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Opinion Paper

SECONDARY XYLEM PARENCHYMA – FROM CLASSICAL TERMINOLOGY TO FUNCTIONAL TRAITS

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Terminology plays a crucial role in describing and understanding the morphological and anatomical variation in living organisms. The huge diversity in plant species and their many morphological and physiological adaptations to a wide range of ecosystems is reflected in an enormous anatomical variation of woody tissues. This is perhaps somewhat surprising given that angiosperm wood consists of essentially three cell types only: imperforate tracheary elements (fibres and tracheids), vessel elements, and living parenchyma cells. However, variation in the dimensions and the arrangement of these cells provide a challenge to anyone who aims to describe and understand quantitative and qualitative differences between wood samples. The challenge lies not only in the consistent application and interpretation of terms (Lens *et al*. 2012), but also in how we deal with a dynamic continuum (*i.e*., fuzzy morphology *sensu* Agnes Arber & Rolf Sattler) that includes intergradations, intermediate forms, analogous and homologous features (Sattler & Rutishauser 1997).

While the International Association of Wood Anatomy (IAWA) lists (IAWA Committee 1933, 1964, 1989, 2004) have been successful for identification and classification of angiosperm and gymnosperm wood, there is a lack of an anatomical glossary that goes beyond identification, covering the broad fields related to wood anatomy such as functional and ecological xylem anatomy, evolutionary and developmental wood anatomy, dendrochronology, etc. It is clear that achieving such a general glossary will never be perfect and will require a collaborative effort from many experts in various wood-related disciplines.

This opinion paper attempts to provide a critical review of terminology for wood parenchyma. It is especially concerned with the overlap between the descriptive terms used in systematic wood anatomical treatments and terms with functional implications. Most terminology for ray and axial parenchyma (RAP) has been defined based on the microscopy of transverse and longitudinal sections for wood identification purposes. A number of terms, especially for axial parenchyma, have changed in their usage or gone out of fashion; some of these are discussed here.

Parenchyma in secondary xylem

Parenchyma tissue in the secondary xylem of woody plants represents the living symplastic tissue that is intermeshed with the apoplast (the dead tissues, which include

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the fibres [except living, septate ones] and conductive elements). It plays a crucial but perhaps underrated role in plant physiology. The interest in the subject from a functional perspective has been variable, with a surge of interest during the mid to late 20th century (Braun 1964, 1984; Braun & Wolkinger 1970; Czaninski 1977; Sauter & Kloth 1986) followed by a decline and a resurgence of late (Salleo *et al.* 2004; Martínez-Cabrera *et al.* 2009; Zheng & Martínez-Cabrera 2013; Ziemińska *et al.* 2013, 2015; Spicer 2014; Morris *et al.* 2015). This renewed interest in ray and axial parenchyma (RAP) coincides with advances in image analysis and measurement techniques. Up to this point, a far greater focus has been on the dead conducting cells of wood (vessel elements and tracheids) and the mechanically important fibres of angiospermous wood (Carlquist 2015). As more papers report on wood, it is important to address the terminology used for RAP, as there is a tendency by those outside the discipline of wood anatomy to misuse the terms and provide incorrect information. An overview of the terms related to axial and ray parenchyma are presented in Table 1 and 2.

Functions of ray and axial parenchyma (RAP)

The terminology for describing RAP is important because disciplines outside of traditional wood anatomy are now paying more attention to their function, *e.g.*, plant physiology, functional ecology, plant-ecophysiology, plant pathology, and plant evolutionary-biology. The functions of RAP include: (1) storage and transport of non-structural carbohydrates (NSCs) (*e.g.*, Hoch *et al.* 2003; Salleo *et al.* 2004; O'Brien *et al.* 2014; Plavcová & Jansen 2015), (2) defence against pathogens (*e.g.*, Shigo 1984; Biggs 1987; Schmitt & Liese 1993; Deflorio *et al.* 2008), (3) water storage and capacitance (*e.g.*, Holbrook 1995; Borchert & Pockman 2005; Pfautsch *et al.* 2015), (4) storage of minerals such as calcium oxalate (Trockenbrodt 1995), (5) the transition of sapwood into heartwood (Pinto *et al.* 2004; Spicer 2005; Nawrot *et al.* 2008), and (6) biomechanical contributions, particularly by RP (*e.g.*, Mattheck & Kubler 1995; Burgert & Eckstein 2001; Reiterer *et al.* 2002).

Contact and isolation cells of the ray system

Secondary xylem parenchyma are living cells and are composed of two major cell types, ray parenchyma (RP) and axial parenchyma (AP), which are oriented perpendicular to each other. RP is aligned centripetally and formed from the ray initials of the cambium; AP is aligned axially and formed from the fusiform initials of the cambium (Metcalfe & Chalk 1983).

The cells in wide rays of angiosperms have been further categorised into two subtypes, 'contact' cells and 'isolation' cells, terms used by various authors to describe differing functions between the two (Braun 1964, 1984; Braun & Wolkinger 1970; Sauter & Kloth 1986, Murakami *et al.* 1999; Spicer 2014). Contact cells are in direct association with non-living conducting cells and have the ability to produce tyloses or gums. Isolation cells, which do not make any contact with conductive tissue, might be more specialised for radial transport (Sauter & Kloth 1986). Apart from their function, they also differ in form. Isolation cells are in many cases procumbent, and often have ray cells along their side, which are frequently 'upright cells'. The 'upright' cells, or

Table 1. Anatomical descriptions for terms related to axial parenchyma (AP), along with the definition and source(s) of the term.

