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Systematic Palaeontology (Palaeobotany)

Is porous wood structure exclusive of deciduous trees?

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Abstract

According to the IAWA committee (1989), the ring-porous wood is defined as a "wood in which the vessels in the earlywood are distinctly larger than those in the latewood of the previous and of the same growth ring." This ring-porous structure is mainly present in regions with contrasted seasons. Some authors have mentioned the potential correlation between ring-porous structure and the deciduousness of the trees, but no precise inventory of species has been provided until now to verify this hypothesis. We compared, with the help of Insidewood (2004) and diverse floras, the wood porosity of 1176 species from temperate countries and 3886 from tropical countries as well as their foliage characteristics. As wood features are frequently preserved in fossil specimens, they could constitute an interesting marker of vegetation type and be used to infer the seasonality of the palaeoclimate. ***To cite this article: A. Boura, D. De Franceschi, C. R. Palevol 6 (2007).***

Résumé

Les bois poreux sont-ils exclusifs des arbres décidus ?. D'après le IAWA Committee (1989), le bois à zone poreuse est défini comme un « bois dans lequel les pores du bois initial sont manifestement plus gros que ceux du bois final de l'année précédente et du même cerne. » Ce type de porosité du bois est principalement retrouvé dans les régions à forte saisonnalité. La corrélation potentielle entre cette structure poreuse du bois et le caractère caducifolié des arbres a été mentionnée par de nombreux auteurs, mais aucun inventaire précis n'a été réalisé jusqu'à présent pour vérifier cette hypothèse. Nous avons comparé, grâce à Insidewood (2004) et à diverses flores, la porosité de 1176 espèces de pays tempérés et 3886 espèces de pays tropicaux et le caractère décidu de leur feuillage. Les caractères du bois sont fréquemment préservés dans les spécimens fossiles ; ils pourraient donc constituer des marqueurs fiables du type de végétation et pourraient ainsi être utilisés pour déduire la saisonnalité des paléoclimats. ***Pour citer cet article : A. Boura, D. De Franceschi, C. R. Palevol 6 (2007).***

Keywords: Ring-porous wood; Deciduousness; Leaves; Seasonality

Mots clés : Bois à zone poreuse ; Décidu ; Caducité ; Feuilles ; Saisonnalité

Version française abrégée

D'après le IAWA Committee [27], le bois à zone poreuse est défini comme un « bois dans lequel les pores du bois initial sont manifestement plus gros que ceux du bois final de l'année précédente et du même cerne. »

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Un changement abrupt de taille et densité des vaisseaux permet de distinguer le bois à zone poreuse du bois semi-poreux ou à pores diffus. Cependant, quelques espèces présentent un continuum de ces différents états de porosité, en fonction des conditions environnementales.

Dans les bois à zone poreuse, le bois initial assure l'efficacité de la conduction. L'embolisme, résultant de stress hydrique, induit un blocage des gros vaisseaux de l'année précédente. Le bois final, comprenant de plus petits vaisseaux, est moins efficace, mais présente une meilleure sécurité hydraulique vis-à-vis du phénomène d'embolisme. La structure en zone poreuse du bois est donc considérée comme une adaptation aux climats à forte saisonnalité [14]. Dans ces régions, les espèces à feuillage caduc dominent. Quelques auteurs ont déjà mentionné l'existence d'une corrélation potentielle entre le caractère « bois à zone poreuse » et le caractère caducifolié des arbres [23,36,49], mais aucun inventaire précis n'a été réalisé jusqu'à présent pour vérifier cette hypothèse.

Nous avons donc comparé, grâce à la base de données Insidewood (2004) [29] et à diverses flores, la porosité de 1176 espèces de pays tempérés et 3886 espèces de pays tropicaux, ainsi que le caractère décidu de leur feuillage. Les structures à bois poreux sont présentes dans environ 17 % des espèces étudiées sous climat tempéré et environ 1 % sous climat tropical. Sur l'échantillonnage d'espèces tempérées, 94 % des espèces à bois poreux sont décidues. Les espèces tropicales à bois poreux le sont aussi, pour la plupart. Les résultats obtenus grâce à cette étude nous montrent que, malgré certains problèmes de définition, il existe bien un lien entre les espèces à bois à zone poreuse et le feuillage décidu. L'observation réciproque n'est cependant pas vraie : de nombreuses espèces décidues ont un bois à pores diffus. Il semble, en fait, y avoir des différences de stratégie dans la reprise de la conduction de la sève brute au printemps, les espèces à zone poreuse mettant en place de nouveaux vaisseaux très tôt dans la saison, les espèces à pores diffus rétablissant la conduction dans les vaisseaux formés les années precedents, grâce à la pression racinaire.

