

It is planned to issue a new directory of members early in 1960. We would ask you to check the address you have given us and write us in case of error.

We are without the address of Mr. W.A. Rainford, old address: Post Office Box 325, Livingston, Rhodesia. Perhaps it is possible to reach Mr. Rainford through this medium.

#### Election of the Council Members

The 12 members of our Council have to be elected for a new three-year period. 9 of them are ready to serve again. We have only the announcement of Dr. Bailey, USA, Dr. Chalk, England and Dr. Chattaway Australia, who wish to retire at the end of 1959. As you may have seen from the report of our business meeting in Montreal, we had the possibility of discussing the succession of these three Council members. We therefore suggest a new Council constituted as follows:

Mr. J.D. Hale, F.P.L. of Canada, Ottawa

Dr. E.W.J. Phillips, Princes Risborough

Prof. Dr. B. Huber, Forstbotanisches Institut, München

Prof. Jean Collardet, Centre Technique du Bois, Paris

Mons. Didier Normand, Centre Technique Forestier Tropical, Nogent-sur-Marne

Prof. Dr. A. Frey-Wyssling, Inst. f. Allgem. Botanik ETH, Zurich

Prof. F.R. Milanez, Jardim Botânico, Rio de Janeiro

Dr. W.L. Stern, Yale School of Forestry, New Haven

Dr. B. Francis Kukachka, US F.P.L., Madison

Dr. K.A. Chowdhury, F.R.Inst. Dehra Dun

Dr. H.E. Dadswell, C.S.I.R.O., South Melbourne

Dr. A.B. Wardrop, C.S.I.R.O., South Melbourne

To facilitate the procedure of election, we should like to ask whether you can accept the new structure of the Council. Without your reply by December 15th we assume your consent. If someone were to suggest replacement of one of the Council members by another member of the Association he should write us at an early date to give us time for the final settlement of the question.

Zurich, October 1959

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Zurich, Switzerland

Office: Laboratorium für Holzforschung E.T.H., Universitätstrasse 2

#### EDITORIAL

Several libraries of research laboratories in different countries have evinced their interest in our News Bulletin, so that its contents need no longer be considered as domestic information letters only, but as scientific contributions of a more general significance. We therefore hope to continue publishing short scientific reports and summaries as was the case with the abstracts of the papers presented in the symposia on wood at the Montreal Botanical Congress.

As a result of the appeal to our members for collaboration in this line, we have received a most valuable review on reaction wood by Dr. Wardrop, which we are delighted to publish as a welcome opening paper. Vivant sequentes!

I am glad to state that our financial position, of which this Bulletin gives evidence, enables us to publish two issues of 8 to 10 pages each year.

The new directory of members announced in our last News Bulletin is distributed along with this issue. We would ask each member to check his address and to inform our office continuously of any intervening change.

A. Frey-Wyssling  
Secretary Treasurer



SCIENTIFIC REVIEW

The Structure and Formation of Reaction Wood in Angiosperms  
by A. B. Wardrop

Introduction

The reaction wood of Angiosperms or tension wood may be defined as wood of abnormal structure, the development of which appears to be associated with mechanisms affecting movements of orientation in stems and branches of arborescent plants. That movements of orientation are involved during the growth of trees has long been recognized both under normal environmental conditions and when the environment of the plant undergoes change.

The changes associated with reaction wood formation have for the most part been inferred from the observed modifications in wood anatomy and the fine structure and composition of the tissue elements. Physiological investigations which have been carried out are only of the most exploratory kind.

Anatomy and Fine Structure of Tension Wood

The vessels of tension wood are fewer and smaller than in normal wood and xylem parenchyma tends to be reduced in amount (Onaka 1949). The xylem fibres are characterized by a conspicuously thickened cell wall; part, or all, of which is un lignified (Jaccard 1938, Münch 1937/38, Wardrop and Dadswell 1948-1955, Jutte 1956, Wahlgren 1957).

Two types of tension wood may be distinguished; the compact type in which the fibre cell walls are partially or wholly un lignified in a particular region of the stem, and the diffuse type in which the modified fibres are scattered singly and in groups among normal cells.