Anatomical (descriptive) terms for AP		***Definition / comment***	***Sources for terms***
Apotracheal: *where AP is distant or does not appear to be in contact with a vessel*	*Subcategories*		
	Diffuse	AP scattered randomly, often sparse (*e.g. Carpinus* spp, *Crataegus* spp., *Cornus mas*).	IAWA Committee 1933
	Diffuse-in-aggregates	AP grouped in short tangential lines. No more than 2 cells wide (*e.g. Tilia* spp.).	Kribs 1937
	Reticulate	This is a term for very regular networks of parenchyma bands and multiseriate rays as seen in transverse section.	Record 1944; IAWA Committee 1989
	Banded AP	From one to many cells wide; up to three cells wide – narrow banded, more than three – wide banded. This refers to apotracheal banded AP, as you can also have banded AP that is paratracheal.	Kribs 1937
		Concentric – Many bands. Term no longer in use.	Jane 1956
		Scalariform – Successive fine lines or bands arranged horizontally or in arcs. Important point is that the distance between the rays is greater than the distance between bands (*e.g.* in Annonaceae), and that the rays are wider than the parenchyma bands.	Wagenführ 1961; IAWA Committee 1989
	Marginal AP	Bands of AP at a growth ring boundary. These are mainly apotracheal, though can be paratracheal.	Jane 1934; Hess 1950
		Initial – rarer. Occurs at the beginning of a growth ring (examples: *Cedrela odorata*, *Tectona grandis*).	
		Terminal – most common type. Occurs at the end of a growth ring (*e.g. Magnolia* spp.).	
	Ray-adjacent AP	Diffuse AP clustered along ray margins (*e.g. Staphylea* spp.).	Hess 1950; Carlquist & Hoekman 1985

(continued)

(Table 1 continued)

Anatomical (descriptive) terms for AP		***Definition / comment***	***Sources for terms***
Paratracheal: *where AP is in association with a vessel*	AP Scanty Paratracheal	A term agreed upon by the IAWA committee (1964) as preferred to vasicentric scanty (Kribs 1937). An incomplete sheath of AP surrounding a vessel or occasional AP cells touching the vessel (*e.g. Fraxinus* spp., *Laurus nobilis*).	IAWA Committee 1964, 1989
	AP Vasicentric	Where paratracheal parenchyma form a complete oval or circular sheath around a vessel or vessel group.	Jane 1934; IAWA Committee 1964, 1989
	AP Aliform	Paratracheal AP with lateral extensions, often wing-like, forming a diamond-shaped outline referred to as lozenge-aliform. It can either completely surround the vessel or can be to one side (*e.g. Inga* spp. and *Brosimum* spp.). Both winged-aliform and lozenge-aliform were designated as sub-types by the IAWA Committee 1989.	Kribs 1937; IAWA Committee 1989
	AP confluent	Where vasicentric or aliform arragements coalesce. It can completely surround or form to one side of a vessel or vessel group, forming irregular tangential or diagonal bands (*e.g. Parkia pendula*, *Maclura tinctoria*). A special case is banded-confluent, where many vessels are united by tangentially confluent parenchyma.	Kribs 1937; Metcalfe & Chalk 1950; IAWA Committee 1964
AP absent/extremely rare		AP absent or extremely rare intergrades with both apotracheal (diffuse) or scanty paratracheal. In order to make sure that the AP is absent or extremely rare it is necessary to view longitudinal as well as transverse sections (*e.g. Salix*, *Populus*, *Scottellia*). Septate fibres are often present where AP is rare or absent (Wheeler *et al*. 2007).	IAWA Committee 1989

Table 2. Functional descriptions for terms related to ray and axial parenchyma (RAP), along with the definition and source(s) of the term.

Functional terms for RAP		***Definition / comment***	***Sources for terms***
	Subcategories		
	Accessory tissues	Parenchymatous tissues in association with the conductive system (vessels and tracheids) via pit membranes (half-bordered or with reduced borders). Through these close pit contacts a functional unity exists between the accessory tissues and the conductive system. Concerns both angiosperms and gymnosperms.	Braun 1984
	Vessel-associated cells	Specialised RAP that are in contact with the vessels, as per term. Czaninski (1977) coined the term in preference to contact cells; however, both are used interchangeably today.	Czaninski 1977
	Paratracheal contact	Concerns only AP in actual contact with the vessels. Concerns angiosperms only. Braun (1984) coined this term as a means of specifically referring to angiosperms, where the term paratracheidal was coined in reference to only conifers. Not in use today.	Braun 1970, 1984
	Paratracheidal	AP in direct contact with tracheids. Gymnosperms only (not including those with vessels). The use of this term has been discontinued.	Braun & Wolkinger 1970
	Contact cells	These are specialised RAP in direct contact with the vessels, a term that is in wide use today and used interchangeably with the term ‘vessel-associated-cells’. Connected to vessels via half-bordered pit pairs or pit pairs with reduced borders.	Braun & Wolkinger 1970 Sauter 1972, 1988 Braun 1984
	Isolation cells	Confined to the ray system, and used to describe cells that have no contact with any conductive tissues. Probably, more specialised for radial transport.	Sauter & Kloth 1986 Murakami 1999
Vessel-distant AP	Storage cells (storage parenchyma)	RAP cells that have a common function in the storage of NSCs. These are not classified as specialised cell types. These can also contain tannins and crystals, such as calcium oxalate and tend to have more numerous plasmodesmata connections (Bonnemain & Fromard 1987; Czaninski 1987).	Czaninski 1977

‘erect’ ray cells, have the same orientation as the axial parenchyma, and may perform the same function as diffuse axial parenchyma in forming contacts between conduits and parenchyma, or simply contact between other parenchyma only (Holl 1975; Carlquist 2001). Conifers, on the other hand, have predominantly uniseriate rays, and therefore have contact cells only in their ray structure, where all ray parenchyma cells have some contact with tracheids.

