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IAWA Journal 37 (2), 2016: 127–151



Opinion paper

WOOD ANATOMY AND TRAIT-BASED ECOLOGY

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ABSTRACT

The largest part of forest biomass consists of wood. A global estimate of carbon stored in lignified tissues rises up to 400 Pg. Given these quantities, there is a growing interest of implementing wood research in diagnoses and evaluations of the carrying capacity of the global ecosystem and its forests. The question arises how disciplines like wood anatomy could respond to the increasing demands of a trait-based ecology, understood as a paradigmatic shift in addressing global changes. Dendrochronology and ecological wood anatomy, traditionally operating within the paradigm of species-based ecology, developed robust methods to address ecological questions. However, sampling strategies and database design will likely be different when wood traits are to be used to study individual tree performance, including responses to stress.

Aiming at optimally involving wood research in trait-based ecology, some trait concepts are analysed. The value of the IAWA standard lists of wood anatomical features as starting points for trait databases is recognized. A summary of the functionality of wood is given to inform the trait-research community of basic aspects of tree performance. The time dimension is highlighted, as well as the foundations for understanding bio-hydraulics, bio-mechanics and metabolism of wood and relevant traits.

Guidelines are given for sampling strategies and database concepts. Prospects of time axis construction and system integration are discussed, as well as the importance of standardizing for size.

Keywords: Functional traits, wood anatomical features, traits database, global ecology, forest ecology, tree performance, stress effects.

INTRODUCTION

Wood science finds its classical justification in the prominence of lignified plant tissues in both living nature and material culture. Research on wood supports technological investigations as well as botanical disciplines like taxonomy and physiology. There is an additional and strongly growing interest that is driven by the commonly accepted understanding that forests are crucial to assure ecological functions and services at different geographic scales. Locally, forests provide resources for the economy in a potentially sustainable way and assure environmental protection. Globally, they play a key role in the climate regulation of the planet. The scientific essence to which these

discussions can be reduced is the thermodynamics of the global ecosystem of the earth. Forests comprise indeed a large share of the free energy of terrestrial systems, energy that is available to perform work, or, in ecological terms, energy that is useful to produce goods and deliver services. Deforestation and forest degradation signify higher levels of entropy, lower potential to perform work and, therefore, less goods and services and reduced survival means for mankind. Despite high levels of deforestation and forest degradation, especially in the tropics, the remaining forests still continue to sequester carbon dioxide: there is an estimated net sink of $1.1 \pm 0.8 \text{ Pg C year}^{-1}$ (Pan *et al.* 2011). This phenomenon can be understood as a global indicator for relatively stable stocks of organic carbon and concomitant amounts of free energy stored in forests.

The major part of the energy in forests is stockpiled in organic molecules and woody biomass in particular. The carbon stock of the world's forests is estimated as $861 \pm 66 \text{ Pg C}$ (tropical forests represent 55% of this carbon, while the boreal belt holds 32% and the temperate forests 14%). On average 44% of the carbon is present as organic soil compounds, 42% as live biomass (below and above ground), 8% as dead wood and 5% as litter (Pan *et al.* 2011), but there are large differences between biomes, with a higher proportion of carbon in living biomass in the tropics and more carbon in the soil of the boreal forest. Interestingly the largest part of the forest biomass consists of wood and bark: above ground this rises up to 98% in tropical and temperate forests and 87% in boreal forests (Malhi *et al.* 1999), but also below ground much of the carbon is kept in woody materials, including coarse roots, a part of the detritus and even a substantial part of the fine roots contain lignified tissues. Heterotrophs (less than 1% according to Gosz (1978)), tree foliage and herbaceous plants, although functionally vital, constitute only small fractions of the carbon stocks. Chave *et al.* (2009) estimate that 400 Pg carbon is stored in wood globally. These are reasons enough to include wood research into investigations of planetary carbon budgets and hence global change.

Because thermodynamics of the earth is to a large extent regulated by forests and wood is by far the largest component of their biomass, it seems evident that the study of the fitness of small and large biotic systems could profit from research methodology that has been developed in wood science and wood anatomy in particular. The question arises which wood anatomical protocols could be adopted by an ecological methodology documenting a diagnosis of the carrying capacity of the global ecosystem and its forests. This type of diagnosis copes indeed with a dire need for information supporting evaluations of stress effects on trees, of human impact on biodiversity and the global ecosystem. Sampling strategies and database design aiming at maximizing the ecological information content of the research material will not necessarily be the same as those that give rise to the scientific collections with reference specimens for taxonomy and wood identification. Although the two approaches share many features (often called traits in the context of ecosystem studies), care is to be taken in the choice of plant feature databases feeding the ecosystem models. The most common, most reliable and the easiest accessible databases on wood anatomical features are not constructed for ecosystem studies. They should therefore not blindly be incorporated

into predictive models. Wood anatomy is indeed traditionally species-based research. Involving wood anatomy into a trait-based ecology in the sense of Kattge *et al.* (2011) needs a reflection on existing data and established methods.

Here I aim at interpreting the plant trait concept from a wood anatomical angle and explore how wood research could be useful for ecosystem modelling. The objective is to outline some opportunities of wood anatomy for trait-based ecology and to draw the attention of the wood anatomical community, traditionally working within the paradigm of species ecology, to the needs for data of predictive modelling and global change research. I will discuss the broad categories of wood anatomical features and their general functions, potentially helpful for discussions within the trait-research community. I give directions for implementing wood research into trait-based ecology. I show how trait-based ecology links to established disciplines like wood anatomy and dendrochronology and what are the opportunities and the potential threats of this liaison.

TRAIT CONCEPT

The dynamics of the planetary system and its large biotic systems is often addressed with the help of mathematical ecosystem models (Moorcroft *et al.* 2001; François *et al.* 2006; Kim *et al.* 2012; Joetzer *et al.* 2015). These models often rely on extensive data of so-called plant traits. The term “trait” has diverging meanings in different scientific disciplines like genetics, ecology and population dynamics (Violle *et al.* 2007). Where the genotype can be understood as the assembly of genes (genome, plastome, chondrome), the phenotype is being considered as the association of traits (Mohr & Schopfer 1995).

Still there is a lot of confusion in the terminology, but Violle *et al.* (2007) emphasize the importance of defining traits on the organismal scale: traits are seen as “*any morphological, physiological or phenological feature measurable at the individual level, without reference to the environment or any other level of organisation.*” For the TRY database (Kattge *et al.* 2011), plant traits are understood as “*morphological, anatomical, biochemical, physiological or phenological features of individuals or their component organs or tissues.*” They are considered as a key to understanding and predicting the adaptation of ecosystems in the face of biodiversity loss and global changes.

