Aspects of the Aging Process in Cambium and Xylem

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The aging processes in a living tree are of a very complex nature; they occur at different time intervals and in different dimensional spaces. The aging processes within a vegetation period are most obvious in the leaves: the swelling bud develops into young, pale leaves in spring, which grow to full size and obtain a firmer epidermis. After weeks and months they become discoloured after the first early frosts in autumn; the aging process, beginning when the leaves develop, gradually comes to a standstill, necrobiosis sets in and takes a rapid course. In the same space of time, cambium and xylem have also undergone an aging process which, however, is a process that will continue after the winter rest period and after the resumption of vegetation activity. Cambium and xylem thus age both with the rhythm of unit time and the integral passage of time. — While there is no lower limit to unit time, it can at most comprise a period of vegetation; long-term development is unlimited. In the measurable range the most aged trees are over 4,000 years old, as determined on *Pinus pinaster* trunks of a virgin pine forest in the higher regions of Arizona. However, this limit is entirely accidental and applies only unilaterally to the group of ring forming trees of temperate climatic zones. The biological phenomenon of the timelessness of organisms or organs capable of dividing thus becomes decisive for the individual age of tree: if the aging process is not subject to qualitative modifications as in the above example of the leaves, necrobiosis will at best involve certain tissues and not the individual as such. Individuals in which the aging process occurs only in the quantitative respect lose their age, they become time-less. Life as such is timeless; aging and death are fixed points in life due to environmental circumstances which do not as such correspond to its basic concept. However, of the more highly organized organisms, only individual tree relics are witnesses to this unbroken vitality.

Aging Processes in Cambium and Xylem

Cambium is defined as initial tissue which comprises the actively dividing fusiform- and ray-initials. The cambial zone comprises the phloem- and xylem-parent-cell tissues and their daughter cells which are not yet differentiated. The width of the cambial zone is variable and depends on the vegetational rhythm while the width of the cambium is commonly constant and comprises only one layer of cells. — In the xylem, the individual elements are grouped into tissue units which perform specific functions: tracheid or fibre ground-tissue is designed to perform mechanical functions, the tracheid- or vessel-system for the conduction of water and the ray and parenchyma tissue for storage.

In Scheme 1 the aging process in cambium, cambial zone and xylem is divided into processes occuring

Scheme 1. Aging Process in Cambium and Xylem

Tissue		Unit time *dt*	Time *t*
Fusiform initial layer	Quantitative aging	— Deceleration of division process	— Length growth of initials to maximum value — Growth in number of initial cells
Ray initial layer	Quantitative aging	— Deceleration of division process	— Growth in number of initial cells — Increase of ray matrix
Mother cell tissue	Quantitative aging	— Cell differentiation — Formation of secondary and tertiary walls	
Mechanical tissue	Qualitative aging	— Loss of protoplasm — Complete lignification	
Conducting tissue	Qualitative aging	— Loss of protoplasm — Complete lignification	— Pit closure in longitudinal tracheids — Closure of vessels by tyloses
Storage tissue	Qualitative aging	— Cells lose ability to divide	— Formation of heartwood substances — Formation of tyloses — Gradual necrobiosis

(Tissue groups, left margin: **Cambium + Cambial Zone** spans Fusiform initial layer, Ray initial layer, Mother cell tissue; **Xylem** spans Mechanical tissue, Conducting tissue, Storage tissue)

within a time unit and such as continue over several time units. The morphologically detectable changes within the cambial zone here designated as the quantitative expression of aging have been described mainly by I. W. Bailey, M. W. Bannan and H. E. Dadswell and collaborators in fundamental studies. Within unit time, they comprise, according to measurements taken by M. W. Bannan (1955), a retardation of divisions in the initial layer. The retardation in the dividing process, however, substantially determines the later formation of cambial derivatives: in the cambial zone, bipolar length- and surface-growth of the cells not highly differentiated are possible under morphogenetic laws; outside this zone, however, the shape and size are permanently fixed. In the event of rapid division in the cambium, daughter cells remain in the cambial zone and thus under the action of the growth promotion for only a short time; in the other case, where division is slow, there is sufficient time for a lasting development of both the cell unit as such and the cell wall in particular. This regularity can be found again, according to measurements made by I. J. W. Bisset and H. E. Dadswell (1950) in the interrelationship between fibre length and ring formation. — Along with the differentation of cells, the cell-wall construction is completed (A. B. Wardrop, 1964). The concept that cell-wall formation from the early development of the primary membrane via the secondary wall to the tertiary lamella is a specific phenomenon of the aging of plasma may be unfamiliar but fits well into the overall picture of cambium aging without the aid of mechanistic principles of explanation.

