TERMINAL XYLEM AND INITIAL PARENCHYMA IN ANATOMICAL INVESTIGATIONS –

A REVIEW OF DEFINITIONS

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ABSTRACT: The term 'terminal parenchyma' (TP) is commonly used, although it has been applied in two different trends of studies, in two different meanings. Papers concerning differentiation of wood elements use the term 'terminal parenchyma' to describe a specific parenchyma tissue, whereas in examinations of cambial initials rearrangement recorded in consecutive layers of wood, authors apply the same term to the last layers of wood, produced at the end of the growing season. Those last layers may consist solely of parenchyma cells, or may include latewood vessels or fibres. It seems reasonable to preserve the 'terminal parenchyma' term as referring to actual parenchyma tissue. To describe a layer of xylem elements deposited at the end of each growing season (with no reference to their actual type) the usage of 'terminal late xylem' (TLX) term is more appropriate.

Regarding parenchyma tissue localised on the borders of annual increments, several definitions, like 'marginal' or 'boundary' parenchyma, have been introduced. Because of the fact that examinations of secondary xylem development are in the main stream of scientific research, it seems to be essential to improve the definition of every phenomenon and every structure of xylem. The aim of this review was to precise these definitions.

KEY WORDS: terminal xylem, terminal late xylem, terminal parenchyma, initial parenchyma, terminal layer

Seasonal activity of vascular cambium

In temperate climate the formation of secondary xylem mainly occurs in spring and early summer, so only during few months of the year, when temperature is high enough, called the growth season (Priestley 1930; Brown 1935; Frankenstein et al. 2005). Tropical trees sometimes do not exhibit annual cycles of wood formation or, if they do, the limiting factor seems to be water accessibility instead of low temperature (Kozlowski 1965; Dave and Rao 1982; Venogupal and Kirshnamurthy 1987; Dünisch et al. 2002; Leon-Gomez and Monroy-Ata 2005; Marcati et al. 2006; Westbrook et al. 2006). Growth periodicity has been described in species growing in tropical regions where dry season occurs with less than 50 mm precipitation per month (Worbes 1995). Dormant phase of deciduous trees is characterised by leaves' shedding (Medway 1972; Alvim and Alvim 1976) and subsequent decrease of wood growth (Mariaux 1969). The response to drought period differs among examined species (Worbes 1999), thus it seems to be genetically determined.

The secondary xylem formed at the beginning or ending of cambial activity is called earlywood and latewood respectively. Tracheary elements in earlywood and latewood usually differ in such features as thickness of cell walls or cell diameter, hence the mechanical and hydraulic properties of earlywood and latewood also differ (Haberlandt 1928). The consecutive rings comprising earlywood and latewood, called annual increments or growth rings (particularly distinct in ring-porous trees) are usually visible macroscopically. False growth rings have been described in several tropical trees, usually as a result of drought periods inducing the formation of latewood xylem elements (Worbes 1999).

Process of secondary xylem formation can be diversified into several stages, to some extent independent. The first stage involves multiplicative periclinal divisions of cambial fusiform cells, both initials and their derivatives – secondary xylem or phloem mother cells. When cambial derivatives move away from cambium, the next stage occurs – xylem mother cells grow in a way specific for their type. Cell fate determination presumably occurs very early,

before expansion phase begins (Catesson and Roland 1981; Catesson 1989). Together with growth of protoplast, an apposition of primary cell wall occurs (Fahn 1990; Larson 1994; Beck 2010). The last stage – differentiation – occurs after cessation of growth and usually includes: apposition of secondary cell wall, lignification, formation of perforation plates (vessel elements) and apoptosis (vessel elements, tracheids, fibres).