Since the term “trait” strictly needs to be reserved for descriptions at the level of individual plants, the sampling unit should definitely be an individual (Kleyer & Minden 2015). Measuring a trait does not require information external to that individual, including both environmental factors or other integrating biotic systems like populations, communities or ecosystems. Standing biomass and vegetation cover are measured at the plot level and should therefore not be considered as traits.

Starting from their concise definition, Violle *et al.* (2007) also underline the importance of studying traits along environmental gradients. The length of the gradient that is being studied has important consequences for sampling strategies and available databases. When the gradient of interest falls within the distribution limits of a species (or clade), the trait should show enough intraspecific variability to be tested for its responsiveness. When the gradient is long enough to encompass different vegetation

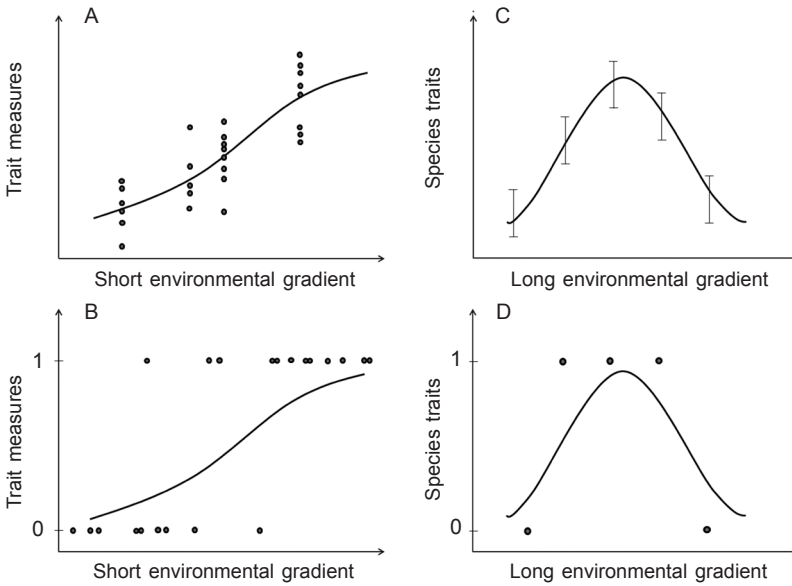


Figure 1. Trait analysis along short and long environmental gradients. Quantitative traits are measured on 26 individuals on four discrete positions on a short gradient (A). Qualitative traits are scored for 21 individuals spread along a short gradient (B). Underlying models for variation of traits along a short gradient are likely linear or S-shaped. Dots are trait measures corresponding to individual trees. For long gradients trait values that are representative for species can be extracted from available databases. Mean values and standard deviations of quantitative traits of 5 species (C) and representative values of qualitative traits of the same 5 species (D) are plotted on a long gradient. The shape of the response curves is often unimodal showing minima, maxima and optimal values.

types, traits can be used that are constant for a species or that are expressed as mean values for that species (Fig. 1). Since botanical information is often summarized on the level of species, there are more databases allowing analysis of interspecific variability along long gradients than intraspecific changes caused by small-scale environmental fluctuations. Using species values of traits implies that these values are representative for that species and its general habitat. Some traits show very high intraspecific variability and should only be used with care in analyses of long gradients.

This emphasis on environmental gradients implies that a study of traits is conceptually different from descriptions and comparisons of specimens aiming at taxonomical reviews or establishment of identification tools in a context of enforcement of timber trade regulations. Individuals that are atypical for a taxon might indeed be interesting because of their traits and, as such, for evaluations of stress effects (Table 1). Variability as such is more important in trait analysis than in a taxonomic approach searching for discriminating features between species. Features that are constant within a species are taxonomically more interesting than those that are strongly variable. In contrast with comparative botany, variability along a gradient is more interesting in the context of trait analysis. On the other hand, features that are constant or characteristic for a species

Table 1. Taxon diagnosis and trait-based ecology both use wood anatomy but have different objectives. Taxon diagnosis aims at comparing different clades and therefore uses the most representative specimens. Trait-based ecology put emphasis on explaining variability of trait measures.

	Descriptive wood anatomy for taxon diagnosis	Wood anatomy for trait-based ecology
Aim	Descriptions of species or other level taxa	Descriptions of individuals and their components
Material	Representative specimens from standard positions in the woody plant Adult stem wood	Individuals with known position on an environmental gradient Adult stem wood, juvenile tissues of stem, branches, roots; scaling for size
Methods	Finding characterizing features to distinguish taxa Summarizing information with mean values and standard deviations	Establishing probability distribution functions of features Explaining variability in terms of environmental responses
Angle	Different microscopic levels	Integration of microscopic and macroscopic levels
End product	Taxonomic classifications	Ecosystem models
Paradigm	Mechanistic explanation of functions of features	Traits in relation to performance of individuals

are to be understood as a proxy for the general functioning of that species, including its populations and individuals. They are an expression of the evolutionary adaptation of a taxon to a general habitat, but they do not allow addressing the responses of a single organism to short term events, including extreme ones. Vestured intervessel pits in the secondary xylem are a typical example of a wood anatomical feature that is characteristic for a certain taxon. There is no doubt that this feature is relevant for the functioning of individual trees and more particularly for their hydraulic performance, even if the precise function is far from being elucidated (van Vliet 1978; Jansen *et al.* 2004, 2009). This feature does not seem to be variable among individuals of a species. The InsideWood database (Wheeler 2011) reveals that almost 36% (> 2000 species) of the species contain vestured pits, but this feature is coded as “variable” for only 37 species which is probably to be understood as uncertainty in the observation rather than environmentally driven variability.

Traits and wood

Violle *et al.* (2007) mention different types of traits, such as ecophysiological, life-history, demographic, biological, performance, response, effect, hard and soft traits. They define functional traits as: “*morpho-physio-phenological traits which impacts*

fitness directly via their effects on growth, reproduction and survival.” This definition is a general one for the plant kingdom and deserves some interpretation and slightly different emphasis for more particular contexts like wood research. When working with woody plants it is self-evident that some wood traits show clear links with growth (tree-ring width for instance), less with reproduction and most traits help the survival of the tree through their role in hydraulics (*e.g.* cavitation resistance), mechanics (*e.g.* buckling resistance) or biological defence.