The three physiologically distinguishable tissues of the xylem are differently affected by aging within a time unit. The cells of the storage tissue lose their ability to divide; most retain their protoplast and are capable of active metabolism. This has initiated alterations in the activity of the tissue which are here referred to as the qualitative expression of aging. These qualitative changes lead to necrobiosis. The storage tissue is affected thereby only after the passage of several time units while the mechanical and water-conducting tissues are affected as a rule early after differentiation in that their cell units lose the protoplasts and are appropriated to strengthening and conducting functions as empty shells.

Beyond the time unit, cambium and xylem are subjected to aging processes which may be regarded as the summation of individual effects. In the cambial range, they occur as a quantitative development; in the xylem, however, they are qualitative. This differentiation indicated basic differences between the cambium and its derivatives: as the process of qualitative aging under optimal conditions is absent in the meristem, the latter will hardly be subject to the laws of necrobiosis. According to measurements taken by I. W. Bailey (1923) this is also seen in the morphology of the cambium when the length of the fusiform initials that continously increase in the first period of about one hundred years later asymptotically approach a parallel with the time axis. This dependence is applicable only to nonstoried cambium. Along with the phylogenetic development, the formative tissue thus loses part of its morphological dependence on time in that no increase in the length of the initial cells or only minor changes can be

observed in the storied cambium. — Independently of changes in the individual initial cells, their number increases in the rhythm of anticlinical divisions. The order of anticlinical divisions has·been determined by M. W. Bannan. His observations reveal that a fusiform initial in young conifer cambium can divide anticlinally three or four times per year ·and only once in an aged cambium; moreover, the products of division show considerably greater vitality in the young formative tissue than in the old in terms of the degree of their ability to divide.

The aging process in the xylem over extended periods involves mainly the storage tissue. Very decisive phenomena are observed which initiate the transformation of sapwood into heartwood and end in the necrobiosis of the storage tissue. The other tissue units are morphologically and physiologically fixed; the changes still occuring there are of a passive nature and relate mainly to the bordered-pit closure in tracheids, the blocking of vessels by tyloses and the deposition of heartwood substances in the cell walls.

Aging of Plasma and Cell-wall Formation

Since the micellar structure of cell walls found in the polarization microscope by A. Frey (1926) could be made accessible to direct observation in the electron microscope, the structural principle of the lignified cell wall may be regarded as known. While the discussion on the order of individual cell-wall lamellae is not yet terminated, more and more return to the view proposed by A. Frey-Wyssling in 1935 that the common central lamella and the primary walls adjacent thereto on either side (compound middle lamella) are followed by a three-layered secondary wall and a tertiary wall on both sides. What is fundamental for the structure of the cell wall in individual lamellae is the particular orientation of microfibrils: In the primary wall the fibrils are oriented crosswise similar to a real fabric, in the secondary walls, however, in parallel, the principal direction not infrequently changing from one lamella to the next. The tertiary wall is then deposited by the plasma as an amorphous terminal lamella against the cell lumen. Simply and generally defined, any cell wall having a cross-wise network of fibrils can be regarded as primary, while membranes with parallelized fibril texture are of secondary origin. — Primary, secondary and tertiary cell walls, however, are not only morphological units. As they represent stages which follow one another with the passage of time, they become the quantitative definition of the aging of the cytoplasm building them. The formation of new cell walls is dependent on cells capable of dividing and thus occurs only within the cambial zone. — Fig. 1 shows the deposition of a newly formed ray cell wall and reveals that this primary membrane is laid down during the telophase of nuclear division. It is likely that such wall formation occurs spontaneously in a random fashion following the principle of maximum disorder. The young cell wall is then enlarged by the plasma appropriated to the new cell and transformed into the secondary and tertiary stage by apposition. — The plasma unit appropriated to a cell in the formation of the primary· wall, is in unused young condition and under the special action of the nucleus which is capable of division; in contrast the deposition of the secondary cell
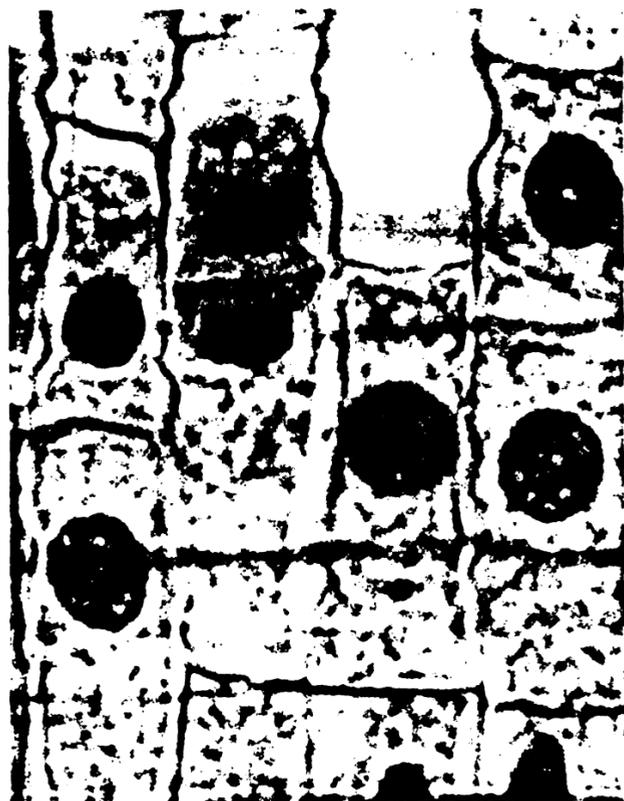
Fig. 1. Ray matrix in the cambial zone of *Picea abies* (Radial section). Telophase in dividing cell with new formed cell wall × 1135 (Microphotography by B. Meier)