The separateness of growth from differentiation may be demonstrated by a comparison of typical morphology, i.a. dimensions of earlywood and latewood elements. The diameter of earlywood vessel elements is much bigger than that of their cambial ancestors, which is the result of their considerable lateral growth during development (Larson 1994; Beck 2010), characterised as intrusive in circumferential and symplastic in radial direction (Wilczek et al. 2011b). Fibres' axial dimension is several times that of their cambial ancestors and results from intrusive growth (Larson 1994; Jura et al. 2008; Beck 2010). Although latewood elements exhibit almost all distinctive morphological features (e.g. perforation plates in vessel elements), dimensions and shape of these cells resemble those of the cambial fusiform cells. Similar pattern of xylem elements development was observed, when a sample of developing wood was compressed mechanically (Bauer and Eschrich 1997). It seems that specific change of cells' dimensions during development of xylem elements is related with the occurrence of intrusive growth, which may be omitted without the disturbance of following differentiation.
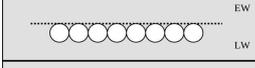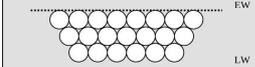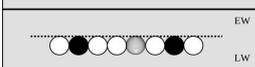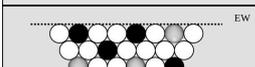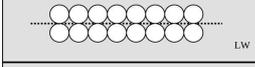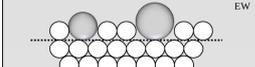
Parenchymatous cells at the borders of annual increments

At the borders between latewood of the given annual increment and earlywood of the next one, one or several layers of parenchymatous cells usually occur. Most species of temperate climate and some tropical ones produce parenchyma cells as the last layers of an annual increment, which has been commonly described as 'terminal parenchyma' (TP) (Holden 1912; Hejnowicz and Krawczyszyn 1969; Amobi 1974; Fisher 1981; Carquist 2001; Worbes 1999; Trouet et al. 2001; Dünisch et al. 2002; Deflorio et al. 2005; Robert et al. 2010). The detailed analysis revealed that the last formed layer of annual increment may consist not only of parenchyma cells, but also fibres (Barnett 1992; Dünish et al. 2002; Deflorio et al. 2005; Lisi et al. 2008) or latewood vessels (Marcati et al. 2006). Small solitary vessels were also observed in darker rings

of tropical trees wood, occurring between consecutive growth rings, although the typical boundary between rings was indistinct in those species (Ogata et al. 2001).

It was observed that some tropical trees, like *Terminalia tomentosa* and *Gmelina* sp., usually produce layers of fibres at the end of the growing season, and deposit the continuous or discontinuous layer of parenchyma cells as the first layer of the new annual increment, hence such parenchyma was defined as 'initial parenchyma' (Chowdhury 1934, 1936, 1953; Venogupal and Kirshnamurthy 1987; Détienne 1989; Dünish et al. 2002). Initial parenchyma develops from undifferentiated derivatives of cambial initials deposited on the xylem side in the previous year and overwintering in undifferentiated state (Dave and Rao 1982; Barnett 1992). In some other tropical trees there was observed neither terminal nor initial parenchyma, as in the case of *Magnifera indica* (Rao and Dave 1985). Simultaneous occurrence of terminal and initial parenchyma, like in *Robinia pseudoacacia*, was rarely observed (Carlquist 1980).

Next to 'terminal' and 'initial parenchyma', there was also introduced the term 'marginal parenchyma' as a layer of parenchyma tissue occurring at the boundary of growth rings. This term did not distinguish between the actual nature of parenchyma tissue: terminal or initial (Hess 1950; Gourlay and Kanowski 1991, Gourlay 1995; Wiemann et al. 1998; Westbrook et al. 2006; Lisi et al. 2008). However, the same term was also used to describe initial and terminal parenchyma occurring simultaneously (Carlquist 1980, 2001; Mainieri et al. 1983; Mainieri and Chimelo 1989; Marcati et al. 2006). We propose to specify those two definitions of marginal parenchyma as 'wide meaning' and 'narrow meaning' respectively (Fig. 1). Another term related with parenchymatous cells is 'boundary parenchyma', with no specification of terminal nor initial character of the tissue (Jane 1956; Patel 1974, 1978, 1987, 1988, 1990; Meylan and Butterfield 1978; Butterfield and Meylan 1980; Knowles and Beveridge 1982), i.e. in the same sense as the wide meaning of 'marginal parenchyma'.

Cells' configuration	TX	TL	IP	TP	MP(b)*	BP	MP(n)
	X	X	-	X	X	X	-
	X	-	-	X	X	X	-
	X	X	-	-	-	-	-
	X	-	-	-	-	-	-
	-	-	X	-	X	X	-
	-	-	X	-	X	X	-
	-	-	-	-	X	X	X
	-	-	-	-	X	X	X
	-	-	-	-	X	X	X
	-	-	-	-	X	X	X

Legend:

○ - parenchyma cell
◉ - vessel element
● - fibre
.... - growth boundary

MP(n) = TP+IP

MP(b)* = TP+IP, TP, IP

TX – terminal xylem;

TL – terminal layer;

TP – terminal parenchyma;

IP – initial parenchyma;

MP(b)* – marginal parenchyma (broad meaning);

MP(n) – marginal parenchyma (narrow meaning);

BP – boundary parenchyma;

EW – earlywood;

LW – latewood.

