Introducing wood anatomical and dendrochronological aspects of herbaceous plants: applications of the Xylem Database to vegetation science

Ulf Büntgen, Achilleas Psomas & Fritz H. Schweingruber

Abstract

Objectives: Although more than half of the Earth’s landmass is covered by non-forest vegetation and forests only account for ca. 20%, the majority of wood anatomical and dendrochronological studies still centre on trees and their timber products of secondary meristem growth. Comprehensive assessments of the anatomy, taxonomy, physiology and dendrochronology of herbs are, however, still missing. We therefore aim to evaluate the importance of stem anatomical and dendrochronological aspects of herbaceous plants for vegetation science, and further intend to explore if species-specific differences in xylem anatomy can be linked with patterns of life form, plant size and site ecology.

Locations: Numerous extra-tropical sites within six biogeographic regions on six continents, spanning an elevational gradient of 4400 m from sea level to the alpine zone.

Methods: We employ the Xylem Database to investigate well-established and newly defined wood anatomical and dendrochronological traits in 3347 dicotyledonous tree, shrub and herb species from 140 families and 952 genera. The obtained site information is placed in a global context of vegetation cover.

Results: We demonstrate that plants included in the Xylem Database broadly represent the diversity of growth forms, habitats and life histories of extra-tropical dicots, thus validating its potential for a range of uses within vegetation science. An unexpectedly rich catalogue of xylem anatomical and dendrochronological features is found in the stems of almost all dwarf shrub and herb species, with the quantity and diversity of their characteristics being comparable to larger plants, including most tree species. Annual rings are formed independently of life form, plant size and site ecology. Secondary growth, which is an expression of plant age, defines the main principle of terrestrial angiosperm development.

Conclusions: Based on a first assessment of the Xylem Database, we suggest merging the traditionally separated research communities of wood anatomy and dendrochronology (including dendroclimatology and -ecology), as well as expanding their joint application to all non-forest, extra-tropical vegetation types. Moreover, we recommend overcoming the theoretical life form separation of trees, shrubs and herbs. This conceptual advancement will likely provide annually resolved insight on the past dynamics of dry matter production and carbon allocation for many marginal vegetation zones beyond the geographic limits of forest growth, which are particularly vulnerable to environmental change. Our study may further stimulate timely efforts in comparing plant morphological and wood anatomical characteristics with phylogenetic reconstructions.
Introduction

Ontogenetic assessments of the functioning of stems and roots so far mainly concentrate on tree species (Evert 2006; Meinzer et al. 2009), whereas in-depth knowledge on the functionality of stems and roots in smaller plants, such as shrubs, dwarf shrubs, herbs and grasses, is generally limited to only a few cases (Schenk & Jackson 2002). Large-scale data sets of plant traits that are based on anatomical descriptions and which also represent the natural life-form diversity are predominately restricted to literature reviews (Metcalle & Chalk 1957; Kattge et al. 2011). Despite a few examples among shrub species (Gregory 1994; Carlquist & Hoekman 1985 and references herein), trees still dominate systematic and comparative wood anatomical reports (see Hoekman 1985 and references herein), and a comprehensive xylem anatomical evaluation of shrubs, dwarf shrubs and herbs is currently missing (Wheeler et al. 2007).

Although the majority of studies in wood science still centre on the anatomy, taxonomy, physiology and dendrochronology of trees, a few exceptions indicate a wide range of diverse characteristics in the anatomy of different shrub species (Greguss 1945) and herbs (Zoller 1949; Dietz & Ullmann 1997; Schweingruber & Dietz 2001; Evert 2006; Schweingruber & Büntgen 2013). Some studies also reveal the dendrochronological potential of arctic shrubs (Hallinger et al. 2010; Macias-Fauria et al. 2012; Schweingruber et al. 2013b), temperate shrubs and herbs (Poschlod et al. 2011; Nobis & Schweingruber 2013), as well as shrubs from Mediterranean environments (De Micco & Aronne 2009; Battipaglia et al. 2010; Crivellaro & Schweingruber 2013; Zimowski et al. 2014). Nevertheless, tree ring researchers, and more specifically dendroclimatologists, so far primarily focus on the development of long chronologies from climate-sensitive trees (Fritts 1976) and wood material from historical, sub-fossil and even archaeological samples (Büntgen et al. 2011). At the same time, this emerging community broadly overlooks more than half of the Earth’s landmass that is covered by smaller, non-forest vegetation types (Friedl et al. 2010).