Arrangements of the axial parenchyma system

Paratracheal axial parenchyma (AP)

AP is situated between the rays and is aligned vertically. These cells may be highly grouped around the vessels, which is termed ‘paratracheal’, or alternatively, the AP cells may completely surround the vessel as regular layers, a condition referred to as ‘vasicentric’ (*e.g.* in *Phoebe porosa*, *Enterolobium cyclocarpum*, *Olea europaea*). However, more commonly, the AP is scanty paratracheal, or may be either aliform or confluent in arrangement. The scanty paratracheal arrangement is very frequent, occurring in up to 28 % of all hardwoods (Wheeler *et al.* 2007). Aliform is wing-shaped with lateral extensions and is further subdivided into ‘lozenge-aliform’ (*e.g. Microberlinia brazzavillensis*, *Qualea rosea*) or ‘winged-aliform’ (*e.g. Jacaranda copaia*, *Terminalia superba*, *Brosimum* spp.). The term ‘confluent’ describes paratracheal arrangements that coalesce or where aliform types completely surround or are to one side of two or more vessels together (*e.g. Parkia pendula*, *Peltogyne confertiflora*). Both aliform and confluent have been considered a sub-set of abundant vasicentric (Kribs 1937; Carlquist 2001); however, this usage is not very common. The term ‘scanty paratracheal’ (see *Catalpa ovata*; Fig. 1c) describes a situation where the AP does not completely sheath the vessel or a vessel group, or where they are just occasionally making contact with the vessel (*e.g. Pistacia vera*, *Laurus nobilis*, *Fraxinus excelsior*) (Hess 1950; Metcalfe & Chalk 1950; Plavcová & Jansen 2015). Unilateral paratracheal parenchyma is of rare occurrence, and if present, often found alongside other paratracheal arrangements. It describes paratracheal AP that forms to one side of the vessels and is shaped in a semi-circular fashion (*e.g. Peltogyne confertiflora*). The terms abaxial and adaxial describe paratracheal AP arranged to either side of a vessel and have been fused into the term ‘unilateral’ and generally discontinued as descriptors because in most wood samples or sections of mature stems the orientation with respect to the cambium and pith is not obvious (IAWA Committee 1989).

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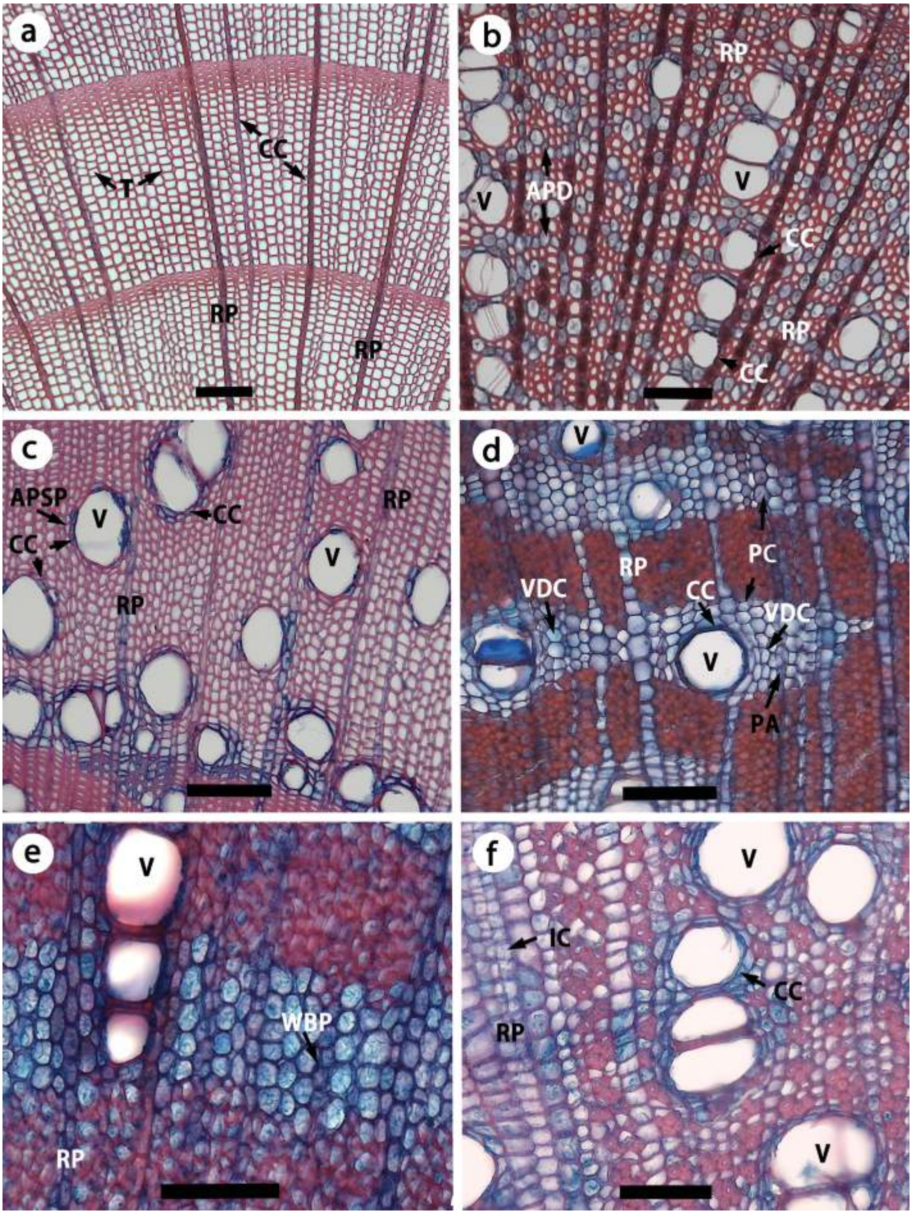
Figure 1. Light microscopy images of the transverse sections of one conifer and five angiosperm species showing different axial parenchyma (AP) and ray parenchyma (RP) cell arrangements where both functional and anatomical terms are shown for (a) *Picea abies* (Pinaceae), a temperate species with no axial AP present, and where all the uniseriate RP are contact cells (CC) having direct contact with the tracheids (T), (b) *Quercus robur* (Fagaceae), a temperate species with axial parenchyma diffuse (APD), (c) *Catalpa ovata* (Bignoniaceae), a temperate species with axial parenchyma scanty paratracheal (APSP) shown here as contact cells, (d) *Amherstia nobilis* (Fabaceae), a tropical species with AP in paratracheal arrangements called paratracheal aliform