* the term 'marginal parenchyma' in a broad sense (equivalent to 'boundary parenchyma') is used, when the type of parenchymatous cells present at the border of increments is not strictly specified (thus, it may be initial parenchyma, terminal parenchyma, or both).

Fig. 1. Diagram illustrating possible applications of particular terms discussed in the paper. Horizontal dotted lines represent boundaries of growth increments. Cells below the line belong to the previous increment.

Sometimes, even in the same genus or species, the terminal or initial character of parenchymatous cells seems to be controversial, especially in some species living in tropical climate, like *Cedrela*. Mainieri et al. (1983), Mainieri and Chimelo (1989) described parenchyma layer as marginal (in narrow meaning) in this genus. *C. fissilis* was examined by Boninsegna et al. (1989) and *C. odorata* by Détienne (1989) and Botosso et al. (2000). In these cases axial parenchyma was recognised as initial. Other species of this genus have been examined and axial parenchyma was described as terminal (Détienne et al. 1982; Détienne and Jacquet 1983). Recent research revealed that in *C. fissilis* both terminal and initial layer of parenchyma occur, which has been defined as 'marginal parenchyma' (Marcati et al. 2006).

Even though the recognition of initial or terminal parenchyma might be difficult in some species, which may be the reason of some vagueness, these terms are clear and exact. Marginal parenchyma in the wide meaning and boundary parenchyma seem to describe exactly the same thing. Although the term 'marginal parenchyma' was firstly introduced in the wide meaning (Hess 1950), it has been commonly used in a narrow meaning afterwards (Carlquist 1980, 2001; Mainieri et al. 1983; Mainieri and Chimelo 1989; Marcati et al. 2006), so it seems to be reasonable to use it in a narrow meaning.

TLX and the examinations of cambial rearrangement

The examinations of changes of cambial initials' arrangement are mostly based on the analysis of tangential and transversal sections of secondary xylem. Gymnosperm trees have been widely examined, mainly because their tracheids hardly grow intrusively during wood development, thus they almost exactly reflect the arrangement of cambial initials existing before wood deposition (Hejnowicz 1961, 1964, 1968; Hejnowicz and Krawczyszyn 1969; Pyszyński 1972; Włoch 1976, 1985, 1987; Włoch et al. 2001, 2002). Examinations of the same type, concerning angiosperm trees' wood, are much more difficult, because xylem elements' mother cells show robust intrusive growth during wood maturation, thus the arrangement of cells is almost impossible to trace. This is why the most attention was paid to axial parenchyma cells, which do not grow intrusively during their development, and hence keep shape and dimensions of their ancestors – fusiform cambial initials. We can assume that a layer composed solely of parenchyma cells reflects the arrangement of fusiform initials existing at the moment of deposition of this layer of wood. The method comparing last layers of consecutive annual increments has been frequently applied for the angiosperm trees growing in temperate climate, since these layers usually consist of parenchyma cells and reflect the arrangement of cambial initials (Cumbie 1967; Hejnowicz and Krawczyszyn 1969; Hejnowicz and Romberger 1973; Krawczyszyn 1977; Włoch 1985, 1987, 1988; Włoch and Bilczewska 1987). When comparing those layers, described as 'terminal late xylem' (TLX), in subsequent annual increments, the annual changes can be demonstrated (Hejnowicz and Krawczyszyn 1969; Hejnowicz and Romberger 1973; Hejnowicz and Zagórska-Marek 1974; Krawczyszyn 1977). The term 'terminal layer' (TL) was used to describe the last layer of parenchymatous cells formed at the