Les caractères anatomiques du bois liés au type de porosité sont fréquemment préservés dans les spécimens fossiles. Ils pourraient, grâce aux résultats obtenus dans cette étude, être utilisés comme marqueurs du type de vegetation, afin de déduire la saisonnalité des paléoclimats.

1. Introduction

According to the IAWA Committee [27], the ring-porous wood was defined as a "wood in which the vessels in the earlywood are distinctly larger than those in the latewood of the previous and of the same growth ring." An abrupt change in the size and density of vessels between earlywood and latewood enables us to distinguish, in some extent, species with ring-porous wood from others with semi-ring-porous or diffuse-porous wood. In ring-porous wood, such as *Castanea sativa* Mill., *Quercus robur* L., *Fraxinus excelsior* L., annual growth rings are relatively simple to identify, whereas in diffuse-porous wood such as in *Fagus sylvatica* L., *Acer pseudoplatanus* L. and *Liriodendron tulipifera* L. species, the vessels have approximately the same diameter throughout the ring from the earlywood to the late wood, and thus growth rings are less marked. Nevertheless, some species show a continuum between the different states of porosity, depending on the environmental conditions [12]. It is also possible to see a continuum from the diffuse feature to the ring-porous one when looking at the ontogeny of a ring-porous species. Indeed, many ring-porous species show a diffuse-porous wood structure in their first years of growth [12] (personal observations in *Castanea sativa* Mill.).

In wood, the conduit diameter has a major impact on conducting efficiency [42]. According to the Hagen–Poiseuille law, wide conduits are more efficient conductors of water than small ones [47], the lumen conductivity increasing with the fourth power of the lumen diameter [42]. Despite this efficiency to conduct sap, large diameter vessels are more vulnerable to embolism [47].

In ring-porous species, the big vessels of the earlywood provide enhanced sap conduction during the beginning of the growth season. These vessels are usually embolised before the growth stops. Little vessels, of less efficiency for sap conduction, provide conductive safety during the end of the growth season. Ring porosity is thus considered as an adaptation to seasonal climates, providing the reversibility of vessel diameter and vessel density in a single season [14]. Thus, initial wood provides conductive efficiency, final wood conductive safety.

Gilbert [23] considers the ring-porous feature as anomalous regarding to the preponderance of diffuse-porous structure in world floras and outlines the restriction of this feature to a limited geographical region, the North Temperate Area. Since then, several ring-porous species have been described from outside of this zone, but ring-porous species seem to be more or less confined to seasonal habitats.

Bailey and Sinnot [10] underlined a clear relationship between leaf margin and environment in the distribution of the Dicotyledons. Indeed, leaves with an entire margin seem to be predominant in tropical mesic (lowland) regions, whereas leaves with a dentate/non entire-margin are more confined to temperate and cold habitat. This observation was used for palaeoenvironmental reconstruction with the help of statistics on leaf characteristics [50–53]. Leaf habits (deciduous vs. evergreen) seem also to be of great significance in the geographic distribution of taxa. Evergreen species occur in all parts of the world, from the tropics to the Polar Regions, from lowland to sub-Alpine altitudes [2]. More accurate data from satellite imagery [17] or from Woodward [54] and Givnish [24] show that evergreen broad-leaved trees dominate tropical rain forests in aseasonal regions of America, Africa, Madagascar, Australasia, and Islands of the Pacific. Evergreen leathery-leaved trees characterize temperate forests from the southern hemisphere, the Mediteranean scrub, and the wetter temperate rain forest in areas of winter rainfall, on the west sides of continents at mid latitude. Evergreen, needle leaved conifers dominate boreal forests at high latitude in the northern hemisphere. As for deciduous broad-leaved trees, they characterize temperate forests at mid latitude in eastern North America, eastern Asia, and northwestern Europe, but they are also frequent in tropical and subtropical areas, with a pronounced dry season.