(AP) and paratracheal confluent (PC), (e) *Caesalpinia mexicana* (Fabaceae), a subtropical species with wide-banded parenchyma (WBP), and (f) *Ceiba pentandra* (Malvaceae), a tropical species with wide mutiseriate rays showing the isolation cells (IC) between the two most outer layers. All are from stem wood, except *Q. robur*, which was taken from the roots. The sections were stained with a combination of safranin and alcian blue, where the red colour of the former highlights strongly lignified cell walls of the tracheids, vessels and fibres, while the blue stain of the latter highlights both AP and RP. All scale bars represent 100 μm.

There is a complication between the commonly used anatomical definition of paratracheal (Metcalfe & Chalk 1983) and Braun's (1984) functional definition. From a functional point of view, it is essential to have such a term that describes AP in immediate contact with vessels rather than also including vessel-distant AP that is part of a complete paratracheal arrangement. Braun termed vessel-distant paratracheal parenchyma 'interfibrous parenchyma', and devised the more specific term paratracheal-contact cells for the "accessory tissue" of his "hydrosystem", in analogy with the contact cells of the rays. The use of the term 'interfibrous parenchyma' was unfortunate, as it encompassed an array of arrangements that are in themselves quite distinct.

Terms can be essential for the identification of wood; however, from a functional perspective, many of the terms are less valuable because of a morphological continuum. For instance, the difference between a unilateral and a lozenge-aliform arrangement may be functionally negligible, as the only separation between the two is that the latter has a diamond-shaped outline and is present around the whole vessel, an important difference for wood identification purposes. However, the broader terms, such as apotracheal, paratracheal and even scanty paratracheal are certainly important terms for functional studies, as these arrangements have an important association with the vessel in relation to capacitance and defence (Brodersen *et al.* 2010; Plavcová & Jansen 2015; Morris *et al.* 2015). For instance, the lack of such AP arrangements in most conifer species may explain why they require narrow, "safe" tracheids as conductive tissue (Choat *et al.* 2012).

Apotracheal axial parenchyma (AP)

The term 'apotracheal' describes AP cells that are not associated or contiguous with vessels in transverse section. Some random contacts may exist, although these are infrequent (Evert 2006). Diffuse, diffuse-in-aggregates, and marginal AP essentially describes three subcategories of AP that are not in association with vessels. The descriptive terms for AP are when the AP appears distributed in transverse sections. For instance, in the case of diffuse there are a number of sources that describe AP as being isolated and irregularly dispersed, which is true when viewed as a single transverse section. However, from a functional point of view this is not the case, as such cells cannot be isolated from surrounding symplastic tissue because all parenchyma cells are to some degree interconnected with each other (Zimmermann & Tomlinson 1966; Zimmermann 1971). All diffuse parenchyma types are networking with both the vessels and the ray system. This was demonstrated by Zimmerman (1971) who showed that an isolated group of AP will sooner or later contact other AP and/or RP.

Alternatively, AP might act as a transport bridge between rays, thus by-passing the vessels altogether, as is the case with the AP pattern diffuse-in-aggregates or the narrow bands of axial parenchyma. The latter term 'diffuse-in-aggregates' describes where they form tangential lines, of no more than one cell wide between rays, although in transverse section one may or may not see diffuse-in-aggregates contacting rays (Metcalfe & Chalk 1950; Carlquist 2001). Examples of diffuse-in-aggregates include *Tilia* spp. (Malvaceae) and *Dalbergia stevensonii* (Fabaceae). Diffuse AP are more commonly associated with temperate species. In tropical tree species where AP is absent or rare, there is a higher incidence of septate fibres (Wheeler *et al*. 2007). Here, septate fibres are presumably taking over the functional role of AP, where examples include: Achariaceae, Araliaceae, Burseraceae and Salicaceae. Both Araliaceae and Salicaceae are found in temperate and tropical biomes. *Kalopanax septemlobus* (Araliaceae) is an excellent example of a temperate species with absent or extremely rare AP, but with an abundance of septate fibres taking over the functional role.

The term 'banded' applies to AP that is one to many cells wide, and this is further subdivided into narrow-banded and wide-banded apotracheal AP (see *Caesalpinia mexicana*; Fig. 1e). Although banded arrangements are mostly apotracheal, they can be paratracheal, where they are clearly associated with the vessels. Under the IAWA Committee (1989) it forms a separate group of arrangements that includes the arbitrary, overlapping sub-categories (1) axial parenchyma bands more than three cells wide, (2) axial parenchyma in narrow bands or lines up to three cells wide, (3) axial parenchyma reticulate, (4) axial parenchyma scalariform and (5) axial parenchyma in marginal or in apparently marginal bands. Wide bands (more than three cells wide) are much more common in tropical trees, perhaps acting as a dynamic barrier against the inward advance of decay, thus replacing the growth ring of temperate species, a static barrier where highly lignified fibres slow the spread of decay; this is Wall 2 of the CODIT model, an acronym for Compartmentalisation of Decay in Trees (Shigo 1984). Although wide banded AP are more common in the trees of the tropics than in temperate regions (*e.g*. Meliaceae and Moraceae), they still have a rare overall occurrence with only a 9% of the world's woods having this characteristic (Wheeler *et al*. 2007). A quick check of 834 species with wide bands (InsideWood database: Wheeler *et al*. 2007) showed a much higher incidence of wide parenchyma bands with growth rings absent or indistinct (748 species out of the total) indicating that in the absence of growth rings, parenchyma may be taking on a defensive role. When the wide bands run via vessels, they intergrade with confluent AP, a pattern under the umbrella of paratracheal. A term was in use to describe this as 'banded confluent' (Jane 1970), which acknowledged that bands are not always circumferentially continuous, but can be as a result of there being a considerable amount of confluent parenchyma that form together to appear as bands. There are, of course, gradations in the continuity of the bands and they can appear independent of vessels or extend from vessel to vessel where then the distribution of the bands appears related to the position of the vessel.