wall — and particularly of the tertiary cell wall is by an aged plasma under the action of the nucleus which is no longer capable of division. In this context, the differences between the irregular texture of the primary wall, the parallel texture of the secondary wall and the amorphous texture of the tertiary wall may be regarded as the quantitative indication of plasma aging. It is in the nature of aging to display youth, maturity and senescence; the stage of maturity is commonly the one richest in energy while youth and senescence are poorer in energy. In the change from the irregular texture to the parallel order and finally to the amorphous stage, the three aging stages can be recognized and at the same time identified as the products of different formative energy. If the reactivating energy of the three cell walls required for their disintegration is taken as the measure for the formative energy required, it can readily be shown that the energy curve of aging is at a maximum in the mature stage of secondary cell wall formation. — The morphological order can thus be defined by its energy content as with the ferromagnetism of thin layers. Spontaneous magnetization occurs in a ferromagnet below Curie temperature independently of an exterior magnetizing field as per the thermodynamic theory of molecular fields (E. Kneller, 1962). This magnetization, however, is homogenous only in small areas (the Weiss area) and corresponds to the so-called zero structure in which the magnetization vectors mutually cancel each other. If an exterior magnetic field is allowed to act on a ferromagnet, its spontaneous magnetization will change in accordance with the field intensity applied: the magnetization vectors of the Weiss areas are successively oriented in the direction of the exterior magnetic field; the irregular structure of the zero-phase changes into a parallel structure which can be made visible by the so-called Bitter bands. The condition of parallelization is richer in energy than that of the zero phase. — This should be regarded merely as an analogy and not as a mechanistic attempt to explain the structure of parallel texture in secondary walls.

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Transformation of Sapwood into Heartwood