Quantification of the total terrestrial stem and root biomass (Jackson et al. 1996), averaged over a large variety of different plant ages, often neglects information on species-specific longevity and the appropriate level of annual resolution that can be reached through simple ring counting instead of cross-dating (Fritts 1976; see also details below), which would ultimately provide an important temporal component for evaluating carbon fluxes over various spatial scales. Imprecise age information of species specific to community-wide biomass production will subsequently translate into sizeable model uncertainties of regional to global water, energy and carbon cycles and budgets (Keenan et al. 2013; Pearson et al. 2013). Plot-scale observations of vegetation patterns and dynamics from the northern latitudes and some higher elevation settings (Emmendorf et al. 2012; Pauli et al. 2012), extending well beyond the distributional limits of current forest growth, are generally too short to capture the full spectrum of biotic responses to climatic changes (Wu et al. 2012). Evaluation of the complex effects of climate variability on plant productivity further requires the inclusion of small plants, such as shrubs and herbs, which may exhibit both fast and slow rates of biomass turnover.

Here, we aim to introduce the Xylem Database (http://www.wsl.ch/dendropro/xylemdb/) and use it to illustrate the potential importance of wood anatomical and dendrochronological aspects of herbaceous plants for vegetation science. In doing so, we further intend to describe species-specific xylem anatomical characteristics and dendrochronological features, and relate patterns in the observed findings to differences in life form, plant size and site ecology. We illustrate that this unique compilation of nearly 3,500 species from six biogeographic zones on six continents broadly represents the diversity of extra-tropical dicotyledonous plants, and thereby provides a new resource for the analysis of functional traits in the context of global vegetation cover.

Methods

A total of 3347 individual herbaceous species from six biogeographic zones on six continents has been collected during the past 40 yrs (Schweingruber et al. 2012). The somewhat haphazard sampling design resulted in an exceptional compilation of well-preserved above- and below-ground stem parts from plants in 140 families and 952 genera. These samples ideally capture the entire stem part between the hypocotyl and the primary root (root collar) and thus contain the oldest remaining plant tissues. Thus, all collected stem sections should include the maximum number of formed and preserved rings, enabling ring properties, plant ages and recruitment dates to be most accurately estimated. As the correct determination of plant ages depends on an uninterrupted process of annual ring formation and the subsequent detection of annual ring boundaries (Dietz & Fattorini 2002; Schweingruber & Büntgen 2013; Schweingruber et al. 2013a,b), all material originates outside the tropics (Fritts 1976). Here, we do not consider the seasonal tropics. We also excluded damaged individuals from sites with extremely poor soil and/or nutrient conditions, material from mechanically disturbed sites, as well as samples from exceptionally large individuals that often represent intensively fertilized settings.
To assess xylem characteristics, as well as plant age and annual increment, ethanol-saturated stem parts of each plant sample were sectioned in three anatomical directions, double-stained with safranin and astrablue, mounted and microscopically analysed and measured under transmitted and normal polarized light. More specifically, a small axe was used to expose the transition zone between the root and the stem (i.e. the root collar) of all dwarf shrub and herb specimens. Alternatively, a small saw was employed to obtain larger disc samples from trees and shrubs, while increment borers were utilized for coring the largest individuals. All samples were individually stored in labelled plastic bags filled with 40% ethanol that additionally contain information on plant height, life form, site ecology, sample locality, altitude and the collection date (Schweingruber et al. 2012). Stem parts were divided under wet conditions, without embedding, but applying disposal blades in a sliding microtome (Typ Reichert; Gartner & Nievergelt 2010). Cuboid sections of approximately 1-cm length were cut from large stem parts and thin and soft stems of herbs were clamped in cork and fixed in a microtome holder (Schneider & Gartner 2013).