Marginal AP, coined by Hess (1950) is banded, but laid out at the beginning or at the end of a growth ring, termed, respectively, initial and terminal. Usually only one type is present in a species, although some species have both, for example *Robinia pseudoacacia*, although this rarely occurs (Carlquist 1980). We do know that in a number of temperate species apotracheal terminal parenchyma participate actively in defence, particularly against brown rot fungi (Schwarze & Fink 1998, Schwarze *et al*. 2000, 2003; Schwarze 2007). However, this anatomical trait has a worldwide distribution, from temperate to subtropical and tropical biomes, and studies conducted were biased to species of temperate origin. The InsideWood database (Wheeler *et al*. 2007) reports 1782 from a total of over 5000 species to have marginal parenchyma.

From a descriptive to a functional terminology

Braun (1970, 1984) tried to include both gymnosperms (with the exception of the Gnetales) and angiosperms (not including vesselless genera) by referring to RAP in association with either tracheids or vessels as 'accessory tissues' of his hydrosystem, a term now mostly discontinued in modern publications. This was a very specific functional term used by Braun (1984), where he makes a distinction between tropical and temperate trees. Braun suggested that in tropical trees accessory tissue tends to have little or no starch because the sugars are in a state of constant remobilisation. By contrast, temperate trees have starch in the accessory tissues, but it is broken down earlier than in surrounding parenchyma (Sauter 1966; Braun 1984; Essiamah & Essiamah 1985). The accessory tissues further included the functional terms 'paratracheidal parenchyma' and 'paratracheal contact parenchyma', two terms referring specifically to AP of both gymnosperms and angiosperms, respectively. Braun's (1984) usage of the term 'paratracheidal' was perhaps to make a distinction between the tracheids of conifers and the vessels of angiosperms, particularly for tropical conifers, which have, on average, more AP than their temperate counterparts, such as in many genera of the Podocarpaceae (Morris *et al.* 2015). The contact cells of the rays were also included in Braun's accessory tissues (Braun 1964, 1970, 1984).

The term 'contact cell' (see Fig. 1) was also coined for any parenchymatous cell in contact with a vessel (Sauter 1966, 1973). More recent papers have been using the original Sauter (1966) application of the term 'contact cell' (Bonsen & Kučera 1990; Améglio & Cruiziat 1992; Sokołowska 2013; Zwieniecki & Holbrook 2009; Secchi & Zwieniecki 2012). Isolation cells, from a functional and spatial perspective, not only apply to the ray structure; vessel-distant cells (see *Amherstia nobilis*; Fig. 1d) within a large group of paratracheal AP (surrounding a vessel) are in effect isolated to the same degree as those of the ray system, and may have similar functions.

Irrespective of the difference in cambial origin between RP and AP, there is a striking analogy between them as both have contact cells and vessel-distant cells, and many common functions are shared. For instance, contact cells from RP and AP (1) both have different pits, which are either half-bordered or simple, possibly functioning in the hypothetical release of sugar into vessels as opposed to those that just store NSCs (Sauter 1972, 1973; Braun 1984), (2) both can form tyloses during heartwood formation when the pit aperture exceeds 10 μm, or gums when the width falls below this figure, although tyloses occur largely from the RP during the transition to heartwood (Chattaway 1949), while elsewhere in the sapwood, in response to pathogens etc., tyloses can occur where pits exceed 3 μm (Bonsen & Kučera 1990), (3) both have a protective layer (Schmid 1965), also referred to as the amorphous layer when referring to vessel-associated RP and AP (Fujii *et al.* 1980, 1981), and (4) both have similar enzymatic activity marked by high mitochondrial counts and carbohydrate storage/mobilisation cycles (Sauter 1973; Essiamah & Eschrich 1985; Alves *et al.* 2001). While, on the other hand, isolation cells (see *Ceiba pentandra*; Fig. 1f) of the ray structure, and paratracheal vessel-distant AP have: (1) no pit-mediated direct contact associations with vessel elements, (2) high plasmodesmatal densities, as no plasmodesmata are at the interface between a contact cell and a vessel (Bonnemain & Fromard 1987;

Czaninski 1987), and (3) long-term storage capacities (large vacuoles) with generally slow mobilisation cycles, most evidently in temperate species (Braun 1984). In fact, during autumn, RAP that does not have contact with vessels accumulate oxalate, tannins, or large quantities of starch, a trend not shown in contact cells (Buvat 1989).

Czaninski (1964, 1977, 1987) in the 1960s coined the term 'vessel-associated cells' (VACs) as a term for AP and RP in contact with vessels that share common functions. It was first used in the case of *Robinia pseudoacacia* for the small 'specialised cells' surrounding the vessels, and represented a more precise description than just 'contact cells'. The VACs were used as a means to further divide cells from those with a common function, such as storage of NSCs, into those with more 'specialised' functions, like the production of tyloses, or the secretion of defensive compounds into the vessel. Czaninski (1970) also coined the term 'storage cells' for vessel-distant AP, which are distinguished from VACs (or contact cells) by their larger lumen and vacuole size.