Numerous authors have tried to explain patterns of leaf life span [2,19,33,39,40]. All these hypotheses were already summarized [15,24]. Evergreen trees can photosynthesize during a longer period, including parts of the unfavourable season; they can begin photosynthesizing earlier and continue later than deciduous ones. Moreover, as they keep their leaves for more than one year, evergreen species have a lower amortized cost of constructing the carbohydrate skeleton. They also have a lower amortized cost of replacing nutrients, making them advantageous on nutrient poor sites. However, evergreen leaves often have to be tougher and thicker.

Deciduous trees, as for them, have a higher rate of photosynthesis per unit leaf mass during favourable periods than evergreen ones have, and reduce their transpiration rate during the unfavourable season.

Phenological phenomena such as swelling, elongation and opening of buds or elongation of the stems and leaves, maturation of the leaves, flowering, and fruiting are often associated with specific stages in cambial activity and certain structural variations in the ring [22].

Bailey [9] outlined a link between the apparition of ring porosity, the acquisition of a pronounced resting period and the beginning of the deciduous habit. Since then, this potential correlation between ring-porous structure and the deciduousness of the trees has been mentioned by several authors [23,36,49], but no precise inventory of species has been provided until now to verify this hypothesis.

The aim of this study is to increase our knowledge of the relationship between wood and leaf habit, in order to provide more ecological deduction from fossil angiosperm record, especially from the very abundant fossil wood. We have first verified this potential relationship between ring-porous structure and deciduousness by drawing up a list of ring-porous species from temperate and tropical environments and by comparing this anatomical wood feature with their leaf habit. Then, we tried to understand the divergences between these two features by considering physiological processes.

Could some of the differences in life history, habit or phenology of trees be explained in terms of differences in hydraulic architecture?

2. Material and method

For this study, we mostly used data on wood anatomy from the Insidewood database [29], but also from wood Atlases [28,41]. We considered that the sampling of the studied species present in the database reflects more or less the global biodiversity occuring in nature.

In order to compare these wood data with foliage characteristics data of the plants, we used numerous published – or online – floras [38] and herbaria (‘Muséum national d'histoire naturelle’, Paris), where descriptions of the leaves, particularly leaf habits, and plants from various parts of the world are available.

We considered the geographical regions defined by Brazier and Franklin [13].

We first tried to list all temperate European ring-porous species. Then we compared their wood porosity with their leaf habits. Following what, we listed on one hand temperate species with ring-porous wood and on the other hand tropical species with ring-porous wood. We finally associated these tropical species with their leaf habit and environment.

3. Results

3.1. European temperate species

We found 193 European species wood descriptions. Among these species, nearly 15% are only ring porous, 10% are only semi-ring porous, and 27% are only diffuse porous. The other species show two or three features of porosity. The ring porosity feature can be present in almost 27% of the European temperate species (Fig. 1).

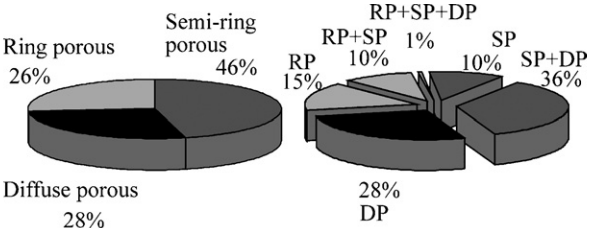

Fig. 1. Growth ring patterns distribution in European temperate species (RP, ring porous; SP, semi-porous; DP, diffuse porous).
Fig. 1. Distribution des différents types de porosité au sein des espèces tempérées européennes (RP, bois à zone poreuse ; SP, bois à zone semi-poreuse ; DP, bois à pores diffus).

As regards the relationship between wood porosity and leaf habit in the European temperate areas (Fig. 2), it appears that 94% of the species that are ring porous are also deciduous. Among these ring-porous species, only two shrub species show at the same time a ring-porous structure of their wood, as well as a semi-evergreen leaf habit for the first one and an evergreen leaf habit with a strong spring growth for the second one.

It is also clear that the reciprocal phenomenon is not true. Some deciduous species have a semi-ring-porous or a diffuse-porous wood.

