboratory this year. He brought with him a very interesting, special form of never-dried cellulose which was prepared by the water-washing of a film slightly coagulated under a saturated vapor conditions from a LiCl-DMAc (dimethylacetoamide) solution. Electron microscopy revealed that this material had no diffraction pattern and corresponded to the so-called 'amorphous cellulose' well-known to the industrial community. The cellulose forms a clear gel which is easily malleable and can be stretched. When this cellulose was stretched over a 3.0-mm TEM grid and allowed to dry in the presence of negative stain, individual highly ordered glucan chains could be resolved. Because this cellulose is ordered yet has no crystallinity, we have termed this new form, *quasi-tactic cellulose* meaning, 'somewhat ordered'. Manuscripts on this new form of cellulose are now in preparation [10].

THE TERMINAL COMPLEX (TC)—A MACROMOLECULAR ENZYME COMPLEX FOR CELLULOSE MICROFIBRIL ASSEMBLY

Early evidence from freeze fracture and current findings

In the 1960s with the advent of freeze fracture which revealed replicas of the interior of membrane surfaces, investigators began to notice highly ordered, multiparticulate protein subunits in association with cell membranes, particularly the plasma membrane. It was these ordered particles that led Preston [11] to propose the *'Ordered Granule Hypothesis'* for the biogenesis of cellulose microfibrils. Preston hypothesized that ordered multiple enzyme complexes reside in the plasma membrane, and that the geometry of the complex determines the direction of microfibril assembly. No actual ordered membrane complexes had been observed until Brown & Montezinos [12] imaged a linear particulate complex in

association with the tip of a growing microfibril in the alga, *Oocystis apiculata.* This was followed by a number of other examples, including a so-called 'rosette-terminal complex' which has been found to be exclusive for all land plant cellulose assembly, including mosses, ferns, liverworts, and certain green algae [13]. In all organisms so far examined, there have been only two major types of TCs: linear or rosette. Considerable variation in the linear TC is found in the number of subunits as well as the arrangement of subunits. Perhaps the most novel form is from the yellow green alga; *Vaucheria* in which the linear TC has subunits arranged in diagonal rows [14].

Another very interesting recent variation is the linear TC found in the tunicate, *Metandrocarpa uedai* [7]. Here, there are large 14.0 nm particles that lie on the periphery of the linear complex, and small 7.2 nm particles which lie inside a furrow created by the TC. Tunicates synthesize almost exclusively cellulose Iβ. The TC is novel in that the peripheral subunits may have greater spacing than any found from TCs which synthesize predominantly cellulose Iα, suggesting that the TC subunit aggregation pattern may determine the suballomorph type which is assembled. If this is true, then is may be possible in the future to genetically engineer 'spacer proteins' into TCs to alter them in such a way that they may assemble only cellulose Iβ. The biotechnological implications of such research will be discussed below.

Proof for the function of the rosette-TC

Is the TC complex first imaged by Brown & Montezinos in 1976 [12] really an enzyme complex, or is it a replication artefact? Until recently, independent evidence for the rosette-terminal complex was lacking until Kudlicka & Brown [15] imaged intact rosette-TCs from a digitonin-solubilized plasma membrane preparation capable of assembling cellulose I microfibrils *in vitro* when supplied with UDP-glucose. This discovery lays to rest any doubts about the role of the TCs in cellulose biosynthesis and paves the way for some truly exciting new research on the control of microfibril assembly by experimentally altering TC structure (see the section on molecular biology).

Correlation of TC subunit structure with protocols for microfibril assembly

Once the two-stage crystallization concept had been elaborated [8] and proven independently [9] was it reasonable to correlate these patterns with known TC geometry. In 1996 [13], I gave the first detailed examples of all of the TCs known at the time and described how the TC geometry correlates with microfibril size and shape. The most important aspects relate to the number of catalytic sites within each TC subunit and the final association into hydrophobic glucan sheets. If a given microfibril's dimensions are known, then it is relatively easy to calculate the total number of glucan chains. If the number and distribution of TC subunits are known, then it is possible to assign the number of catalytic sites for each subunit, then, using stage 1 of cellulose crystallization into a single hydrophobically associated glucan chain sheet, the number of chains contributing to this sheet can be deduced. For example, each TC subunit of *Valonia* has over 10 catalytic sites. Three subunits produce a massive glucan chain sheet 30 chains thick. The next tier of three TC subunits generates the second sheet that associates with the first sheet by H-bonding and so on until the microfibril is fully assembled. Thus, the length of the linear TC controls the microfibril width in this instance. In *Vaucheria* [14] there is only one catalytic site per TC subunit, and a very different microfibril is assembled. In both case, the chains are parallel and the allomorph is cellulose I.