There is another definition of “trait” that interestingly originates from the context of wood research. Lachenbruch and McCulloh (2014) presuppose an explicit designation of a relevant period of time: “*any morphological or chemical measure that does not change over the period in which a performance is examined*” where “performance” should be understood as a “*quantifiable level at which a plant unit accomplishes a function over a particular period of time.*”

In the Lachenbruch & McCulloh (2014) definition the term “functional” is not over-emphasized. This makes sense as most plant features are at least potentially functional and mechanistic explanations for direct links between trait measures and physiological functions are still a matter of debate. There is certainly a growing amount of interesting experimental data (Hacke 2015), but the discussion about the function of some features is still riddled with controversy and speculation, like there is the function of cell wall thickness for avoidance of implosion of conduits. At the same time it is certain that secondary tissues of trees and their constituting cells are typically polyfunctional. Discussions of their functions would therefore profit from a systemic approach (Gartner 1995), where interactions between components are considered rather than single components out of the context of an organism. Even when the precise physiological function of most of the traits is not yet elucidated, there is often a statistically significant correlation between many traits and the performance of the individual. This justifies that ecosystem models continue to use trait databases for their ecological diagnoses, evaluations and predictions. These correlations are probably the reasons why these modellers adopted the trait approach with enthusiasm. They expect reducing the complexity of heterogeneous communities like tropical rainforests, even when uncertainty prevails about causal relationships between tree performance and traits. At the same time there is a real danger for over-interpretation when correlations between fragmentary datasets are observed.

The IAWA lists of standardized features

Wood trait analysis presupposes good definitions, not in the least because of the unavoidable quantitative approach. Also the terminology needs to be rich enough to cover the wide spectrum of wood phenomena. The terminology of wood anatomical features is extensive and exceptionally well defined in the IAWA feature lists for hardwood and softwood identification (IAWA Committee 1989, 2004). This terminology provides also access to a vast body of knowledge on the structure and function of wood. This knowledge is crucial to design new research on growth responses of trees to extreme events, or more generally, to explore the performance of individual trees, including the functionality of the secondary xylem, its properties and its traits.

Research on ecophysiological processes and functions profit from easy access to the wood anatomical terminology and relevant literature. To give a basic example: projects including measurements of vessel sizes better refer to the IAWA lists because of at least two reasons. First of all there are clear instructions on what conventionally should be measured. The IAWA lists also caution that vessels of ring-porous species should not be pooled. It is indeed essential to keep early- and latewood vessels apart since they are functionally fairly different. The earlywood vessels are formed using photosynthates of the previous growing season, assure 90–95 % of the water transport and allow an early response to water availability on dry sites, while latewood vessels are probably essential for sustaining minimal sap flow after embolism of the earlywood vessels. A further search in the wood anatomical literature even suggests that earlywood vessels occasionally need to be split into those of the first formed band and the later ones (García-González *et al.* 2016; Kitin & Funada 2016).

Most of the IAWA features are qualitative. They should in principle be coded as either present or absent. When the presence of a feature is unclear or changes between and within individuals there is a possibility to add information on its variability. Some of the qualitative features can be transformed easily into rank variables. Vessel size (tangential diameter of vessel lumen) is typically described by the presence and absence of four different classes, but for analytical reasons these classes allow for a ranking which has a higher information content than presence absence data in the separate classes. The IAWA coding also allows values for mean and standard deviation and text-based information. The main purpose of the IAWA feature lists is description of taxa and identification of unknown wood. However the lists are certainly a good basis for assembling information of traits of individuals. Rather than establishing from scratch new lists of wood anatomical traits, I recommend to make optimal use of the IAWA lists for defining and selecting wood anatomical traits. Trait research is strongly interested in verifying whether responses along gradients are linear, unimodal (with different tolerances) or multimodal. Adaptation of the IAWA feature lists to trait research should therefore focus in the first place on expanding the quantitative information content.

Ecological wood anatomy and dendrochronology

Wood-trait analysis is a rather novel approach driven by the current scientific needs and by ecosystem modelling in particular, but its methodology is very closely allied to classical ecological wood anatomy and to dendrochronology.

Ecological wood anatomy, successfully applied since the seventies of the 20th century by Carlquist (1975, 1980, 1984) and Baas (1976) and many others (Wheeler *et al.* 2007) is to be understood as ecophyletic wood anatomy where correlations are being studied between wood anatomical features characterizing the species and the general habitat conditions where the species occurs. As early as 1985, the existence of another type of ecological wood anatomy has been acknowledged where not the species features are studied, but the phenotypical modifications of the wood structure in response to changing environmental conditions (Baas & Miller 1985). This field of study is also since long the topic of forestry-related research where the effect of the environment (and its manipulation through management) on tree growth and wood quality is being

studied. This second meaning of “ecological wood anatomy” is essentially the same as what now could be called “wood anatomical trait-based ecology”.

The other closely related discipline is dendrochronology. When understood in the broadest possible sense, dendrochronology is the study of events through time that are recorded in tree features like growth rings. Growth is certainly an important aspect of performance analysis of individual trees, which directly links growth-ring studies to the trait concept. Many dendrochronological studies aim at developing mean chronologies through the principle and the methodology of cross dating which focuses on phenomena at the population level. A growth-ring study in the context of trait-based ecology can obviously also incorporate non-crossdatable series (from trees that do not show growth that is synchronic to a population), certainly when signals in stressed individual trees are the subject of study. This does not mean that the cross dating approach is not important in trait-based ecology: cross dating is a robust method for quality control of measurements and for assuring that every single ring is associated to the calendar year where it was formed.

Wood anatomical feature categories and traits

Some of the wood anatomical characters combine clearly different functions. Tracheids and septate fibres combine mechanical functions with hydraulic and metabolic ones, respectively. All of the other cell types/tissues in wood are probably to a certain extent potentially polyfunctional. Categorizing wood anatomical features into separate functions will always sound artificial to some extent. Here I discuss the aspects of large IAWA categories that seem to be relevant for a trait-based ecology and for ecosystem modelling. There are many other features that are not well-known outside of the wood anatomical community, but contain certainly information on tree performance, such as storied structure, cambial variants (Robert *et al.* 2014) and mineral and organic (De Micco *et al.* 2016a) inclusions. The IAWA features lists (IAWA Committee 1989, 2004) give a very convenient overview of these.