Another term, 'transfer cells', as coined by Gunning *et al.* (1968, 1974) and normally used in unison with the phloem, had its use extended to xylem parenchyma in association with vessels. Chafe (1974) stated that the contact cells might function as transfer cells owing to a similar structure as those in the phloem. While as useful an analogy as it may have sounded, the term used in this context seems to have expired, because vessel-contact cells lack the elaborate wall invaginations typical of true transfer cells. These days, the terms VACs and contact cells can be used interchangeably for angiosperms, while contact cells is a suitable term when also referring to conifers.

Conclusion and outlook

Terms we coin and define for RAP are critically important for how we interpret them, and therefore use them in the right context, especially in relation to xylem function. Rather than a revision of terms, the main message here is that it is important to be mindful of what term to use and where correctly to use it, whether it be from a functional or structural perspective.

More attention should be paid to the three-dimensional structure and arrangement of RAP, which remains poorly explored despite the development of novel techniques such as high resolution computed tomography and image analysis tools (*e.g.*, alignment and stitching tools; Huggett & Tomlinson 2010; Brodersen 2013). Moreover, precise descriptions in combination with exact quantification are highly desired to make progress in the field of functional and ecological wood anatomy (Scholz *et al.* 2013; von Arx *et al.* 2013, 2015). We also hope that training of new students will be offered in such a way that they will develop a special eye for detail and accuracy, which is required to capture the maximum information available in wood. Many of us would indeed be surprised by how many details are presented in old literature such as the works by Moll & Janssonius (1909–1936).

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REFERENCES

Alves G, Sauter JJ, Julien J-L, Fleurat-Lessard P, Améglio T, Guillot A, *et al*. 2001. Plasma membrane H$^+$-ATPase, succinate and isocitrate dehydrogenases activities of vessel-associated cells in walnut trees. J. Plant Physiol. 158: 1263–1271.

Améglio T & Cruiziat P. 1992. Alternance tension/pression de la sève dans le xylème chez le noyer pendant l'hiver: rôle des températures. C.R. Acad. Sci. Paris, sér. III, 315: 429–435.

Biggs AR. 1987. Occurrence and location of suberin in wound reaction zones in xylem of 17 tree species. Phytopathol. 77: 718–725.

Bonnemain J & Fromard L. 1987. Physiologie comparée des cellules compagnes du phloème et des cellules associées aux vaisseaux. Bull. Soc. Bot. France 134: 27–37.

Bonsen KJM & Kučera LJ. 1990. Vessel occlusion in plants: morphological, functional, and evolutionary aspects. IAWA Bull. n.s. 11: 393–399.

Borchert R & Pockman WT. 2005. Water storage capacitance and xylem tension in isolated branches of temperate and tropical trees. Tree Physiol. 25: 457–466.

Braun HJ. 1964. Zelldifferenzierung im Holzstrahl. Ber. Deut. Bot. Ges. 77: 355–376.

Braun HJ. 1970. Funktionelle Histologie der Sekundären Sprossachse I. Das Holz. Encyclopedia of Plant Anatomy IC, part 1. Borntraeger, Berlin.

Braun HJ. 1984. The significance of the accessory tissues of the hydrosystem for osmotic water shifting as the second principle of water ascent, with some thoughts concerning the evolution of trees. IAWA Bull. n.s. 5: 275–294.

Braun HJ & Wolkinger F. 1970. Zur funktionellen Anatomie des axialen Holzparenchyms und Vorschlage zur Reform seiner Terminologie. Holzforschung 24: 19–26.

Brodersen CR, McElrone A, Choat B, Matthews M & Shackel K. 2010. Dynamics of embolism repair in grapevine: *in vivo* visualisations using HRCT. Plant Physiology 154: 1088–1095.

Brodersen CR. 2013. Visualizing wood anatomy in three dimensions with high-resolution X-ray micro-tomography. IAWA J. 34: 408–424.

Burgert I & Eckstein D. 2001. The tensile strength of isolated wood rays of beech (*Fagus sylvatica* L.) and its significance for the biomechanics of living trees. Trees 15: 168–170.

Buvat R. 1989. Ontogeny, cell differentiation, and structure of vascular plants. Springer-Verlag, Berlin, Germany.

Carlquist S. 1980. Further concepts in ecological wood anatomy with comments on recent work in wood anatomy and evolution. Aliso 9: 499–535.

Carlquist S. 2001. Comparative wood anatomy. Systematic, ecological, and evolutionary aspects of dicotyledon wood. Ed. 2. Springer-Verlag, Berlin, Germany.

Carlquist S. 2015. Living cells in wood. 1. Absence, scarcity and histology of axial parenchyma as keys to function. Bot. J. Linn. Soc. 177: 291–321.

Carlquist S & Hoekman D. 1985. Wood anatomy of Staphyleaceae: ecology, statistical correlations and systematics. Flora 177: 195–216.

Chafe SC. 1974. Cell wall formation and 'protective layer' development in the xylem parenchyma of trembling aspen. Protoplasma 80: 335–354.

Chattaway MM. 1949. The development of tyloses and secretion of gum in heartwood formation. Aust. J. Sci. Res. B-Biol. 2: 227–240.

Choat B, Jansen S, Brodribb TJ, *et al*. 2012. Global convergence in the vulnerability of forests to drought. Nature 491: 752–755.

Czaninski Y. 1964. Variations saisonnières du chondriome dans les cellules du parenchyme ligneux vertical de *Robinia pseudoacacia*. C.R. Acad. Sci. 258: 697–682.

Czaninski Y. 1977. Vessel-associated cells. IAWA Bull. 3: 51–55.

Czaninski Y. 1987. Généralité et diversité des cellules associées aux éléments conducteurs (cellules de contact sensu lato). Bull. Soc. Bot. Fr. Actual Bot. 134: 19–26.

Deflorio G, Johnson C, Fink S & Schwarze FMWR. 2008. Decay development in living sapwood of coniferous and deciduous trees inoculated with six wood decay fungi. For. Ecol. Man. 255: 2373–2383.