BIOCHEMISTRY

Investigations with *Acetobacter xylinum*

This is a fascinating topic with some very interesting recent discoveries. In the 1950s the nucleotide sugar, UDP-glucose, was first implicated in cellulose biosynthesis in the gram-negative bacterium, *Acetobacter xylinum* [16]. It was not until 1987 when Ross *et al*. [17] discovered cyclic diguanylic acid as a regulator of cellulose synthesis in *Acetobacter,* that the *in vitro* research accelerated. In 1989 my graduate student, Fong Chyr Lin, synthesized cellulose II *in vitro* from *Acetobacter* extracts and purified the enzymes using trypsin and product entrapment [18]. He found three polypeptides (83, 93 and 97 kDa) implicated as potential catalytic subunits for UDP-glucose binding and polymerization into β-1,4 glucan chains. In 1990, in collaboration with Richard Drake [19], we identified the 83 kDa polypeptide as the

catalytic subunit using the photoaffinity labeling probe, azido-UDP-glucose. This allowed us to concentrate on amino acid sequencing of this polypeptide which led to the first isolation and sequencing of a gene for cellulose biosynthesis by Saxena, Lin & Brown in 1990 [20]. Since then, Dr Saxena has made many advancements in this field, some of which will be described below in the molecular biology section.

Higher plants

Resolving the enzymes associated with cellulose biosynthesis in higher plants has been enormously more difficult and challenging than *Acetobacter*; however, we have accepted this 'challenge' and have made some promising new discoveries which should soon enable identification of the proteins involved in cellulose biosynthesis in higher plants which include our most important economic cellulose crops. For this reason, we have devoted a large proportion of our research efforts into isolation and purification of enzymes and associated proteins in cellulose and callose (β-1,3 glucan) biosynthesis, using mung bean, cotton, and *Arabidopsis* as the major model systems.

The first complete separation of cellulose and callose assembly

One of the most severe problems in cellulose biochemistry is the activation of callose synthase in membrane-solubilized preparations. There have been a long series of discussions on whether the glucan synthase complex can switch between callose and cellulose assembly, depending on such factors as wounding, induction, etc. Using native gel electrophoresis, we have achieved the first complete separation of β-1,3 and β-1,4-glucan synthase activities *in vitro*. Cellulose synthase activity is confined to the upper, loading well of the native gel, and only callose synthase activity is found in the interface between the stacking and running gels [15]. Electron microscopy of particles from the stacking gel reveal only cellulose (as determined by cytochemical staining with CBHI-gold) and often particles associated with the tips of cellulose I microfibrils. On occasion, complete rosette arrangements are observed. Frequently rosette-type fragments or clusters of subunits are found. We believe these are the same rosette structures that we first observed in 1980 [21].

The β-1,3 glucan assembly in the stacking/running gel interface contains only callose, often associated with *single* particle subunits, not rosette particle subunits. Furthermore, the single particle subunits are slightly larger than the subunits associated with cellulose assembly.

What is the 'true' structure of the cellulose/callose synthesis assembly machine in higher plants? It is important to understand that a generalized 'impression' or view of cellulose biosynthesis from a TC rosette complex is based on *two-dimensional* data from the hydrophobic domains of a fractured plasma membrane. We examined thin sections of cells known to be active in synthesizing cellulose where linear TCs would be expected [22]. We discovered that the TC structure is much more extensive than presented by freeze fracture, and that much of it faces deep into the cytoplasm as most of an iceberg would remain under water. Thus, it is not unreasonable to hypothesize that on the cytoplasmic side of the plasma membrane, the callose synthase subunits could be associated with the rosette subunits, and when damaged, this association could be lost, and callose synthase would be activated. If this structural organization is correct, it is easy to understand why such a TC structure would never be derived from the perspective of a fractured membrane. A re-investigation of TCs using high resolution TEM and delicate fixation techniques could yield important new structural information about TCs and also be a test for biochemical probes such as antibodies to TC proteins to verify *in situ* structure with biochemical evidence.