end of growing season (Włoch 1988), although the author has not specified whether it can be used to describe the layer comprising other cell types. In our opinion, excluding cell types other than parenchymatous from TL definition is not justified. Later, the same author introduced a similar term – 'terminal xylem' (TX) (Włoch 1985, 1987), which has also been used by Barceló (2005). TX definition is wider than TL definition, as it may be applied to more than one layer of cells (Fig. 2). It may also be applied to describe e.g. wood of some tropical species, which do not exhibit distinct differentiation into earlywood and latewood, but possess terminal xylem, usually as a continuous layer of parenchyma cells. An example may be the wood of *Millettia laurentii*, presented by Richter and Dallwitz (2000).
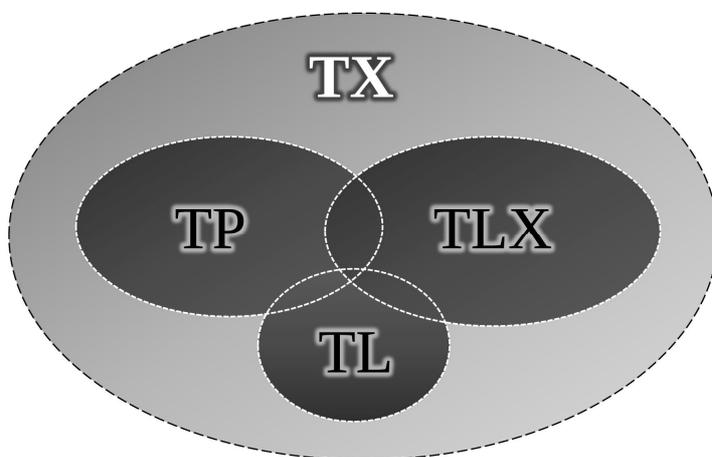

Fig. 2. Diagram illustrating semantic capacity and relations between terms applied in direct examinations of cambial rearrangement. TX – terminal xylem (bright grey oval bordered with black dotted line): the widest term, as it does not indicate the character of cells and may refer to many layers of cells. TLX – terminal late xylem (dark grey oval bordered with white dotted line): used to describe last layers of wood produced at the end of the growing season (as opposed to cases of false rings formation). TP – terminal parenchyma (dark grey oval bordered with white dotted line): applied, when last deposited layers consist solely of parenchymatous cells. TL – terminal layer (dark grey oval bordered with white dotted line): used to describe only the last layer of wood (also in false rings), with no strict indication of parenchymatous cells (therefore, to a certain extent, it corresponds to TP, TLX and TX application range).

In studies of cambial initials' rearrangement in temperate climate trees, with terminal late xylem consisting solely of parenchyma cells, the term 'terminal parenchyma' was also introduced (Włoch and Wawrzyniak 1990; Kojs et al. 2004 a,b, Jura et al. 2006; Wilczek et al. 2011a). Application of 'initial parenchyma' for this type of investigation may be questionable, because of frequent occurrence of large vessel elements (Marcati et al. 2006), locally modifying the arrangement of cells. Moreover, the parenchymatous cells are often scattered and do not form a continuous layer (Chowdhury 1953).

It seems reasonable to distinguish between terminal xylem (TX) and terminal/initial parenchyma. The definition 'TX' relates to the layer of cells displaying the same pattern as cambial initials, due to the absence of intrusive growth during maturation of xylem elements, rather than morphological features of xylem cells. The research of cambial initials rearrangement is focused on analyses of cells shape, contacts between cells, cells arrangement alterations, which are recorded in secondary xylem elements unless the intrusive growth is absent and the arrangement of cells during wood maturation remains unaffected. Therefore, while examining the layer (or layers) of wood with cells arrangement reflecting that of cambial initials, the term TX seems to be appropriate. The differentiation process, which is independent from growth, is irrelevant in these examinations. The definition 'TX' may be applied either to the layers composed solely of parenchyma cells or the layers containing fibres and latewood vessel elements in addition to parenchymatous cells.

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TERMINALNY KSYLEM I INICJALNA PARENCHYMA W BADANIACH ANATOMICZNYCH – PRZEGLĄD DEFINICJI

Streszczenie

W artykułach dotyczących różnicowania elementów drewna stosuje się nazwę „parenchyma terminalna" do opisu tkanki miękiszowej. Jednak w badaniach pośrednich przebudowy układu inicjałów kambium pojęcie to odnosi się do ostatnich warstw przyrostu rocznego. Warstwy te mogą składać się z komórek parenchymatycznych, ale mogą również zawierać włókna i naczynia. Wydaje się uzasadnione stosowanie nazwy „parenchyma terminalna" do opisu komórek miękiszowych, a do opisu ostatnich warstw przyrostu rocznego (nie odnosząc się do typu komórek) bardziej odpowiednia wydaje się być nazwa „drewno terminalne" (TX).