3.2. Temperate vs. tropical species

Among the 5329 species with described wood, 1176 are temperate, whereas 3886 are tropical. The other ones can be found in both temperate and tropical areas. Over these studied species, 274 are ring porous.

In temperate areas, ring porous wood structure occurs in 17.7% (208/1,176) of the studied species. Ring porosity is more frequent in the northern hemisphere (24.8% of the studied species) than in the southern one (3.5% of the studied species).

In tropical countries, ring porosity occurs in only 1.1% of the total number of studied species (43/3886).

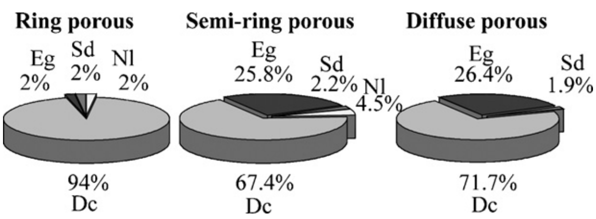

Fig. 2. Growth ring patterns and the associated leaf habit in European temperate species (Eg, evergreen species; Dc, deciduous species; Sd, semi-deciduous species; Nl, no leaf).
Fig. 2. Type de porosité et feuillage associé au sein des espèces européennes tempérées (Eg, espèces sempervirentes ; Dc, espèces décidues ; Sd, espèces semi-décidues ; Nl, feuillage absent).

3.3. Tropical species

Among all the studied species, we found 43 tropical species with a ring-porous wood structure. Most of them are deciduous, but a few appear to have evergreen habit. Ninety percent of the ring-porous species have also a wood with simple perforation, and 35% with spiral thickenings. Both of these wood anatomical characters are known to be an adaptation in cold and dry habitat [14,30]: simple perforations provide a better conduction and spiral thickenings allow to refill embolised vessels.

4. Discussion

Regarding the obtained results, it first appears that it is not always easy to distinguish among all the porosity features, most probably because definitions are not very clear. Authors do not agree on the definition of ring-porous, semi-ring-porous, and diffuse-porous wood. Most of the definitions given to these three states of porosity are based on a qualitative estimation made by the observer [12,18,21,27]. Therefore, definitions vary from one author to another and consequently there is not always an agreement on the assigned categories [36]. Both temperate species *Jasminum fruticans* L. and *Rosmarinus officinalis* L. that show a ring-porous structure of their wood and a (semi) evergreen habit are a good example of this phenomenon. Indeed, both of them can be ring-porous, according to Insidewood [29], whereas in Schweingruber [41], they both are only semi-ring porous.

In temperate climates, ring porosity is frequent and associated with autumnal deciduousness. In tropical areas, the ring-porous structure is very rare. This feature happens in most cases, in species from regions of alternate wet and dry seasons that present at the same time a deciduous leaf habit.

In these species, the dry season triggers leaf fall [1]. In tropical regions, the annual rainfalls condition the forest type [7]: 2000 mm of annual rainfall usually corresponds to the minimum required by the evergreen forest, 1500 mm of annual rainfall is the limit between moist deciduous and dry deciduous forests, and 900 mm corresponds to a change in the structure and floristic composition of the dry deciduous type [34]. A relationship between the percentage of deciduous trees in the forest and the number of dry months exists [8]. Axelrod [6] shows that in actual forest there is an increasing defoliation pattern with increasing seasonal drought. However, in our listing of ring-porous species from tropical areas, we found several species that show both ring-porous structures and an evergreen foliage. Four patterns of leaf phenology in tropical trees have been distinguished [32]: (1) leaf fall before bud break, the entire tree remaining leafless or nearly so for a few weeks to several months; (2) leaf fall associated with budbreak; (3) leaf-fall completed well after bud break; (4) continuous production and loss of leaves. These patterns can explain, in some extent, our results. Indeed, a few tropical species are known as evergreen species (*Cinnamomum camphora* (L.) J. Presl., *Magnolia grandiflora* L., *Grevillea sp*., and *Persea Americana* Mill.), but have a complete change of foliage each year. The abscission of the previous year's leaves occurs as the new growth develops on the tree [1]. The young leaves are responsible for the increase of cambial activity, size, and density of vessels through the production of auxin [3]. The earlywood formation is thus mainly induced by the leaf growth. This should be particularly true on trees that loose leaves and then produce new leaves on the overall crown simultaneously. Nevertheless, these tropical species do not present any ring-porous structure of their wood.