Another important perspective is that in order to generate a cellulose I microfibril known to contain at least 36 glucan chains, all six subunits of the rosette TC would need to be specifically associated with one another. One subunit by itself would be able to generate only six glucan chains, and this is insufficient to produce crystalline cellulose. In all probability, the so-called 'amorphous' cellulose could be produced here, or single glucan chains could fold and crystallize into cellulose II. To be discussed in the molecular biology section below is an interesting case where a radial swelling mutant of *Arabidopsis* lacks intact rosettes, yet synthesizes noncrystalline β-1,4 glucans [23].

Sources of UDP-glucose for cellulose biosynthesis

It is generally accepted that UDP-glucose is the donor for glucose in the polymerizing reaction; however, a recent investigation [24] has shed light on what may be an alternative pathway through membrane-bound sucrose synthase (SuSy) activity. This enzyme has been found to be associated with the plasma membrane of cotton fibers, and it has been suggested that SuSy 'channelizes' UDP-glucose directly to the TC by converting sucrose to fructose and UDP-glucose. Such an efficient directed exchange may explain how a plant cell can more efficiently direct precursors to the sites for specialized, amplified synthesis of cellulose, such as xylem elements, and the secondary wall cellulose deposition in cotton fibers. Thus, there could be several different pathways for UDP-glucose utilization. Of course, how all of this is controlled, regulated, and targeted, will be among the most exciting research in the near future (to be discussed below in the Future Research section).

Proteins associated with cellulose synthase—their possible roles

We and others have found that during product entrapment, many other proteins are found associated with cellulose synthase activity. Among these are annexin-like molecules [25] which have UDP-glucose binding activities. The role of annexin in cellulose biosynthesis is not known. It may help to switch UDP-glucose to the callose synthase during wounding or specific developmental stages.

In addition, we have found a 170-kDa polypeptide which was co-purified with cellulose synthase and appears to be a UDP-glucose binding polypeptide which may be a plant homolog of yeast β-1,3 glucan synthase [26]. This work suggests that at least cellulose and callose assembly may be mediated by two different synthase activities in higher plants.

Many other proteins have been proposed to have some role in cellulose biosynthesis [27]; however, it remains to be proven that these proteins actually are necessary and precisely how they interact with the catalytic subunit to initiate and direct the assembly of cellulose. Polypeptides in signal-transduction are expected to play important roles in cellulose biogenesis. The sites of regulation could be very diverse, ranging from ER-assembled polypeptides, to Golgi-modified products, and finally to the directed and targeted exocytosis of TC complexes and their activation to assemble cellulose. The story does not end there. Cellulose microfibril assembly also is under the influence of the cytoskeletal system and is highly coordinated in terms of temporal and spatial regulation. During cell aging, it is possible that other sets of cellulose synthases may take over roles in wall assembly. This seems likely during secondary wall synthesis in xylem differentiation and fiber differentiation in the cotton ovule epidermis.

Obviously, the foremost focus on cellulose biosynthesis has centered on the catalytic subunit and how it functions in glycosylation (more on this below); however, I envision for the future a great emphasis on cellulose synthase-associated proteins and their role in the spatial and temporal regulation of important metabolic processes. The bottom line is that our preconceived notions of a simple polymerization reaction giving rise to β-1,4 glucans, are inaccurate, and the levels of complexity and diversity of cellulose biosynthesis are only becoming apparent as we discover new enzymes and genes associated with the process.

MOLECULAR BIOLOGY

The first sequencing and cloning of a cellulose synthase gene

In May 1990, Dr Saxena and I attended the annual meetings of the American Society for Microbiology in Los Angeles, California. There, we presented our data on the first cloning and sequencing of a gene for cellulose synthase. Because of our earlier work [18] on the purification of the 83 kDa polypeptide in *Acetobacter,* we were in a position to obtain the amino acid sequence of this polypeptide. We found the n-terminal amino acid sequence of the 83 kDa polypeptide, and Dr Saxena quickly identified and sequenced the gene responsible for cellulose biosynthesis. While we were the first to publicly disclose the discovery of a gene for cellulose synthase and to publish (an abstract), it was not until our full-length article was published later in 1990 [20] that all of the details emerged. Using mutational analysis, scientists at the Cetus Corporation, published their full length article on the cellulose gene sequence a few months earlier [28], and they incorrectly identified the catalytic subunit as we showed later [29].