The sapwood/heartwood relation in living trees has time and again been the subject of comprehensive studies. The literature relating thereto has been largely collated by H. E. Dadswell und W. E. Hillis (1962). In their assumptions, these authors largely adhere to the conventional subdivision into sapwood trees (e. g. *Alnus incana*), ripewood trees (e. g. *Abies alba*) and trees with regular (e. g. *Pinus* species) or irregular (e. g. *Fagus silvatica*) heartwood formation. This terminology is contestable because it is based mainly on macroscopically visible characteristics and takes too little account of the cytology of the aging storage tissue. Indeed, many indications argue for the assumption that the transformation of sapwood into heartwood represents the final phase of an aging process in a living tree. The newly formed xylem is subject to qualitative aging in that the mechanical and conducting cells as a rule lose their protoplasts while the storage cells lose their capacity to divide within a time unit (e. g. a period of vegetation). In both cases, this initiates necrobiosis which occurs at different rates but finally leads to the death of cells and tissues. These necrobiotic processes should generally be regarded as the final phase of xylem aging and manifest themselves in the transformation of sapwood into heartwood. It should here be observed that heartwood formation can only proceed from the storage tissue and that this change is gradual in its action. Differences can be measured, in the first place, in the sapwood portion, but they also reveal themselves in the quality of heartwood formation. In young trees, the sapwood zone commonly reaches from the cambium to the pith; in older trees it usually comprises only a number of peripheral rings. Exceptions are found in the species previously as so-called "sapwood trees" which possess sapwood-type wood also in the vicinity of the pith. Too little is as yet known of the actual changes in the living tissue of these types in the vicinity of the pith, but we have good evidence of that the cytological aging of cells (A. Frey-Wyssling and H. H. Bosshard, 1959) at advanced tree ages is basically the same as in heartwood forming woods, with the exception that it begins later. Apart from these so-called sapwood trees, the transformation into heartwood usually begins regularly, but at least three modifications requiring to be observed: (1) woods having light heartwood (cf. ripewood trees). They clearly reveal necrobiosis of the storage cells without building large quantities of pigmented heartwood substances. Occasionally, however, coloured heartwood substances are found in the individual storage cells so that it must be assumed that their precursors are formed in the cambium of these woods as well, but obviously remain unpigmented. (2) Woods with obligatory-coloured heartwood (cf. trees with regular heartwood formation). In this group, which may also be known as the oak type, pigmented heartwood substances are invariably formed in the storage tissue, and are generally capable of penetrating into the cell walls of all tissue units. (3) Woods with facultative coloured heartwood (cf. trees with irregular heartwood). This group may be designated as the ash type. The brown heartwood of an ash need not occur in all samples and need not affect the entire heartwood portion. In

addition, the pigmented heartwood substances are commonly retained as wall coating or droplike inclusions in the cells of the storage tissue. In this case, the cell walls are not impregnated either in the storage tissue or in the rest of the xylem (H. H. Bosshard, 1955). — According to H. Erdtman and E. Rennerfelt (1944) precursors of the heartwood phenols are formed in the cambium and are capable of diffusion towards the heartwood border radially from the sapwood through the ray cells. In so doing, they are most probably subjected to oxypolymerization, which causes pigmentation and higher molecularity. It is conceivable that the polymerization process is so controlled in respect of time with the necrobiotic processes in the obligatory-coloured heartwood species that the heartwood substances are small enough when the plasma-semi-permeability ends to emerge into the adjacent tissues from the storage cells through the cell-wall filters. — In the facultative-coloured heartwood species the tendency to form coloured heartwood may be genetically less fixed so that it requires particular exterior influences to initiate the relative reactions. In this case, too, the pigmented heartwood substances are formed in the storage tissue; very likely, their synthesis sets in earlier in the still active sapwood so that when the cell dies they are of such high molecularity that they can no longer penetrate through the cell walls. In this case, the coincidence in respect of time necrobiotic processes and the synthesis of heartwood-substances would be decisive for the type of sapwood/heartwood transformation.
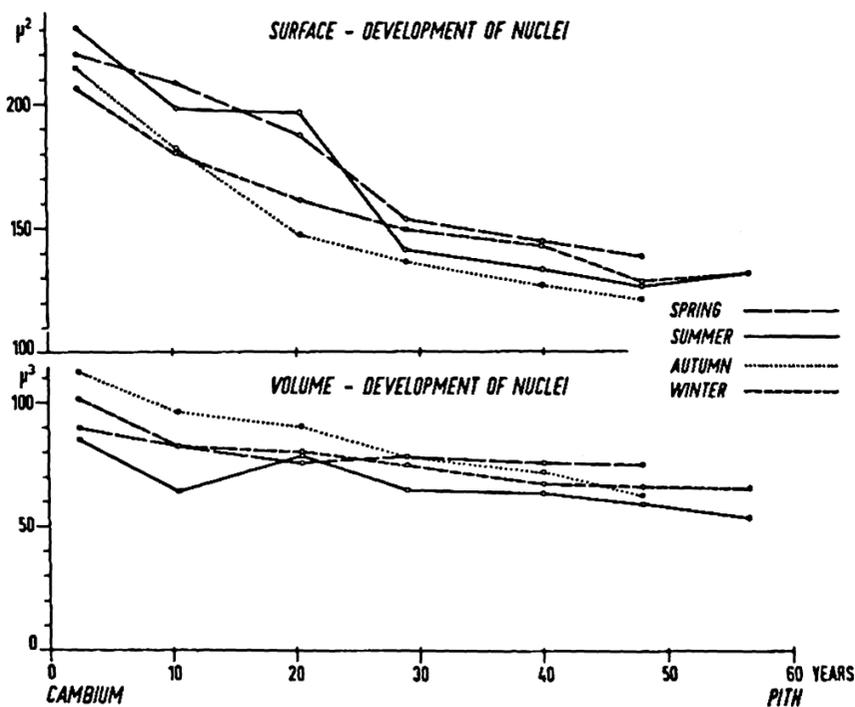