Growth rings to rank traits on a time axis

Where foliar traits fail to predict absolute growth rate (Poorter *et al.* 2015) tree-ring widths allow the evaluation of productivity in a quite direct way. Growth rings observed in a transverse section from pith to bark mirror the dynamics of cambial activity during a period as long as the age of the cambium at the height of the section. They are a result of a periodic phenomenon and should be without any doubt considered as a phenological trait and links wood anatomy in a straight line to the trait concept *sensu* Violle *et al.* (2007). Cambial activity as a phenological trait has the disadvantage that it is taking place underneath the bark and needs indirect methods to be assessed, including dendrometer measurements (high resolution dendrometers register also shrinking and swelling of tissues), periodic sampling of the cambial zone, inflicting artificial wounds by needles, pins, window-like incisions (Mariaux 1967) and even electric pulses (Nakai *et al.* 2015). The cambium is indeed very sensitive and registers different kinds of signals from the environment, including climate, insect attacks and mechanical impact (De Micco *et al.* 2016b). The major advantage of cambial activity, understood as a phe-

nological trait, is that the fluctuations are registered in xylem (information on a period as long as tree life if the wood around the lower parts around the pith is intact) and phloem (information only readable for one or a limited number of years (Gricar *et al.* 2016)).

The importance of growth rings in an approach of tree performance analysis cannot be overestimated, also according to the trait concept of Lachenbruch and McCulloh (2014) because this concept presupposes the explicit definition of the period for which the performance is being studied. Even if most of the wood traits continue to have a clear link to the performance of a tree many years after being established, some traits are only significant for the year that they were formed (vessels of ring-porous species, conducting phloem). Some other wood features gradually lose their functionality such as pith at the lower parts of the stem and other seedling features. Time series of tree-ring anatomical features are important to understand the functional role of xylem plasticity over the life span of trees (Abrantes *et al.* 2013).

Even if the link to performance is relatively clear, ring-width series probably need different interpretation as a trait than tree-ring descriptors in classical dendrochronology. The year to year variability is in dendrochronology traditionally more important than evaluating the biomass increment. A better proxy for biomass increment is volume growth for which basal area is a better expression than growth-ring width. Many growth-ring descriptors exist both based on width and on wood density measurements. They represent a large potential for valorising wood anatomical and dendrochronological methods for ecosystem modelling.

IAWA features related to growth rings are the categories distinct, indistinct, absent and variable (IAWA Committee 1989). For softwoods there are additional features describing the transition between earlywood and latewood (IAWA Committee 2004). The classical dendrochronological terminology (Bräuning *et al.* 2016) can easily be transposed to trait-based ecology. More intra-ring features are linked to the so-called intra-annual density fluctuations (De Micco *et al.* 2016b) or other growth zones inside separate rings (Dié *et al.* 2012). In the TRY database a category growth-ring distinctness is incorporated, next to plant growth rate which could be expressed as ring width. Some of the dendrochronological features are listed by Wimmer (2002), who makes the distinction between continuous and discontinuous features.

Studying growth rings as traits implies measuring them. Measuring ring widths presupposes a discrete starting point and an end point. If growth rings are anatomically distinct, there is an abrupt transition from one ring to the next, allowing a swift measurement. For indistinct rings the transitions are only gradual which means that it is not possible to associate each single cell to one growth ring (Tarelkin *et al.* 2016) and an explicit convention is needed for measurements, *e.g.* the distance between two density maxima (Verheyden *et al.* 2004). This type of structures are often difficult to date exactly and a distinction should be made between intra-annual density fluctuations (De Micco *et al.* 2014, 2016b) and density maxima at tree-ring borders.

Vessels, tracheids and biohydraulics

Structure and function of water transport systems control to a large extent productivity and survival of trees (Brodribb 2009) and wood anatomical traits are therefore

often studied from the point of view of hydraulics. Wood hydraulics deals with three different biophysical properties (Anderegg & Meinzer 2015): conductivity, safety of the pathway, and capacitance.

Long-distance water transport of gymnosperms is through tracheids. Their lumen diameter ranges from 5 to 80 μm , the length is less than 5 mm and they comprise 90 % of conifer xylem (Hacke *et al.* 2015). Water transport in hardwoods is predominantly through vessels. A vessel diameter could be 300 μm and more. Especially lianas could have vessels that are easily seen with the naked eye. Some individual vessels of *Cissus* species have a vessel diameter of 700 μm (Ewers *et al.* 2015). Mean vessel diameter is 51.4 μm (from measurements on 3102 specimens) and mean vessel element length is 549.5 μm (2964 specimens) according to the far from complete database of TRY (Kattge *et al.* 2011). When functional, tracheids and vessels are part of the apoplast (Mohr & Schopfer 1995). Vessel systems (consisting of different connected vessels) start from the periphery of the stele in the roots and end in the mesophyll tissues of the leaves. The functional apoplast is full of water but a substantial proportion of the conductive tissues of an adult tree is blocked by cavitations, tyloses and vessel deposits (De Micco *et al.* 2016b). Some degree of cavitation can be repaired (Holbrook *et al.* 2001), but many embolisms are irreversible.

Sizes and abundance of vessels and other conduits are variable among individuals. Wide vessels assure efficient water conduction, as the volumetric flow rate increases with the fourth power of the vessel radius following the Law of Hagen-Poiseuille. Large vessels are however more vulnerable to cavitation. Small diameters of the hydraulic conduits seem to be important for evergreen species to cope with embolism caused by freeze-thaw periodicity (Zanne *et al.* 2014).

Also following the Law of Hagen-Poiseuille is that the volumetric flow rate is inversely related to the length of the path. This means that vessels and tracheids need to be wider at the lower parts of the trees and taper towards the higher parts to assure optimal transport and a stable hydraulic resistance with progressing growth in height (Anfodillo *et al.* 2013; Lazzarin *et al.* 2016). Indeed, xylem conduits narrow from roots to stem and further to the branches and leaf petioles (Tyree & Zimmermann 2002; Brunner *et al.* 2015). Tall trees are expected to have wide vessels at the base of the stem and small trees and shrubs narrow ones. Trait-based ecology needs to take into account the strong relation between height grow and general site conditions. Trees grow taller on fertile, mesic soils at lower altitudes than on poor soils, arid conditions at higher altitudes. In forestry this is traditionally being quantified with a site index which is an expression of the height of a tree at a certain age. Vessels are expected to be narrower in drier forests and woodlands because trees are on average much smaller (Barajas-Morales 1985; Olson & Rosell 2013). The general trend of variation of vessel dimensions with height, which has been repeatedly confirmed also for other anatomical features (Lazzarin *et al.* 2016), is to be understood as valid for an idealized plant. Vessel sizes indeed fluctuate often on a pith to bark gradient (Verheyden *et al.* 2004) and can reflect interesting environmental signals like precipitation seasonality, including the El Niño effect in parts of Eastern Africa. This phenomenon allows to treat vessel sizes as dendrochronological variables (García-González & Fonti 2006). They can also reflect the reaction of the

hydrosystem on pruning (Giantomasi *et al.* 2015), bark removal (Delvaux *et al.* 2013) and the development of buttresses (where vessels are smaller).