Since these initial investigations, the genes responsible for cellulose biosynthesis in *Acetobacter* and other prokaryotic organisms have been thoroughly characterized [30–32]. The genes in the cellulose synthase operon of *Acetobacter* have provided clues to the complex assembly of crystalline microfibrils from a gram negative bacterium. Barriers include the LPS layer and peptidoglycan envelope which must be 'traversed' by a pore-like protein complex to export the cellulose from the catalytic center on the cell membrane to the exterior (presumably accomplished by the ACS-C gene). The ACS-D gene appears to play a major role in the crystallization of cellulose, for when this gene is disrupted, only cellulose II is assembled in agitated culture [30].

Gene sequences provide clues to the mechanism of action of glycosyl transferases

In 1994 Dr Saxena visited the laboratory of Dr Bernhard Henrissat in Grenoble and learned about the technique of hydrophobic cluster analysis (HCA). Dr Henrissat was successfully using this approach to characterize various cellulases. We decided to collaborate on glycosyl transferases using the ACS-AB gene from *Acetobacter* as the model for a processive glycosyl transferase, and examples of nonprocessive glycan synthases. In 1995, we published our first work in the characterization of the multidomain architecture of β-glycosyl transferases [33]. The important findings from this investigation showed the following: (a) processive and nonprocessive β-glycosyl transferases can be clearly segregated on the basis of HCA; (b) the catalytic residues were found to be based on conserved Asp residues, two for the nonprocessive examples, with a single domain, and three for the processive examples, with two domains; and, (c) a QXXRW conserved sequence motif was found for all processive β-glycosyl transferases. From this work, we also concluded that during polymerization, two UDP-glucose molecules simultaneously bind adjacent to each other, but at a 180° orientation, thus giving a 'double addition' of two glucose residues for each catalytic event. This logic was based on the difficulty of explaining what rotates relative to what in the polymerization via the addition of a single glucose residue since every other glucose residue in β-1,4-glucans is oriented 180° with its neighbor; e.g. the glucan chain has a twofold screw axis.

In this study, we also proposed that the glucose additions take place from the reducing end. It is likely that this is not the case, based on a recent study by Koyama *et al*. [4] in which they convincingly demonstrated in *Acetobacter xylinum*, the site of glucose addition from the nonreducing end.

The multiple domain hypothesis for *Acetobacter* cellulose synthase is confirmed in higher plant glycosyl transferases

We first presented our work on HCA publicly in 1995 at the American Society for Plant Physiology Meetings in Charlotte, NC. Dr Deborah Delmer heard Inder Saxena's presentation, and after the Meetings, she began a search of the databases for gene sequences with the DDD QXXRW motif which we found characteristic for processive β-glycosyl transferases. She and her colleagues found a similar sequence in cotton and rice and defined a CelA homolog for cellulose synthase and described this in 1996 [34]. The CelA genes encoding the catalytic region for cellulose synthase in cotton and rice have lengthy hypervariable regions; however, they all contain the three characteristic aspartic acid residues in two domains and the QXXRW motif.

Independently, Richard Williamson's group in Canberra [23] found similar gene sequences from an *Arabidopsis* temperature-sensitive mutant, the roots of which underwent a radial swelling, probably due to the lack of reinforcement from the cellulose. These mutants produce less crystalline cellulose and in addition, a large quantity of noncrystalline β-1,4 glucans. Freeze fracture of the mutants indicated the absence of TC rosettes. This point is very interesting inasmuch as the mutation may be related to the control of TC integrity, in which case the absence of rosette TCs would suggest that perhaps the individual subunits are present and fully active. In this situation, only six glucan chains could associate, and this would be too few chains to produce a crystalline structure. Thus, it is possible that the so-called 'noncrystalline' β-1,4 glucans of the mutant, may be due to the TC alteration. With the concomitant decrease in crystalline cellulose in the *Arabidopsis* mutant it is highly suggestive that the mutation affects the crystallization phase rather than polymerization; however, this is curious since the site of the mutation has been mapped to the same catalytic domain that we first described in *Acetobacter* [33] and also found in cotton and rice [34].