Chemical processing, including sample bleaching, staining and dehydration, was performed for each slide and only small amounts of liquid were carefully dropped to enable the surplus to run off into a container. Brown sections containing oxidized phenols were bleached with Eau de Javelle (NaClO) for 10 min and then washed with tap water. All wood sections were simultaneously double stained for 2–3 min with astrablue and safranin at a ratio of 1:1 (astrablue: 0.3 g in 100 ml distilled water with 2 ml acetic or tartaric acid; safranin: 0.4 g in 100 ml distilled water). Samples were then washed with different ethanol concentrations between 60 and 95%, and a drop of xylol was placed on each section before ultimately covering the material with Canada balsam and a cover slip. To prevent thin sections from buckling, both the slides and cover slips were sandwiched between PVC and subsequently placed on iron plates, with additional magnets on the topside pressing the samples flat during their ultimate 24-h drying at 60 °C.

Red-stained structures represent lignified cell walls, whereas blue-stained sections refer to non-lignified cell parts. The utilization of polarized light and microscopy further allowed secondary cell walls to be distinguished from primary walls (Chaffey 2002; Schweingruber et al. 2012, 2013a,b). Gartner & Schweingruber (2013) describe in detail the entire chain of preparation steps that range from very soft to very hard material and from extremely small to extremely large samples.

All samples were processed at the Swiss Federal Research Institute WSL, and only technically perfect slides were ultimately considered for xylem anatomical and dendrochronological analyses. Members of the International Association of Wood Anatomists (IAWA; Wheeler et al. 1989) have successfully defined wood anatomical features within numerous tree and shrub species by using single-stained slides (i.e. only safranin was employed as dye) and applying high-amplification microscopy. The resulting inventory (http://insidewood.lib.ncsu.edu/), which describes the state-of-the-art catalogue for wood identification (though mainly focusing on tree and shrub species), was herein considered as a basic framework for the additional pinpointing of new herb-specific characteristics in wood anatomy and dendrochronology. In this regard, it is useful to mention that we created micro-sections of each sample. This step follows standard procedures in traditional wood anatomy and is commonly done for each specimen that is newly assessed at the Swiss Federal Research Institute WSL. All wood anatomical features as defined by the IAWA inventory (http://insidewood.lib.ncsu.edu/) were then determined and classified. Moreover, we detected novel characteristics, which have so far not yet been described for trees and other larger plant species. These newly perceived wood anatomical traits might be well distributed among the entire stem and thus possibly occur within the pith, the xylem or the cambium. It should be further noted that differences between woody and non-woody cell walls were only detectable with the use of polarized light after application of a so-called double staining (safranin and astrablue).

The MODIS Global Land Cover Type product (http://modis.gsfc.nasa.gov/) was utilized to represent the Earth’s current vegetation cover (Friedl et al. 2002). This satellite-based data set of global land-cover maps provides thematic characterizations of the Earth’s surface that capture biotic and abiotic properties and that are closely tied to the ecological condition of land areas (Friedl et al. 2010). It contains five classification schemes that describe land-cover properties derived from observations covering yearly input of Terra- and Aqua-MODIS data at a spatial resolution of 1 × 1 km. Data from 2009 together with the primary land-cover scheme of 17 classes defined by the International Geosphere Biosphere Programme (IGBP; http://www.igbp.net/) were used and aggregated into three broader units: (1) forests (evergreen needle-leaf forest, evergreen broad-leaf forest, deciduous needle-leaf forest, deciduous broad-leaf forest, mixed forest); (2) beyond forests (closed shrublands, open shrublands, woody savannas, savannas, grasslands, permanent wetlands, croplands, urban and built-up, cropland/natural vegetation mosaic); and (3) others (snow and ice, barren or sparsely vegetated).
Results and Discussion