Essiamah S & Eschrich W. 1985. Changes of starch content in the storage tissues of deciduous trees during winter and spring. IAWA Bull. n.s. 6: 97–106.

Evert RF. 2006. Esau's Plant anatomy: meristems, cells, and tissues of the plant body: their structure, function and development. Ed. 3. Wiley, Hoboken, New Jersey, USA.

Fujii T, Harada H & Saiki H. 1980. The layered structure of secondary walls in axial parenchyma of the wood of 51 Japanese angiosperm species. Mokuzai Gakkaishi 26: 373–380.

Fujii T, Harada H & Saiki H. 1981. Ultrastructure of 'amorphous layer' in xylem parenchyma cell wall of angiosperm species. Mokuzai Gakkaishi 27: 149–156.

Gunning BES & Pate JS. 1974. Transfer cells. In: Robards AW (Ed.), Dynamic aspects of plant ultrastructure: 441–479. McGraw-Hill, London, UK.

Gunning BES, Pate JS & Briarty LG. 1968. Specialized "transfer cells" in minor veins of leaves and their possible significance in phloem translocation. J. Cell Biol. 37: 7–12.

Hess RW. 1950. Tropical wood: classification of wood parenchyma in dicotyledons. Trop. Woods 96: 1–20.

Hoch G, Richter A & Korner CH. 2003. Non-structural carbon compounds in temperate forest trees. Plant Cell Environ. 26: 1067–1081.

Holbrook NM. 1995. Stem water storage. In: Gartner BL (Ed.), Stems and trunks in plant form and function: 151–174. Academic Press, San Diego, USA.

Höll W. 1975. Radial transport in rays. In: Zimmermann MH & Milburn JA (Eds.), Transport in Plants I. Phloem transport: 432–450. Springer-Verlag, Berlin, Heidelburg, New York.

Huggett BA & Tomlinson PB. 2010. Aspects of vessel dimensions in the aerial roots of epiphytic Araceae. Int. J. Plant. Sci. 171: 362–369.

IAWA Committee. 1933. Glossary of terms used in describing wood. Trop. Woods 36: 1–12.

IAWA Committee on Nomenclature. 1964. Multilingual glossary of terms used in wood anatomy. Konkordia, Winterthur, Switzerland.

IAWA Committee. 1989. IAWA list of microscopic features for hardwood identification. IAWA Bull. n.s. 10: 219–332.

IAWA Committee. 2004. IAWA list of microscopic features for softwood identification. IAWA J. 25: 1–70.

Jane FW. 1934. Terminal and initial parenchyma in wood. Nature 133: 534–534.

Jane FW. 1970. The structure of wood. (Ed. 2, revised by Wilson K & White DJB). A. and C. Black, London, UK.

Kribs DA. 1937. Salient lines of structural specialization in the wood parenchyma of dicotyledons. Bull. Torrey Bot. Club 64: 177–186.

Lens F, Cooper L, Gandolfo MA, Groover P, Jaiswal P, Lachenbruch R, Spicer R, Staton D, Stevenson DW, Walls RL, *et al*. 2012. An extension of the Plant Ontology project supporting wood anatomy and development research. IAWA J. 33: 113–117.

Martínez-Cabrera HI, Jones CS, Espino S & Schenk HJ. 2009. Wood anatomy and wood density in shrubs: responses to varying aridity along transcontinental transects. Amer. J. Bot. 96: 1388–1398.

Mattheck C & Kubler H. 1995. Wood – the internal optimization of trees. Springer-Verlag, Berlin, Germany.

Metcalfe CR & Chalk L. 1950. Anatomy of the dicotyledons. Clarendon Press, Oxford, UK.

Metcalfe CR & Chalk L. 1983. Anatomy of the dicotyledons. Ed. 2. Vol. II. Wood structure and conclusion of the general introduction. Clarendon Press, Oxford, UK.

Moll JW & Janssonius HH. 1909–1936. Mikrographie des Holzes der auf Java vorkommenden Baumarten, 6 vols. Brill, Leiden.

Morris H, Plavcová L, Cvecko P, Fichtler E, Gillingham MAF, Martínez-Cabrera HI, McGlinn D, Wheeler E, Zheng J, Ziemińska K & Jansen S. 2015. A global analysis of parenchyma tissue fractions in secondary xylem of seed plants. New Phytol. doi:10.1111/nph.13737.

Murakami Y, Funada R, Sano Y & Ohtani, J. 1999. The differentiation of contact cells and isolation cells in the xylem ray parenchyma of *Populus maximowiczii*. Ann. Bot. 84: 429–435.

Nawrot M, Pazdrowski W & Szymanski M. 2008. Dynamics of heart-wood formation and axial and radial distribution of sapwood and heartwood in stems of European larch (*Larix decidua* Mill.). J. For. Sci. 54: 409–417.

O'Brien MJ, Leuzinger S, Philipson CD, Tay J & Hector A. 2014. Drought survival of tropical tree seedlings enhanced by non-structural carbohydrate levels. Nature Clim. Change 4: 710–714.

Pfautsch S, Renard J, Tjoelker MG & Salih A. 2015. Phloem as capacitor: radial transfer of water into xylem of tree stems occurs via symplastic transport in ray parenchyma. Plant Physiol. 167: 963–971.

Pinto I, Pereira H & Usenius A. 2004. Heartwood and sapwood development within maritime pine (*Pinus pinaster* Ait.) stems. Trees-Struct. Funct. 18: 284–294.

Plavcová L & Jansen S. 2015. The role of xylem parenchyma in the storage and utilization of non-structural carbohydrates. In: Hacke UG (Ed.), Functional and ecological xylem anatomy: 209–234. Springer, Switzerland.