Fig. 2. Surface- and Volume-Development of nuclei in ray cells of ash (*Fraxinus excelsior*) in the four seasons (Measurements by U. Hugentobler)

Necrobiosis of the storage tissue was formerly described as the alteration of the nucleus which e. g. in conifers, gradually tends from an ellipse towards circular configuration becomes pycnotic and finally disappears. In describing the necrobiotic conditions, the degree of slenderness of the nucleus was previously employed. At present, other measured values are being tested for their significance. By way of example, the calculation of nucleus surfaces (Fig. 2) has proved to be useful. To begin with, the basis was the assumption that the activity of the cell should largely be attributed to surface reactions at the border between nucleus and

plasma. Indeed, results show that the nuclei in sapwood in the vicinity of the cambium are provided with larger surfaces than in the sapwood adjacent to the heartwood, which is true for all seasons. In addition, cell surfaces are larger in the active spring and summer months than in autumn and winter. — On the whole, the concept of the transformation from sapwood into heartwood which is the final stage of the aging process in the storage tissue, proves to be very useful in the organization of these complex problems.

Summary

In this brief paper only some aspects of aging in cambium and xylem have been considered. It is important that aging is quantitative in the meristem and qualitative in the xylem. Along with the change in the essential cell property — the capacity to divide — necrobiosis of the storage tissue is initiated in the final phase of xylem aging, which finally causes the sapwood to be transformed into heartwood. In addition, aging of wood within a time unit and in time generally is discussed. Aging of the plasma in the cell results in specific cell-wall structure while the aging of the meristem accounts for the formation of rings in springwood and summerwood. — The growth laws found by K. Sanio (1872) and the differences later established between juvenile and adult wood (B. J. Rendle, 1958), however, relate to the aging process in the cambium, which extends through decades and which can be measured by the continuous increase in the length of the fusiform initials. In this respect, it is particularly significant that the highly developed storied cambium assumes an exceptional position where the morphological dimension of the fusiform cells is already found in the juvenile condition.

Aspekte der Alterung von Kambium und Xylem

Zusammenfassung

In der Kürze des vorliegenden Beitrages sind im wesentlichen nur einige Aspekte der Alterung von Kambium und Xylem genannt worden. Wichtig ist der Hinweis, daß es sich im Meristem um eine quantitative Alterung handelt, im Xylem aber um eine qualitative. Mit der Veränderung der wesentlichsten Zellqualität — der Teilungsfähigkeit — wird in der Endphase der Alterung des Xylems die Nekrobiose des Speichergewebes eingeleitet, die schließlich zur Umwandlung des Splintes in das Kernholz führt. Weiter wird die Alterung des Holzes innerhalb einer Zeiteinheit und mit der Zeit im allgemeinen dargestellt. Dabei sind vor allem die Vorgänge im Bildungsgewebe momentan. So bedingt die Alterung des Plasmas in der Zelle spezifische Zellwand-Strukturen, die Alterung des Meristems den eigentlichen Jahrringaufbau in Früh- und Spätholz. — Die von K. Sanio (1872) gefundenen Wachstumsgesetze und die später erhobenen Unterschiede des jugendlichen und des alten Holzes (B. J. Rendle, 1958) gehen indessen auf die sich über Jahrzehnte hinziehende Alterung des Kambiums zurück, meßbar an der stetigen Längenzunahme der Fusiform-Initialen. Von besonderer Bedeutung ist in dieser Hinsicht die Ausnahmestellung der hochentwickelten Stockwerk-Kambien, in denen das morphologische Maß der Fusiforminitialen schon im Jugendstadium gefunden wird.

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Zur Morphologie der Tracheiden in Zellstoffen aus skandinavischem Birkenholz

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Einleitung

Nach gängiger Meinung setzen sich die europäischen Laubhölzer aus drei Zellelementen zusammen: den Sklerenchymfasern, den Gefäßen und den Markstrahlzellen. Hinzu kommt noch als viertes Element ein meist nur geringer Anteil an Längsparenchymzellen. Dagegen bleiben die Tracheiden meist unbeachtet. Weder Huber und Prütz (1) noch die Holzeigenschaftstafel „Birke" (2) bringen eine Bemerkung über Birken-Tracheiden. Nur das holzanatomische Werk von Greguss (3) erwähnt stichwortartig die Existenz dieses seltenen Zellelements im Birkenholz. In einer neueren Arbeit widmet Huber (4) den Tracheiden und Fasertracheiden der Angiospermen eine ganz allgemein gehaltene, kurze Notiz.