Discussions of trait data should be aware that measured conductivity is not more than 50 % of the predicted conductivity by the Hagen-Poiseuille law. Vessel diameter is indeed a very simplified prediction of conductivity (Ewers *et al.* 2015) as vessel sizes and abundances only explain a fraction of the conduction. Phenomena at the pit level are at least as important as conduit sizes. Passage of sap flow through the pits in conifers represents 64 % of the total tracheid resistance (Hacke *et al.* 2015). Intervessel pits in angiosperms account for more than 50 % of the hydraulic resistance (Choat *et al.* 2008). Many fine pit structures play a role in sap flow. Conifer pit membranes show much larger pores than the typical membranes of angiosperms (Hacke *et al.* 2015). The thickness of pit membranes seems to be the best anatomical correlate of embolism resistance in angiosperms (Li *et al.* 2016).

Water is moved by differences in water potential and transpiration is by far the main driver. The water potential gradient consists of an osmotic, a gravimetric and a pressure potential (Vergégnest 2015). The osmotic water potential is caused by solutes in cell sap and is more negative with high solute concentrates like in living cells. The gravimetric potential is important for high trees and rises with the height. Xylem conduits are mostly under tension and the pressure potential is accordingly negative. Because of turgor pressure the pressure potential is positive in living cells. A full understanding of water transport in the xylem should also take into account that water transport is possible without transpiration as a result of pressure generated in the roots or even in the stem. Root and stem pressures are of importance at higher latitudes in early spring when trees are still leafless and when starch is being mobilized. Similar xylem pressures are possible at very high humidity in the tropical rainforest where intense guttation shows that water in the vessels of many trees is quite often under positive pressure (Mohr & Schopfer 1995). There are also records of fog water uptake via the leaves feeding a subsequent reversal of the sap flow to belowground pools that can be as high as 26 % of the daily transpiration of cloud forest saplings (Eller *et al.* 2013). Also for conifers needle water uptake has been observed (Hacke *et al.* 2015). Similarly there is evidence of redistribution of deep soil water through the superficial roots to undep soil layers (Meinzer *et al.* 2004). Nocturnal transpiration and night-time sap flow has been recorded across a range of biomes. A substantial part of this is for refilling the tree stem with water which has been depleted during the day (Zeppel *et al.* 2013).

An overview of quantifiable features (including descriptors for conduit sizes, intervessel contact walls, pit dimensions) and derived properties like vulnerability is given in Scholz *et al.* (2013). The IAWA feature list for hardwoods (IAWA Committee 1989) gives an overview of most of the existing vessel characteristics. Many of these, like perforation type, presence of vascular tracheids and vessel arrangement, are definitely functional for sap flow and tree performance in general.

Xylem conductance appears to be also influenced by the concentration of chemical compounds in the xylem sap. A two-fold increase in xylem conductivity was observed at higher K⁺ ion concentrations (Zwieniecki *et al.* 2001). This effect may be related to shrinkage and swelling of polymers in the vessel pit membranes.

Fibres, tracheids and biomechanics

Given the large amount of energy that trees invest in tissues for which the major functionality is support, it seems to be important to consider the mechanical function of wood as of similar importance as the hydraulic function. The mechanics of a whole tree is the combined result of mechanical properties of the wood and size and the morphology of the tree. Also the phenomenon of the so-called motricity or posture control (Fournier *et al.* 2013) is relevant for a mechanical understanding of wood traits.

The mechanical function of wood is mainly assured by fibres in hardwoods and by tracheids in softwoods. Mechanical properties of wood are mainly determined by cell wall properties. A high proportion of fibres gives strong wood, *i.e.* the capacity to withstand loadings, mainly from weight of tree organs and external impact of wind. The quantity of cell wall material, *i.e.* the proportion of cell wall thickness to cell lumen, assures stiff wood that resists bending deformation (Alméras *et al.* 2004). A second factor explaining stiff wood is the microfibril angle. The main factor for wood deformability (strain at maximum stress) is microfibril angle, next to cell wall proportions. Toughness is assured by cell wall proportions.

To capture the mechanical performance of a standing tree the anatomical fibre and tracheid traits need to be integrated over tree size and architecture. When reading a mechanical signal in wood traits, it is crucial to keep in mind that many examples exist of trees made of weak wood that as a whole support heavy loads of material and resist strong winds during a century or more. It is therefore crucial to take into account measures of tree size and habitus in discussions of mechanical traits. Other factors on a higher level of integration like spiral and interlocked grain contribute to tree mechanics.

Strongly related to fibre and tracheid features is wood density. It is a favourite variable in trait research, probably because extensive databases exist with quantitative information on wood density. Strictly speaking, wood density is to be considered not as a trait, but as a property (Lachenbruch & McCulloh 2014). Wood density has strong correlations to performance, but without direct causality. The higher buckling resistance observed for trees with high wood density reflect probably typical traits of long-lived trees, like thick-walled fibres or heartwood with high concentrations of secondary metabolites. Wood density is very strongly linked to void proportions and fibre cell wall thickness, relationships which are most probably causal. Fortunel *et al.* (2013) found that in 113 Amazonian species fibre traits are the main determinants for wood specific gravity in branches and roots. This wood specific gravity was independent of vessel traits in branches. In roots the influence of vessels on density could be demonstrated, but the positive correlation between the fibre wall fraction and wood specific gravity was particularly high. Measuring basic density (or cell wall thickness) of wood fragments with precise information of their origin (*e.g.* by 3-D scanning of radial cores (De Ridder *et al.* 2011)) in a tree gives information on biomass partitioning within a tree. This is of interest for precise calculations of carbon budgets, but also to address aspects of tree performance, such as presence or absence of buttresses. The anatomy of buttresses suggests that their main function is support. Buttresses of *Khaya ivorensis* shows a higher proportion of fibres than normal stem wood.