A total of 3347 dicotyledonous species from 140 families and 952 genera was compiled during the past 40 yrs. Weighted towards Europe, but still representing global terrestrial vegetation outside of the tropics, this somewhat haphazard plant collection covers six biogeographic zones on six continents and spans an elevational gradient of 4400 m from sea level to the alpine zone (Fig. 1). Mean elevation of all extra-tropical sampling sites is 862 m a.s.l. The compilation includes material from hyper-arid, subtropical, Mediterranean, temperate, boreal, arctic, alpine and even nival habitats. Data represent almost all life forms among seven taxonomic groups (Fig. 1). A total of 2399 samples from Europe, excluding Georgia and Russia (144 and 125), roughly reflects one-third of all existing European dicotyledon species that represent ca. 95% of all dicot families (Tutin 1964–1980). The remaining 679 species are dominated by 325 samples from North America. Unique anatomical insight on Macaronesia and the African Sahara was gained from 157 and 130 species, respectively. Material from the Southern Hemisphere derives from the Andes, Australia and South Africa.

Traditional life-form classification reveals a dominance of 1965 herbs, 556 dwarf shrubs <0.5 cm, as well as 186 trees >400 cm (Fig. 1). This plant size-dependent life-form proportion (small vs large) is representative for the total number of all European terrestrial species (Tutin 1964–1980). Taxonomic classification results in six groups (Cole & Hilger 2010), with 1970 Asterids representing the majority (Fig. 1). The fraction of species within the respective taxonomic group proportionally resembles the total amount and composition of species within the temperate zone of the Northern Hemisphere. Information on site condition, life form, sampling position within a plant hypocotyl, rhizome or stem, as well as the number of annual growth rings and their radial widths is additionally provided for each specimen. All data are freely available from the Xylem Database (http://www.wsl.ch/dendro/xylemdb/index.php).

Although approximately corresponding to the natural life-form diversity of Central European plant species (Ellenberg 1996), our data set is expected to under-represent the huge number of annual herbs and dwarf shrubs that may sporadically germinate after short-term precipitation events, which are known to occur frequently in arid environments, such as parts of the Mediterranean Basin and other subtropical regions (Whittaker 1975). At the same time, our data set may slightly overestimate the proportion of larger plants, as it integrates ca. 80% of trees and shrubs, but only ca. 30% of dicotyledonous herbs (Aeschimann et al. 2004). Any straightforward comparison of our data set with the real world complexity of species diversity is somewhat hampered by the overall relatively vague boundaries that are commonly used for many life-form classification systems (Landolt 2011). Additional bias may arise from imprecise biogeographical categories, as well as a lack of systematic large-scale inventories that comprise not only trees but also shrubs and herbs.

Even though this study is, at least to our knowledge, based on the largest compilation of dicotyledons, it still represents a significantly limited number of samples. In fact, our data only account for ca. 1% of all global taxa, and supplementary evidence from those families that contain many species, such as Lamiaceae, Boraginaceae and Asteraceae, would be particularly beneficial to gain further insight into the elevational distribution of all 3347 sampling sites between sea level in Cyprus (Phagnalon rupestre (L.) DC.) and 4400 m a.s.l. in Argentina (Parastrephia quadrangularis (Mey) Cabr.)
on plant functional traits and their ecological relevance. It should also be noted that monocots, as well as Proteaceae, Cactaceae and many other families from the Northern Eurasian flora were not herein considered. Hence, more data from more biogeographic regions would not only enhance the possibility for further and more comprehensive analyses but would also improve the robustness of any subsequent interpretation.