Foliage abscission patterns appear to be a beneficial adaptation to climates with alternate seasons. The tree defoliates and becomes dormant during the period of unfavourable weather. The majority of the ancient fossil leaves seem to belong to the evergreen type, though it remains quite uncertain. The earliest fossil record of deciduous leaves is in the Glossopteridaceae of the southern hemisphere during Carboniferous (about 300 Ma) [1]. Deciduousness of Angiosperm trees developed during Early Cretaceous (125 Ma) [6]. In both the southern hemisphere during the Carboniferous and the northern one during the Cretaceous, the deciduous habit appeared and evolved in conjunction with the establishment of a strongly seasonal climate.

The annual ring formation began in the Late Carboniferous in the boreal regions [31]. Fossil wood from Early Tertiary is mostly diffuse porous. The earliest known woods of a definite Angiosperm nature show no signs of a ring-porous arrangement, even if well-developed vessels are present. The earliest known ring-porous wood is described from the Cretaceous of Antarctica [37]. According to these palaeobotanical observations, it is advisable to think that both deciduousness and ring-porous structure of the wood appeared at the same time in response to a more seasonal climate.

The relationship between ring porosity and climate has been enhanced by our study. Ring-porous species are always deciduous. However, the reciprocal affirmation is not true, deciduous species can have a ring-porous wood, but also a semi-ring-porous or a diffuse one. The presence of a root pressure in some species can explain this phenomenon [4,25,35].

It seems that in dicot trees, the region that functions in water transport varies among species [48]. In ring-porous species, earlywood vessels of the current year xylem are mainly involved in this transport. These vessels loose their ability to transport water each winter and no refilling with water occurs in them [43,46]. In diffuse porous species, on the contrary, water transport occurs in a large part of the sapwood thanks to the refilling of vessels by root pressure [25,44,48].

In ring-porous angiosperms, the large earlywood vessels are differentiated early in the season and mature quickly, often prior to the full expansion of the new leaves. Small vessels and thick-walled fibres are formed throughout the remaining portions of the growth season [3,22]. These results are consistent with the observation we made last year [11]. We studied the wood formation in the ring-porous species, *Castanea sativa* Mill., and in the diffuse species *Fagus sylvatica* L. We found that wood begins to be formed earlier in the ring-porous species. Indeed, in *Castanea sativa* Mill., the biggest vessels appear with the first leave. In *Fagus sylvatica* L., wood formation begins later, a few weeks after that leaves had already been expanded. Several authors [11,25,26] proved that the early formation of a new vessel in ring-porous species is a strategy to encompass winter embolism, and to supply the new leaves with more efficiency. On the contrary, other species of trees like *Fagus sylvatica* L., utilize root pressure to restore the hydraulic capacity in early spring before the bud break [25,44,48]. During spring, trees begin to take nutriments and mineral elements from the soil through their roots. For some of them, this intake induces root vessels pressurization. The pressure then propagates to the top of the tree, causes "a rise of sap" and the dissolution of the gas in the sap or pushes undissolved gas out of the vessels. This root pressure was measured in several species, which are all semi-ring-porous or diffuse species: woody vines [20,45] *Vitis labrusca* L., *Vitis riparia* Michaux [44], *Acer pseudoplatanus* L. [25], *Acer saccharum* Marsh. [47], *Betula pendula* Roth. [25], *Alnus* [5], *Juglans regia* L. [5], *Fagus sylvatica* L. [16], but seems to be absent in other ones like *Prunus persica* (L) Batsch. [16], *Fraxinus* [25], which are ring-porous.

5. Conclusion

As growth rings show diverse patterns according to species from the tropics and temperate regions, further studies are needed to analyse each observed structure within a growth ring. Detailed studies are necessary to define more precisely this ring-porous feature and examine the tree phenology and leaf production, in order to understand the different observed growth pattern.

Nevertheless, as the growth ring pattern is frequently observable in fossil specimens, the ring-porous wood, even as presently defined, could be an interesting marker of the vegetation type. It could be used to infer the seasonality of the palaeoclimate. Its frequency in different species found in an outcrop could be quantified in order to compare the woods with those of modern vegetations under different climate conditions.

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