Initial studies of the fine structure of tension wood fibres were made by Münch 1937/38 and Jaccard and Frey 1928, who showed that the molecular (micellar) orientation in the un lignified layers of the cell wall was approximately axial. These studies were followed by those of Wardrop and Dadswell 1948 and 1955, Preston and Ranganathan 1947, Jutte 1957, Wahlgren 1957. The various modifications in fine structure which have been observed are indicated diagrammatically in Figure 1. The un lignified ("gelatinous") layer of the cell wall may appear to be uniform in cross-section or markedly convoluted. To some degree this difference appears to be characteristic of certain families or genera. In Acacia, for example, very frequently the tension wood is of the diffuse type with a convoluted layer G.

Anatomical changes involved in the formation of tension wood are associated with changes in composition which have been reviewed by Dadswell et al. 1958.

Cambial Activity and Tension Wood Formation

Growth rings in which tension wood is formed show asymmetry with a greater width of xylem on the side of the stem or branch in which tension wood develops. This asymmetry results either from an increased rate of periclinal divisions in the cambium or from a greater time over which division takes place (Wardrop and Dadswell, 1955). In many species the initiation of tension wood formation by the cambium is paralleled by similar changes in the phloem fibres which also have greatly thickened un lignified cell walls (Metzger, see Münch 1937/38, Onaka 1949, Dadswell and Wardrop 1954).

According to Jaccard 1919 and 1938, the increased radial growth which accompanies tension wood formation is accompanied by a corresponding decrease on the opposite side so that the total cross-section of the wood is no greater than if normal concentric growth had continued.

Stress Development and the Formation of Tension Wood

The existence of growth stresses in woody stems was recognized early and studied extensively by Jacobs, 1938, and Münch 1938. In Angiosperms the outer peripheral xylem was shown to be in a state of tension relative to the xylem near the centre of the stem. Thus when a stem cross-section is cut longitudinally, the peripheral sections contract relative to those from the stem centre. In asymmetrical stems containing tension wood this contraction is greatly enhanced. Again the studies of Jaccard, 1938, showed that when twigs were bent into loops, Figure 2, tension wood developed on the upper side of the loop irrespective of the initial orientation. When such a loop was cut as shown in Figure 2, the segments behaved in such a way as to indicate that the development of tension wood resulted in a contraction of the xylem on the side on which it was formed.

The Occurrence of Tension Wood and Taxonomy

The formation of tension wood is not uniform in all families of Angiosperms. The extensive survey of Onaka, 1949, showed that eccentric development of the stem is usually confined to the upper side of the stem or branch. No eccentric growth occurred in branches and leaning stems of many species, but these were mostly shrubs and vines. Exceptions were seen, however, in Pawlonia tomentosa and Catalpa ovata. Eccentric growth on the lower side of the leaning stems was observed in Gardenia florida and Buxus japonica.

The layer G does not always develop or may only be rudimentary (Oleaceae, Cydoniaceae). It was further pointed out by Onaka, 1949, that in those species in which tracheids and fibre tracheids make the bulk of the xylem, the layer G constitutes most of the wall, but in those species with predominantly libriform fibres the layer G appears to replace or to be formed in addition to the three layers of the normal secondary cell wall. It is not possible to assign with certainty the types of cell wall organization described above with these categories distinguished by Onaka, 1949, but it is reasonable that the first group would correspond to the organization Figure 1 (b) and the second to the organization illustrated in Figure 1 (c) respectively.

It may be noted, however, that different types of cell wall organization were observed to be formed at different times during the growth season (Wardrop and Dadswell, 1955).

Observations of the distribution of tension wood in different families have been made by Necessary, 1955, who considers that its formation is more common in those families in which the xylem is less specialized.

Experimental Formation in Tension Wood

Studies of the formation of tension wood under experimental conditions have been made by Jaccard, 1938, Onaka, 1949, and Wardrop, 1956. These observations relate to three main points of view, viz. that tension wood is formed as a response to stress, to gravity, or as a result of the operation of various intrinsic factors in the plant.



(a) Tension Wood Development as a Stress Response

In the examination of branches and leaning stems of Angiosperms it was early recognized that tension wood occurs on their upper side. Further, if a stem were bent artificially, then tension wood was observed to develop on the upper side, i.e. the side placed in tension. This led to the view that tension wood was a morphological response to the presence of tensile stress in the branch or stem where this stress arose due to the weight of the branch or was artificially induced. Such a view was also consistent with observations on the development of mechanical tissue in herbaceous plants and vines (Vöchting, see Wardlaw, 1952, Haberlandt, 1914).