Others have found similar sequences [35,36] from higher plants. Thus, it appears that the basic multidomain architecture for the catalytic subunit for cellulose synthase first described in our laboratory in 1990 [20] is very similar to all known cellulose synthases. Unfortunately, at this time, no one has succeeded in cloning a functionally intact cellulose synthase from a higher plant; however, this will soon transpire as larger contiguous sequences are synthesized in recombinant organisms. The dawn of manipulation of cellulose synthase via molecular biology is now upon us!

WHAT DOES THE FUTURE HOLD? — BIOTECHNOLOGY IMPLICATIONS

This short review was conceived to bring those up to date who are not specialists in the field; however, it is obvious to anyone who studies carbohydrates, that any controllable manipulation of the biosynthesis of cellulose could lead to important advances in cellulose productivity, quality, and diversity. Thus, the future holds great promise for genetically dissecting and manipulating the genes responsible for cellulose biosynthesis in our major agricultural crops such as cotton and forest trees. Having understood this, what are the most exciting immediate, short-term prospects for 'harvesting' rewards from molecular genetics research?

With the cotton crop, several interesting applications come to mind. If the number of useful fibers per boll could be increased, this would be a great advance for cotton productivity. If the cellulose could be altered by manipulating the crystallinity and degree of polymerization, the strength could perhaps be greatly increased. If the microfibril size, shape, and surface properties could be modified, this may have a dramatic effect on water and dye absorption and retention.

If cellulose production efficiency is a function of temperature, then it would be very important to maximize biosynthetic productivity of cellulose at temperature extremes. For instance, in my home state of Texas, the quality of the cotton crop often is decreased when grown under cool night temperatures [37]. Regulating fiber production and quality when plants are grown under stress conditions could significantly improve the economics of cotton production. Incidentally, the cotton crop in Texas (except in drought years!) is a billion dollar crop, so anything new we can learn about how to improve fiber quality and production would be of value.

Likewise in the forest products industry, cellulose is a major player; however, extracting cellulose in a useful form for pulp and paper often is costly and environmentally detrimental. Thus investigating cellulose/lignin ratios to improve 'extractibility' would appear to be a major goal. By the same token, if the cellulose itself could be stronger, then perhaps less lignin may be required to maintain structural integrity in forest trees. These approaches deserve serious consideration, with greater emphasis on national and international grant support from government and industry.

Cellulose modification via genetic alteration is an important consideration. To produce cellulose derivatives requires considerable expense and involves environmentally sensitive concerns; thus, for example, if cellulose acetate or carboxymethylcellulose could be directly synthesized by living plants and harvested, this could mark the dawn of a new day for farmers and industry cooperatives.

One other point deserves at least the attention of the medical community. Now that we know that the catalytic domain for cellulose synthase appears to be highly conserved, it is not unlikely that cellulose synthase genes may be present and actively expressed in humans. I mention this, for back in the 1960s cellulose was identified by X-ray diffraction from patients suffering from scleroderma [38]. These findings have not been reconfirmed; however, with the advances in molecular biology, it should be relatively easy to determine if humans have genes for cellulose synthase. If so, this may present an interesting new approach for medical applications. Since the tunicates (chordates) synthesize cellulose, it does not seem unreasonable that primates and even humans could synthesize cellulose of one form or another. The evolutionary implications for this broad range of cellulose biosynthesis from organisms as diverse as bacteria to humans marks another saga in a very interesting area of research.

I would like to end this brief review to remind those who want to 'tune in' from time to time to learn more about the status of cellulose biosynthesis, that the Internet now provides a wealth of useful information. I am particularly impressed with the search engines and efficient and rapid supply of up-to-date information in publications, patents, processes, uses for cellulose. Toward that end, I initiated the

CEN or *Cellulose Electronic Network* which is continuing to grow and is an international 'clearinghouse' for information relating to researchers and cellulose. I encourage a visit to the CEN at: <http://www.botany.utexas.edu/infores/cen/> as well as a visit to my home page at the University of Texas at Austin [39] to learn more about our work with cellulose structure and biosynthesis.

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