Aufgrund unserer eingehenden Beschäftigung mit der Morphologie der im Rotbuchenholz vorkommenden Tracheiden (5) haben wir während morphologischer Untersuchungen an technischen Birkenzellstoffen auch deren Tracheiden in den Kreis der zu bearbeitenden Fragen miteinbezogen.

Untersuchungsmaterial

Als Untersuchungsmaterial dienten je ein technisch hergestellter Birken-Papiersulfit- und -sulfatzellstoff. Beide Stoffe stammten aus Schweden; sie waren gebleicht und getrocknet. Die zu untersuchenden Proben wurden mit Brillantkongoblau 2 RW angefärbt (6).

Lichtmikroskopische Untersuchungen

Als Laubholztracheiden werden Zellen angesprochen, die dünnwandig, langgestreckt, beiderseits geschlossen und reich getüpfelt sind. Die beiden Pfeile der Abb. 1 weisen auf eine Zelle hin, die alle genannten Bedingungen erfüllt. Sie liegt mitten zwischen Birken-Sklerenchymfasern, wodurch der Unterschied, der zwischen einer Birken Sklerenchymfaser und einer Birkentracheide besteht, deutlich hervortritt. Die Birkentracheide der Abb. 1 ist 1,15 mm lang und 0,06 mm breit. Diese Zelle ist charakteristisch für Birkentracheiden, woraus man ableiten darf, daß die Birkentracheiden im Durchschnitt etwas kürzer, dafür aber etwas breiter sind als Birken-Sklerenchymfasern.

Bei stärkerer Vergrößerung tritt der Unterschied zwischen den Sklerenchymfasern und den Tracheiden noch viel deutlicher hervor. Abb. 2 zeigt einen Ausschnitt aus Abb. 1. Deutlich wird vor allem die für Birkentracheiden überaus reiche Tüpfelung; tüpfelarme Bereiche der Zellwand trifft man bei Birkentracheiden nur selten an. Dagegen sind die Sklerenchymfasern nur spärlich getüpfelt. Während die Tüpfel der Sklerenchymfasern sich mit ihren Spalten den Längsachsen der Zellen anpassen, bilden die Tüpfel der Tracheide Abb. 2 mit der Längsachse einen Winkel, der — wie bei den Buchentracheiden (5) — im Bereich um 45° liegt.

Abb. 3 zeigt als Teilvergrößerung aus Abb. 1 ein Ende der Birkentracheide. Es ist zwar reich getüpfelt jedoch ebenso geschlossen wie die der Sklerenchymfasern. Auch besitzt es keine leiterförmigen Durchbrechungen, wie sie z. B. bei Buchentracheiden (5) und Birken-Gefäßen (2) auftreten.

Abb. 4 zeigt einen Ausschnitt aus dem mittleren Teil einer anderen Tracheide. Ein Vergleich der beiden Tracheiden Abb. 2 und Abb. 4 läßt jedoch trotz gleicher Vergrößerung keine nennenswerten Unterschiede erkennen, weshalb sich die bei Besprechung der Abb. 1 bis 3 dargelegten Beobachtungen über Birkentracheiden verallgemeinern lassen sollten.

Bei den Untersuchungen an Buchentracheiden (5) erwiesen sich die Übergangsformen zwischen den Tracheiden und Gefäßen einerseits, den Tracheiden und Sklerenchymfasern andererseits als besonders aufschlußreich. Nach unseren Beobachtungen an beiden technischen Birkenzellstoffen scheinen im Birkenholz Zellen, die den Buchen-Fasertracheiden analog wären, nicht vorzukommen. Dagegen fanden sich in den Birkenzellstoffen ebenfalls Fasern, die man als Gefäß-Tracheiden bezeichnen darf.

Abb. 5 zeigt eine für diese seltene Zellform charakteristische Birken-Gefäßtracheide. Mit den Tracheiden stimmt sie in ihrer allgemeinen Erscheinung überein: sie ist langgestreckt und läuft gegen ihre beiden Enden hin spitz zu. Allerdings besitzt sie ein etwas größeres Lumen. Bei genauerer Betrachtung findet man jedoch außer der reichen Tüpfelung ihrer Oberfläche auch noch zwei Bereiche mit leiterförmigen Durch-