Inadequacies in the view that tension wood is a morphological response to stress alone were apparent from the experiments of Hartmann and of Jaccard in which twigs were bent into vertical or horizontal loops. In the former case, tension wood was found on the upper side of the loop irrespective of whether the wood was initially in tension or in compression (Fig. 2) and, in the latter, the tension wood was also consistently on the upper side of the loop so that it appeared that the morphological changes involved in the formation of tension wood constituted a geomorphic response. These and similar experiments led Jaccard to the hypothesis that tension wood is involved in governing the orientation of branches and stems so that they acquire an equilibrium position in relation to gravity.

(b) Intrinsic Factors Governing Tension Wood Formation

The idea of the existence of an equilibrium disposition of stem and branches finds further development in the work on Gymnosperms of Hartmann quoted by Sinnott, 1952. According to this view there is an inherited form of the shoot system which is genetically controlled and in the maintenance of which the development of reaction wood is involved. An example of the sort of experiment upon which this view is based is seen in that of Wardrop, 1956, which is analogous to those carried out by Hartmann and Sinnott. Thus, if a branch of a stem is bent downwards away from the stem, tension wood develops on its upper side. If the branch is bent upwards towards the stem, tension wood develops on the lower side of the branch. Since tension wood formation is associated with a tendency of the stem to contract longitudinally, then in each instance the tension wood is developed in a position which, if free to do so, would result in the branch regaining its normal orientation with respect to the axis. This behaviour points to the operation of intrinsic factors within the plant governing the mutual disposition of its branches with respect to the stem.

The distribution of tension wood appears to be consistent with the view that it is developed in those regions of the stem where a contraction would form part of a process directed towards the maintenance of the normal disposition of the stem and branches. This may be seen as a case of general principle formulated by Russel, 1945: "If... normal structural and functional relations, either external or internal, are disturbed, activities will usually be set in train that are directive towards restoring structural and functional norms or establishing new norms which are adapted to the altered circumstances".

In general this view is also consistent with a series of observations made on the tension wood distribution in normal erect stems (Wardrop, 1956).

(c) Physiological Aspects of Tension Wood Formation

In stems undergoing geotropic recovery it is obvious that the initial response is in the growing point and progresses towards the base of the stem or branch. This is also the case with respect to tension wood formation. If stems are placed horizontally and the tip is removed, no response occurs and no reaction wood is formed. If, however, the response begins and the tip is then removed, recovery continues. Thus, the apex appears essential for the initiation of recovery but not for its continuation (Wardrop, 1956). Further, it was observed by Onaka 1949 and by the author that if an incision is made in the bark on the upper side of a horizontal stem, reaction wood does not develop below the incision unless leaves are left intact in this region. Defoliation reduces the amount of reaction wood formed but, unless the apex is removed, does not inhibit its formation. The participation of auxins in the development of tension wood has been postulated by Jaccard, 1938, Onaka, 1949, Necesany, 1956, but it would seem that auxin is only related to the peripheral distribution of division in the cambium. The application of auxin alone does not induce tension wood formation. The participation of auxin is also suggested by the observation of Strasburger, 1891, that bud development in branches is greater on the upper side of branches of Angiosperms and in the lower side of Gymnosperms. Our own observations have not confirmed this.

The development of tension wood was shown by Jaccard, 1938, to involve the depletion of starch reserves in the stems. Jaccard also records an increase in the osmotic pressure of the cambium on the eccentric side of the stem although the significance of this is unknown.

Jaccard and Frey, 1928, reported that in tangential section the permeability to water in tension wood was less than in normal wood. Onaka, 1949, observed that rise of dye solutions was less rapid in tension wood than in normal wood and attributed this to the smaller vessel diameter. Experiments of the type performed by Lundegardh (Wardrop and Davies, unpublished) showed that in tension wood the total water content and the mobile water was less than in normal wood. The mobile water was calculated to occupy 50 per cent. of the vessel volume in normal wood and 42 per cent. in tension wood, but the vessels occupied 14 per cent. and 7 per cent. in normal wood and tension wood respectively. These results could be regarded as reflecting a greater resistance to conduction of water in tension wood.

A preliminary study of the abnormal lignification of tension wood has been made by Wardrop and Scaife, 1956. The results suggest that the failure of the tissues to lignify must arise from an asymmetrical distribution of phenolic precursor since tension wood is characterized by a high concentration of peroxidase.