Record SJ. 1944. Keys to American hardwood. XII. Parenchyma reticulate. Trop. Woods 74: 31–43.

Reiterer A, Burgert I, Sinn G & Tschegg S. 2002. The radial reinforcement of the wood structure and its implication on mechanical and fracture mechanical properties – a comparison between two tree species. J. Mat. Sci. 37: 935–940.

Salleo S, Lo Gullo MA, Trifilo P & Nardini A. 2004. New evidence for a role of vessel-associated cells and phloem in the rapid xylem refilling of cavitated stems of *Laurus nobilis* L. Plant Cell Environ. 27: 1065–1076.

Sattler R & Rutishauser R. 1997. The fundamental relevance of plant morphology and morphogenesis to plant research. Ann. Bot. 80: 571–582.

Sauter JJ. 1966. Untersuchungen zur Physiologie der Pappelholzstrahlen. I. Jahresperiodischer Verlauf der Starkespeicherung im Holzstrahlparenchym. Zeitschr. Pflanzenphys. 55: 246–258.

Sauter JJ. 1972. Respiratory and phosphate activities in contact cells of wood rays and their possible role in sugar secretion. Z. Pflanzenphysiol. 67: 135–145.

Sauter JJ. 1988. Seasonal changes in the efflux of sugars from parenchyma cells into the apoplast in poplar stems (*Populus* × *canadensis* 'robusta'). Trees 4: 242–249.

Sauter JJ & Kloth S. 1986. Plasmodesmal frequency and radial translocation rates in ray cells of poplar (*Populus* × *canadensis* Moench 'robusta'). Planta 168: 377–380.

Schmid R. 1965. The fine structure of pits in hardwoods. In: Côté WA Jr (Ed.), Cellular ultrastructure of woody plants: 291–304. Syracuse University Press, New York, USA.

Schmitt U & Liese W. 1993. Response of xylem parenchyma to suberisation in some hardwoods after mechanical injury. Trees Struct. Funct. 8: 23–30.

Scholz A, Klepsch M, Karimi Z & Jansen S. 2013. How to quantify conduits in wood? Front. Plant Sci. 4 (56): 1–11.

Schwarze FWMR. 2007. Wood decay under the microscope. Fungal Biol. Rev. 21: 133–170.

Schwarze FWMR, Engels J & Mattheck C. 2000. Fungal strategies of wood decay in trees. Springer-Verlag, Berlin, Heidelberg, Germany.

Schwarze FWMR, Fink S & Deflorio G. 2003. Resistance of parenchyma cells in wood degraded by brown rot fungi. Mycological Progress 2: 26–74.

Secchi F & Zwieniecki MA. 2012. Analysis of xylem sap from functional (non-embolized) and non-functional (embolized) vessels of *Populus nigra*: chemistry of refilling. Plant Physiol. 160: 955–964.

Shigo AL. 1984. Compartmentalisation: a conceptual framework for understanding how trees grow and defend themselves. Annu. Rev. Phytopathol. 22: 189–214.

Sokołowska K. 2013. Symplasmic transport in wood: the importance of living xylem cells. In: Sokołowska K & Sowiński P (Eds.), Symplasmic transport in vascular plants: 101–132. Springer, New York, USA.

Spicer R. 2005. Senescence in secondary xylem: heartwood formation as an active development programme. In: Holbrook N & Zwieniecki M (Eds.), Vascular transport in plants: 457–475. Elsevier Academic Press, Burlington, MA, USA.

Spicer R. 2014. Symplastic networks in secondary vascular tissues: parenchyma distribution and activity supporting long-distance transport. J. Exp. Bot. 65: 1829–1848.

Trockenbrodt M. 1995. Calcium oxalate crystals in the bark of *Quercus robur, Ulmus glabra, Populus tremula* and *Betula pendula*. Ann. Bot. 75: 281–284.

von Arx G, Arzac A, Olano JM & Fonti P. 2015. Assessing conifer ray parenchyma for ecological studies: pitfalls and guidelines. Front. Plant Sci. doi: 10.3389/fpls.2015.01016.

von Arx G, Kueffer C & Fonti P. 2013. Quantifying plasticity in vessel grouping – added value from the image analysis tool ROXAS. IAWA J. 34: 433–445.

Wagenführ R. 1961. Die Klassifizierung des Holz-Parenchyms – ein Beitrag zur Bestimmung der Holzarten. Holztechnologie 8: 281–282.

Wagenführ R. 2007. Holzatlas. Karl Hanser Verlag, Leipzig, Germany.

Wheeler EA, Baas P & Rodgers S. 2007. Variations in dicot anatomy: a global analysis based on the InsideWood database. IAWA J. 28: 229–258.

Zheng J & Martínez-Cabrera HI. 2013. Wood anatomical correlates with theoretical conductivity and wood density across China: evolutionary evidence of the functional differentiation of axial and radial parenchyma. Ann. Bot. 112: 927–935.

Ziemińska K, Butler DW, Gleason SM, Wright IJ & Westoby M. 2013. Fibre wall and lumen fractions drive wood density variation across 24 Australian angiosperms. AoB Plants 5: doi: 10.1093/aobpla/plt046.

Ziemińska K, Westoby M & Wright IJ. 2015. Broad anatomical variation within a narrow wood density range – a study of twig wood across 69 Australian angiosperms. PLoS ONE 10 (9): doi: e0139496.

Zimmermann MH. 1971. Dicotyledonous wood structure made apparent by sequential sections: Film E 1735 (Film data and summary available as a reprint). Inst. Wiss. Film, Göttingen, Germany.

Zimmermann MH & Tomlinson P. 1966. Analysis of complex vascular systems in plants: optical shuttle method. Science 152: 72–73.

Zwieniecki MA & Holbrook NM. 2009. Confronting Maxwell's demon: biophysics of xylem embolism repair. Trends Plant Sci. 14: 530–534.

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