There are empirical relationships between wood density and tree mortality (inverse relationship). This is thought to be essentially biomechanical (Moorcroft *et al.* 2001). Similar relationships are regularly observed between plant functional types and wood density. Pioneer species typically show low density wood and fast primary grow, later successional species grow more slowly and have wood that is denser. Even if these tendencies are empirically confirmed (Chave *et al.* 2006), it sounds too simplistic to classify tree species into functional groups based on their wood density (Kim *et al.* 2012). There are many species that do not respond to this trend at all and therefore the relationship itself is never particularly strong. Moreover characterizing the density of individual trees by a mean species value does not take into account the particularly strong variability of wood density within a tree which is organ dependent, shows an age and a height trend. Many species have a very variable wood density from one individual to another. Basic specific gravity of mature heartwood of *Shorea leprosula* varies by a factor of more than two (Bosman *et al.* 1994). The different anatomical components of density have essentially different functions. Fibre wall thickness assures predominantly biomechanics, vessel size the hydraulics and the secondary metabolites of their cell lumina and cell walls add to decay resistance. Parenchyma, including rays, can have different influences on density. Density as an expression of growth seems to be only of minor importance. When implementing wood density into ecosystem models, it is of great importance to give precise information on the way density is expressed (basic specific gravity, basic density, specific gravity at a certain moisture content) (see definitions of features 193–195 in the hardwood list (IAWA Committee (1989)). It is of similar importance to have precise information on whether the density is measured on heartwood, sapwood, a mixture of both, juvenile stem wood, branch wood, with or without the bark still attached etc.

Where the amount of cell wall material clearly determines biomechanics, the form of cells in a transverse section can be read as an indicator for influences of the environment and tree performance beyond mechanics. The radial diameter is reduced in latewood tracheids of stem wood, but also root tracheids were found to be flatter in trees subjected to severe drought, which is probably to be understood as a reduction in conductivity (Eldhuset *et al.* 2013).

Posture control is another aspect of the mechanics of trees (Fournier *et al.* 2013). Motricity or posture control is assured by the differentiation of reaction wood. Reaction wood is characterized by an eccentric transverse section: softwoods build more material at the compression side, hardwoods at the tension side. Tension wood is anatomically often but not always characterized by a gelatinous layer (a G-layer) at the inside of the cell wall of the fibres (Clair *et al.* 2006; Fournier *et al.* 2013). There can also be multiple layers or there could be no visible difference at all. In softwoods the shape of the compression wood tracheids is rounded. Hardwoods show a very low microfibril angle, softwoods a very high microfibril angle. In hardwoods there is a high content of cellulose in the tension wood, in softwoods a high content of lignin in the compression wood. The main function being mechanical, there is also reported trade-off of compression wood showing a higher vulnerability to drought-induced cavitation, compared to opposite wood (Hacke *et al.* 2015)

Parenchyma and metabolism

Parenchyma in lignified plants shows high variation. The cells vary in size, orientation, form and wall pitting. Tissues are radially or axially orientated. Radial parenchyma forms rays which might be uniseriate like in conifers, but rays can be very large in certain angiosperms. Parenchyma in coniferous wood has three forms (Hacke *et al.* 2015): axial, radial and for most Pinaceae epithelial parenchyma. Axial parenchyma in angiosperms shows on transverse sections patterns that are quite typical for the taxon, but also characterize vegetation types like tropical rainforests showing high occurrences of aliform, banded and confluent parenchyma (Beeckman 1999; Wheeler *et al.* 2007). Epithelial parenchyma surrounding resin ducts are typical for many species of families like Dipterocarpaceae, Burseraceae and Anacardiaceae. Parenchyma cell walls are mostly lignified, but these cells retain a living cytoplasm throughout the sapwood. However, some taxa show complete zones of unlignified parenchyma cells within the secondary xylem (IAWA Committee 1989). This high degree of variation in parenchyma cells and tissues suggests similar variation in functions which can dynamically change during tissue development (Spicer 2014; Morris *et al.* 2016). The function of the axial parenchyma can be taken over by septate fibres especially in some tropical families (Wheeler *et al.* 2007).

Axial and ray parenchyma often form a three-dimensional network within the wood. The contacts between rays and axial parenchymatic strands might be disjunctive and through irregularly shaped cells with finger-like protrusions in between other structures (Kitin *et al.* 2009).

Morris *et al.* (2016) distinguish six discrete functions of wood parenchyma: storage and transport of non-structural carbohydrates, defence against pathogens, water storage and capacitance, storage of minerals, transition from sapwood to heartwood and biomechanics (especially of rays). They argue that the anatomical terminology does not necessarily coincide with different functions. It might indeed be more important from a functional point of view to distinguish between contact cells (adjoining conduits) and isolation cells.

Parenchyma also assures the communication between xylem and phloem. Pro-cumbent cells are likely designed for radial transport, upright cells for linking symplast and apoplast but most of these statements still wait for experimental underpinning.

The xylem parenchyma of juvenile tissues assures contact with parenchyma both in pith and bark through a symplastic continuity, but parenchyma cell walls are also part of the apoplast. The membranes of the vessel-ray and vessel-axial parenchyma pits assure the interface between symplast and apoplast (Spicer 2014).

Parenchyma is involved both in transport of assimilates and water. Parenchyma assures seasonal storage and short- and long-term redistribution of organic and inorganic compounds (Spicer 2014). The high amount of paratracheal axial parenchyma in many tropical hardwoods suggests that this tissue plays also a role in the water balance. This does not mean that extensive axial parenchyma is a necessity in rainforests, since there are many examples of species with similar performance that have only scanty parenchyma.

Parenchyma can show a high water storage capacity, often called the intracellular or elastic water storage (Holbrook 1995; Borchert & Pockman 2005). In some low-density wood, parenchyma may constitute 40–80% of the mass. Parenchyma contributes together with the conduits to the hydraulic capacitance, *i.e.* amount of water released per unit increase of xylem tension (Anderegg & Meinzer 2015), important for delaying stomatal closure (Hölttä *et al.* 2009) through expected effects on night-time refilling of the apoplast. Water losses through transpiration are indeed buffered by water stored in wood tissues: this water can be released into the transpiration stream during the day and recharged during the night. Many trees, especially in tropical dry forests, appear to be well buffered against the impact of seasonal drought. They have access to stored water in the soil or in the stem (Borchert 1999). This stored water enables rehydration during the dry season and subsequent flushing and flowering before the rainy season starts. The rate of water uptake during this dry season rehydration is highly correlated with water storage capacity (Borchert & Pockman 2005), indicating that wood anatomy is a major determinant of drought adaptation.