(d) The Mechanism of Orientation Movements Associated with Tension Wood Formation

The experiments on the development of tension wood in loops by Jaccard, already referred to, demonstrated the development of a contraction associated with tension wood formation. This contraction, it was suggested by Münch, 1937/38, originates in the growth stresses of the stem. The origin of these stresses is to some extent obscure although Jacobs, 1945, pointed out that they may arise in some change, probable



in cell wall texture, associated with the differentiation of the fibres from the cambium. From a study of the stress distribution Jacobs has suggested that an asymmetrical development of the stem alone would bring about an asymmetrical distribution of growth stress which could effect movements of orientation of branches and stems. According to this view the development of tension wood as such does not necessarily form part of the mechanism of movements of orientation, although Jacobs has demonstrated that where tension wood is present the stress development is abnormally high.

A different view of the mechanism of orientation movements has been proposed by Frey-Wyssling, 1952, for the case of the stems undergoing response to gravity. He suggested that the origin of the force leading to bending of the stem lies in the cambium and that forces in excess of the normal osmotic pressure are involved. Frey-Wyssling pointed out that the bending of a growing stem does not correspond to the elastic bending of a rigid body but to the deformation or creep of plastic body under long-time loading. He regarded the reaction wood as being produced by the stem to maintain the orientation achieved after bending as a result of growth forces arising in the cambium. He further pointed out that the cell wall organization of the tissue is particularly adapted for this purpose.

It does not appear that the forces governing recovery of the stem can be osmotic in nature since, as already pointed out, this involves a contraction in length of the stem, and it has been shown that in stems deflected into a horizontal position, geotropic response takes place in those in which the cambium is destroyed, in the lower side of the stem, but does not take place if the cambium is destroyed on the upper side. It is difficult to visualize a mechanism by which this contraction could result if the tissue was in a normal state of turgidity. On the other hand, the asymmetrical development of xylem which results in such a treatment could, in Jacob's observation, give rise to a stress distribution which would cause the stem to recover, especially if the asymmetrical distribution of stress was enhanced by the development of tension wood.

The question thus arises as to the possible source of contractile forces. This has been explained by Münch, 1937/38, in terms of the helical organization of the cell wall, the assumption being made that a pressure exerted by the gelatinous layer on the outer layer would result in a tendency towards cell contraction.

However, in fresh sections, the layer G often appears partially detached from the other layers of the cell wall, especially in those cells in which this is markedly convoluted.

If the possibility that recovery results from the operation of osmotic forces is rejected, then it appears that the force governing recovery must arise during the period of secondary wall formation. The suggestion that this force may result from a volume contraction of the wall during the crystallization of cellulose has been made by Wardrope, 1956, but, like the other mechanisms proposed, no conclusive proof that such a mechanism is operative has been obtained to this stage.

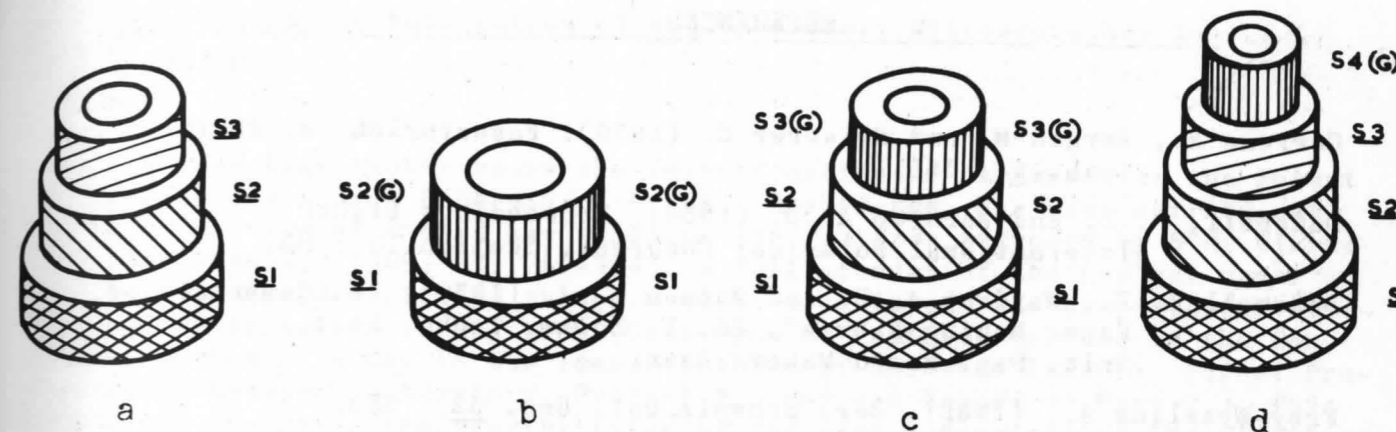


Figure 1

Diagrammatic representation of the organization of the secondary wall in

- (a) normal wood fibres
- (b) (c) and (d) various types of tension wood fibres.

S1 - S4 = successive layers of the secondary wall. G = "gelatinous" layer. A line below the designation of any layer indicates that it is lignified.

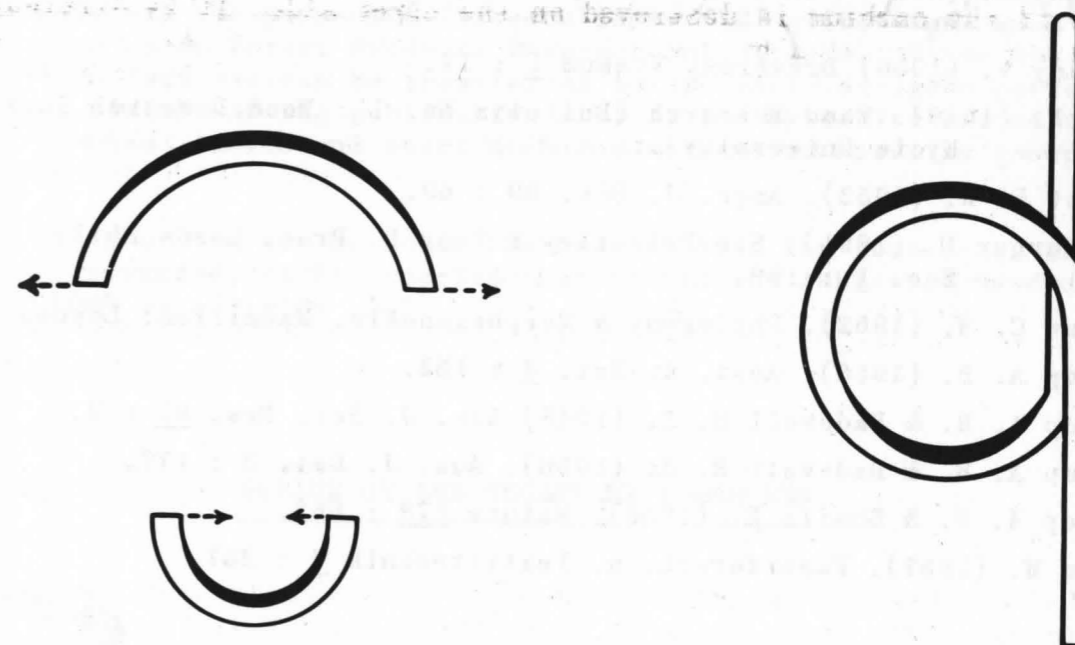


Figure 2

Diagrammatic representation of tension wood formation in a twig bent into the form of a loop. The lower part of the diagram shows the movement of the segments of the loop after cutting (after Jaccard (1938) ).

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Progress in the Publication of the Laboratory Microscope Key to Hardwoods

by J.B. Brazier

For more than twenty years the identification of hardwoods at the Forest Products Research Laboratory, Princes Risborough, has been carried out with the aid of a card key based on the features proposed by S.H. Clarke (New Phytol., 1938, 37, 369-374). A full account of the key has never been formally published though a duplicated report was prepared for limited distribution in May 1939 (Catalogue of Features for Use in the Construction of a Key to the Identification of Hardwood Timbers. Forest Products Research Laboratory, Project 9, Progress Report 4, Part 2.). This served to bring the possibilities of the card key method to the attention of wood anatomists and others and resulted in the technique being widely adopted for the identification of timbers and other biological material. In the light of the experience gained with its almost daily use, a complete revision of the key has been undertaken and is now being prepared as a Forest Products Research Bulletin. This has involved modifications to some of the original key features and the introduction of others not included previously; also the terms and definitions have been amended, where necessary, to conform with the International Glossary of Terms used in Wood Anatomy, sponsored by the Association (Trop. Woods, 1957, No. 107, 1-36). The features used in the key will be fully described and illustrated by a specially prepared set of photomicrographs. About 800 species, representing the 400 or so timbers of commercial interest on the United Kingdom market, have been examined and anatomical data, based, whenever possible, on specimens correlated with herbarium material, have been prepared. These data will be presented for each timber in a coded form on much the same lines as in Forest Products Research Bulletin No. 25, so that the diagnostic features can be transferred to specially designed perforated cards. A feature of the publication will be the extensive use of supplementary notes, tables and short dichotomous keys to specific groups of timbers.