Parenchyma probably plays a role in embolism repair. There is no consensus about the exact repairing mechanisms of the hydraulic system, including refilling of vessels (Clearwater & Goldstein 2005). However, appealing models are proposed explaining conduit refilling and the role of parenchyma cells. It is hypothesized that an increase of osmotically active components, either ions or carbohydrates, are being released into cavitated conduits or surrounding cells. Mechanisms of water transport independent of ion transport like aquaporins (membrane proteins) most probably play an important role (Zwieniecki & Holbrook 2009; Nardini *et al.* 2011). Refilling might be assured through phenomena that are similar to root pressure, accumulation of nutrients in the root apoplast, or stem pressure, soluble sugars released by parenchyma cells (Plavcova & Jansen 2015).

Marginal parenchyma at the boundary between growth rings is likely to be of importance during reinitialisation of cambial activity after dormancy (Trouet *et al.* 2012).

Rays probably also play a mechanical role. This was suggested by the high positive correlation between strength of wood and ray size and abundance when pulled in the radial direction (Mattheck 1995). Also isolated rays showed an unexpectedly high tensile strength (Burgert & Eckstein 2001).

Parenchyma is not always of lower density than the ground tissue. A positive correlation was observed between the ray volume of 50 Japanese hardwoods and the basic density (Fujiwara 1992).

Parenchyma plays also an important role in defence and heartwood formation (Kampe & Magel 2013). In the *Robinia* type of heartwood formation, probably the most common type, are the extractives formed in the parenchyma at the boundary between sapwood and heartwood. In the *Juglans* type the precursors of the heartwood compounds are formed in the sapwood parenchyma and radially transported through the rays.

In some woody plants, especially lianas and stem succulents, some of the un lignified parenchyma cells are able to dedifferentiate, which is important for wound repair.

Parenchyma traits can also be ranked on a time-axis, as shown by Olano *et al.* (2013). They found a positive correlation between the percentage of ray parenchyma of *Juniperus thurifera* and the precipitation in May and a negative correlation between the number of new rays formed in a ring and precipitation during January and February. These findings suggest that variation in wood parenchyma, and ray parenchyma in particular, may improve our understanding of tree responses to environmental changes.

Guidelines for implementing wood anatomy in trait-based ecology

Traits and variability

The performance of trees changes along environmental gradients and through time. In trees and woody plants in general this variation is particularly high. The high genetic and phenotypic variability is a consequence of being long-lived with high probabilities of mutations and high selection pressures. Only a minor fraction of the produced seeds grow up to adult trees (Petit & Hampe 2006).

Traits can be measured with binomial, categorical, ordinal or quantitative scales, but explaining variability among traits is a major issue. Intraspecific variation is interesting for short environmental gradients. Study of long gradients may use trait values that are typical for a species. A clear distinction should be made between variability within trees (between organs, and on a pith-bark or root-to-tree-top transect) and between individuals of the same species. Systematic information on the variability of most of the wood anatomical features is still lacking.

The variability of measures (either traits, properties or individual performance) within a population can be described quantitatively by a distribution function (Mohr & Schopfer 1995). A normal distribution is theoretically obtained when many factors determine a measure independently, and allow a description with only two parameters: the mean and the standard deviation. Many of the wood traits are not distributed normally and cannot be described by mean and standard deviation alone. Characterizing asymmetrical distributions of traits is therefore difficult. Information on mode and median could be of help, but knowledge of the shape of the whole distribution functions is an absolute requirement for correct interpretation of trait measures (Mohr & Schopfer 1995), possibly with the help of robust statistical analysis and modelling. Kattge *et al.* (2011) characterize density distributions of trait data by skewness and kurtosis of raw and log-transformed data and they calculate the departure from normality. Conduit density, conduit area, vessel diameter, conduit lumen area per sapwood area and vessel element length show right tailed and acute peak distributions. Wood density is also right tailed, but shows a wider peak around the mean value. Wood density is the wood feature that is the closest to the normal distribution, with a mean value of approximately 600 mg mm^{-3} (Kattge *et al.* 2011). Choosing a relevant distribution for a response variable is the basis of modelling techniques such as generalised linear modelling and generalised additive modelling. Information on distribution shape of wood traits, upper limit of measures, whether there is overdispersion, zero truncation, mean-variance relationships is hard to find in the literature in an explicit form. Databases should systematically provide this type of statistics in order to optimally incorporate a wood anatomical approach in trait-based ecology.

Traits and stress

A practical definition of stress effects on trees and wood formation is still lacking (Kranter *et al.* 2010). Nevertheless, wood traits can be seen as response variables to environmental impacts. Stress effects could ideally be described in terms of a numerical parameter like there are: tolerance, optimum, lower limit and upper limit of a probability distribution. It is therefore necessary to have information on typical response curves of responsive wood anatomical traits.

Traits and the time axis

A consequence of the trait definition of Lachenbruch and McCulloh (2014) is that traits need to be quantifiable *over a particular period of time*. This means that the period of interest should be clearly defined. A trait measure is indeed supposed to comprise information on the performance of an individual plant, but only during a well-defined period. Juvenile features around the pith of tree stems can certainly provide information on the performance of these trees when they were young, but not necessarily on the performance of big trees. Mature features are more likely to be linked to the performance of adult trees, but it should not be overlooked that the performance of adult trees continue to depend on juvenile tissues in twigs and branches.

Since secondary tissues of trees are the result of gradual accumulation of new cells, the construction of time axes with trait measures and, consequently, the reconstruction of the performance history of single trees is interesting for trait-based ecology. An appealing application of the time-series issue is a systematic comparison of trait values between two subsequent years (Giagli *et al.* 2016).

Modelling of ecosystem dynamics is an important issue for trait-based ecology. These models try to take into account the age-structure of separate populations. This is undoubtedly an area where conceptual and methodological breakthroughs are urgently needed (Violle *et al.* 2007) but where anatomical analysis of growth-ring patterns offers interesting perspectives.

Traits and system integration

Organismal level

Next to the possibility of construction of time series, there is also the integration topic that is of significance. Integration of components into a system of higher hierarchy signifies a classical challenge in ecology. Lachenbruch and McCulloh (2014) avoided this concept in their terminology, but it has certainly an attractive potential in system theory in general (Bertalanffy 1968) and in biotic systems in particular (Allen & Hoekstra 2015). A system of higher integration indeed shows other assets than the sum of the components of this system. The performance of an individual is more than the sum of single traits, it results from the integration of traits. Assembling or integrating traits adds information and gives typical properties (Lachenbruch & McCulloh 2014).