Preparation of the new Bulletin has been in hand for some years and is now well advanced; it is expected that it will be published towards the end of 1960 or early in 1961.

OFFICE OF THE SECRETARY TREASURER

1) Council

All members proposed for the Council have been confirmed and have accepted their election.



2) Financial

a) Statement of receipts and expenditure

Receipts		Expenditure	
	SFr.		SFr.
Subscriptions	872.--	News Bulletin	533.--
Glossary and		Office	314.--
News Bulletin	85.70	Postage	186.50
Subscribers	23.75	Sundry expenses	45.15
Bank interest	99.95	Profit	2.75
	<u>1081.40</u>		<u>1081.40</u>

b) Balance

Balance brought forward	SFr. 4.069.77	* Deposit book	4.001.55
Profit for the year 1959	SFr. 2.75	Postal ch.a.	56.27
	<u>SFr. 4.072.52 *</u>	Cash	14.70
			<u>SFr. 4.072.52</u>

Remarks on the statement of receipts and expenditure:

The profit of the last financial year is extremely low, but compared with 1958, where we had to face a loss of SFrs. 320.--, the financial result of 1959 is not too bad. At all events, it is not our goal to work for profit. As a novelty we have an item "subscriptions". That means that we supply our News Bulletin at the same price to industry libraries which cannot become members. Expenditure is a little lower than 1958. There was no expenditure for stationery and not so much for postage. On the other hand, the amount for our office rose. That is due to the intensive correspondence during the Congress year. The amount entered as office expenditure is at any rate much lower than the effective costs of this type of work.

3) Membership

We are pleased to announce the nomination of 8 members. We are very sorry that we can no longer reproduce publication lists of our new candidates.

Prof. Dr. Pal Greguss, Dozent der Botanik, Universität, Szeged, Hungary

Dr. Helmut J. Braun, Assistent am Forstbotanischen Institut der Universität Freiburg (Br.), Germany

Dott. G. Scaramuzzi, E.N.C.C., C.P. 9079, Rome, Italy

Dr. A. Fahn, The Hebrew University of Jerusalem, Department of Botany, Jerusalem, Israel

Dr. Irving B. Sachs, Forest Products Laboratory, Madison 5, Wisc. USA

Mr. Robert C. Koeppen, Forest Products Laboratory, Madison 5, Wisc. USA

Dr. Dilip Kumar Das, Forest Prod. Laboratory, Chittagong, East Pakistan

Dr. D.S. Richardson, University of Aberdeen, Department of Forestry, Old Aberdeen, Scotland

4) Miscellaneous

- a) In the last News Bulletin we informed our members that the Tree-Ring Society suffered the loss of two of its closest collaborators. We have therefore written a letter of personal encouragement to the secretary of that Society. We are glad to publish the answer to this letter:

Your kind letter of October 6th has been received. In behalf of the Laboratory staff, I wish to express our thanks to the International Association of Wood Anatomists for their interest in this Laboratory and the Tree-Ring Bulletin.

Please be assured that the work in this Laboratory is not only continuing, but expanding. We are gradually adding inductive research to our program and several small projects are now being pursued. We will enlarge on the number and scope of these as we make progress on our initial ones.

The Tree-Ring Bulletin will be continued with Bryant Bannister (of this Laboratory) serving as editor.

The University of Arizona (Laboratory of Tree-Ring Research), The Tree-Ring Society, and Arizona State College at Flagstaff, will co-sponsor a proposed conference on "Forest Tree Growth" to be held here April 11-13, 1960. If you have any interest in such a conference, please let me know, and I will keep you informed as to its development.

Cordially,

sig. Terah L. Smiley  
Acting Director  
University of Arizona, Tucson

- b) The Forest Products Research Bulletin 22 "Identification of Softwoods by their Microscopic Structure" by our member E.W.J. Phillips has been reprinted. There are no changes in the text from the earlier printing. It is available at the price of -/4/- at the Forest Products Research Laboratory, Princes Risborough, Aylesbury, Bucks., England.
- c) Our Council member W.L. Stern has offered reprints of a valuable list of the more important Wood collections all over the world and their relation to renowned Herbaria "The Citation of Wood Specimens and Herbarium Vouchers in Anatomical Research", Taxon 9 (1) (1960). This gift will be distributed with the second News Bulletin of this year.

Zürich, March 1960

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