The relevant level to which tree traits are to be integrated is the organism as a whole. It is indeed definitely the whole plant body which should be seen as an integrated functional unit. The separation of a plant into organs, tissues, cells and cell parts is largely conceptual. Accordingly, hierarchically organised living systems cannot be understood

fully if only elements of them are analysed out of their context. Performance of trees is to a big extent controlled by different wood traits present at different levels of system integration: there are whole tree traits as well as anatomical traits. A tree can react to the environment through modifications of certain features of single cells, as is the case with reaction wood. A reaction is also possible through arranging tissues radially (e.g. vessels of vines are much bigger as soon as they reach a support) or vertically (e.g. spiral grain) (Lachenbruch & McCulloh 2014).

The integration of wood anatomical elements within the higher unit is equally important as a thorough analysis of cell parts, cells and tissues. Cell biology is only one step and not a final goal of biological research of higher systems (Mohr & Schopfer 1995).

Integration of traits to the scale of a tree is essential, since natural selection acts on performance of whole plants. A plant's viability is indeed determined by its performance, rather than its contributing traits and properties. Moreover there can be mutual compensations such that similar performance occurs with rather different traits (Lachenbruch & McCulloh 2014). Typical for trait research is the very complex interaction between different levels of integration and microscopic resolution, such as vessel networks and pit characteristics, as perceived by Lens *et al.* (2011). The integration issue makes it difficult to interpret traits independently from other traits.

Integration of traits implies taking into account the influence of tree size. Size influences nearly all the structural, functional and ecological characteristics of organisms in general and trees in particular. A tree with low density, weak wood can support impressive loading thanks to its size, like it is the case for some emergent rainforest trees like *Ceiba pentandra* and also colossal individuals of *Adansonia*. These species have very light and weak wood, but most of the rainforest emergents have heavy, durable and strong wood.

Moreover there are the scaling laws where many wood anatomical features need to follow mathematical rules rather independent of their general ecophysiological function. This influence of size also confirms the need to standardize for stem size when structural attributes including wood anatomical traits are being compared between individuals (Olson & Rosell 2013; Anfodillo *et al.* 2016). This has important consequences for establishing sampling strategies.

Since plant anatomy is understood to include the study of tissue arrangements in plant organs, the number of wood traits logically also includes features like grain, sapwood width, tree-ring widths, density profiles, water content of fresh wood, stem sapwood cross-sectional area per supported leaf surface area (Huber value), stem circumference, plant height, plant growth rate, stem length, stem heartwood biomass, stem longevity, stem pith type, twig, bark and root characteristics, etc. These are not included in the IAWA feature lists, but are certainly relevant for tree performance and should not be neglected in trait-based ecology supported by the wood research community.

Larger biotic systems

Plants evolved structures necessary for their functioning as an organism, but also as part of larger biotic systems and contribute as such to the functioning of populations and

communities. The organismal performance of certain individuals could be considered as indicative for the population, community or ecosystem behaviour. Scaling-up from plant traits to higher biotic systems requires so-called integration functions (Violle *et al.* 2007). The standing biomass of a community system, like a forest stand, is a simple sum of the masses of individuals, but the mass of a few big trees might be sufficient to characterize the biomass of a stand (Bastin *et al.* 2015).

Less simple integration functions are needed when the climatic response of a tree population is to be captured. The robust dendrochronological methodology is useful for that aim, where that part of the individual tree growth that can be cross dated with other individuals is extracted.

CONCLUSIONS

Forests, woodlands and trees in open landscapes represent important stocks and sinks of carbon. As such they are essential to maintain levels of low entropy and to sustain the carrying capacity of the earth. Woody plants are a major component of forests and a large share of the organic carbon appears as wood. The function of wood in the performance of trees, the position of trees in the functioning of the ecosystem and the role of forest ecosystems in global interactions are reasons enough to give high research priority to woody tissues.

When time and complexity is avoided by science in its classical definitions (Prigogine *et al.* 1984), it seems that a productive implication of wood research into diagnoses and evaluations of the carrying capacity of the global ecosystem implies the usage of models dealing with interactions between components and taking into account variability along time axes. Conceptual breakthroughs are expected in the domain of models for upscaling of wood and tree traits to systems of higher integration levels like populations, communities, ecosystems and biomes.

An interpretation of complexity of wood structures and functions needs to be based on correct terminology covering the wide spectrum of wood anatomical features. Understanding of the function of traits should be based on terminology that describes the variation of plants. Even if a wood anatomical glossary going beyond identification and taxonomy is actually lacking (Morris *et al.* 2016), the IAWA feature lists remain indispensable, thanks to the clear definitions and their comprehensiveness as checklists of *potential* traits.

There is a widely acknowledged need for global databases of wood anatomy (Anderegg & Meinzer 2015) allowing to quantify the relative amount of intra- and inter-specific variation, as well as variation within and between functional groups (Kattge *et al.* 2011). One of the major challenges of plant ecology is indeed defining consistent sets of measurable traits and developing databases allowing the quantification of ecological strategies of plants along gradients (Fournier *et al.* 2013). These databases should incorporate a time dimension since trees are long living organisms storing information on their performance into the traits of the lignified structures. Since measuring of wood traits is often laborious and does not necessarily fit into classical research projects, wood collection curators might reflect on a gradual establishment of collections of research material aiming at underpinning future or long-term projects in the domain of trait-

based ecology. Wood collections are indeed to be considered as interesting archives of wood traits, provided that there are reliable and precise metadata. This would mean a systematic collection of stem discs and of fragments of organs that are possibly less typical for taxon description, like juvenile and root tissues. Especially for the tropics such collections would certainly provide a wealth of study material helping investigations of carrying capacity of ecosystems. As such wood anatomy has excellent and firm foundations to contribute microscopically to global change research.

ACKNOWLEDGEMENTS

Many thanks in the first place to the so-called TG4 team of the EU Cost-Action FP1106, STReESS (Studying Tree Responses to extreme Events: a SynthesiS). We interrupted our daily occupations to come together in scenic locations in Wageningen, Naples, Sarajevo, Hyytiälä, Estoril, Nesuchyne and Kranjska Gora where we all together reflected on the trait concept, stress effect on trees and wood functional features. Many thanks (“in alphabetical order”) to Pieter Baas, Katarina Čufar and Veronica De Micco for taking the time and having the patience to read preliminary try-outs and draft versions of this manuscript. I am very grateful for the input of all the participants of the topic group on wood anatomical functional traits, including all those that gave presentations during our meetings.

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Accepted: 8 April 2016