Height of all (perennial and annual) herb, shrub and tree species within our data set ranges from 2 cm to >40 m (Fig. 2a). However, most plants have heights between 6 and 40 cm, and only a few species indeed exceed >150 cm in height (see also Nobis & Schweingruber 2013 for details). The proportion of species per (well-replicated) height class is uniform (Fig. 2b). Existence of the above- and below-ground stem transition (root collar) allowed the absolute age, herein defined as calendar years, of 1461 out of 2521 small plants within or below their hypocotyls to be estimated (Fig. 2c). The exact determination of plant age was based on rigorous ring counting but did not require cross-dating (App. S1), i.e. the visual synchronization of similar rings from different samples throughout time. Age estimation of the remaining samples was complicated by indistinct ring boundaries that precluded ring counting (see Schweingruber & Poschlod 2005 for a more detailed discussion on methodological challenges associated with dendrochronological age determination). In this regard, it should be noted that simple ring counting of 24 herbs from a garden experiment with known sowing dates associated distinct radial stem increments with precise annual calendar years (Schweingruber & Poschlod 2005). Annual plants and annual shoots, however, always create only one, although often well identifiable, ring. An annual plant is also characterized by secondary growth, which is expressed in both xylem and phloem. Although sometimes rather small, the secondary growth is always located between the xylem, cambium and cortex.

On top of the above-mentioned methodological constraints related to the age estimation of our samples, there may also be genetic reasons. Some plants do not form rings, e.g. certain species do not form distinct ring boundaries. A successive cambium, for instance, is known for Amaranthaceae, and morphological reasons should also be considered. If the hypocotyl zone within a plant has not been found, the counted number of rings most likely does not reflect the correct plant age. The resulting estimate
thus underestimates the true age. This handicap is most critical for larger plants with complex stem, branch and root systems. Most of our estimates tend to underestimate rather than overestimate plant ages, particularly of tree and shrub species, as those values are generally not based on ring counts near the rootstock or at the stem base. Use of the term ‘Maximum age’ is thought correct for annual plants (therophytes), which were harvested at the end of their first and only growing season. Additional bias may originate from plants growing under arid climate conditions, where aperiodic rainfall regimes can trigger intra-annual fibre and vessel bands. These so-called density fluctuations are difficult to distinguish from annual ring boundaries. Ring counting on plants with rotten stem centres or rotten rhizomes only delivers the age of the oldest preserved tissue. Moreover, we are well aware that the herein gathered information on plant ages does not necessarily represent the full range of a species-specific age distribution, but the massive replication of our data set, at least, provides a first insight into aging patterns.

Ages of 1117 dicotyledons with taproots are less than 5 yrs and often only comprise several weeks during which entire rings are formed, such as in Arabidopsis thaliana (Melzer et al. 2008). Xylem around the stem or root centre defines the formation of the first annual ring. Ages of perennial herbs that range between 2 and ca. 50 yrs and ages of shrubs that range between ca. 5 and 200 yrs imply different annual biomass turnover rates. Size, rather than life form separation between annual and perennial herbs and dwarf shrubs, is important to improve understanding of changes in total terrestrial stem and root productivity (see also Schweingruber et al. 2012 for details). The fact that size and life form of plants is not necessarily correlated can be illustrated with two examples of annual plants: sunflowers (Helianthus annuus) can reach a height of 4 m, whereas A. thaliana usually does not exceed 20 cm in height, both under optimal growing conditions.

Knowledge of the age of small plants is further relevant for all studies that seek to understand spatiotemporal changes in vegetation productivity and tissue turnover, particularly within alpine and arctic environments (Weisser et al. 1999). However, a reliable anatomical comparison within and between species is only meaningful if all observations and measurements are based on the hypocotyl or rhizome, which was the case in our study. Precise age estimates are also only possible for small plants with taproots. In contrast, the maximum number of rings in clonal plants (rhizomes) defines the age of the oldest remaining tissues, and thus always underestimates the absolute plant age (Schweingruber & Poschlod 2005). Moreover, it should be noted that the approximation of tissue age, which is particularly relevant to assess carbon turnover, is overall species-specific and climate-dependent: stems of Rhododendron ferrugineum, for instance, can reach >200 yrs old, whereas Potentilla nivalis rhizomes usually do not exceed 10 yrs of age, both growing under alpine conditions. Caution is further advised, as our sampling strategy included only one individual per species. However, a general understanding of plant longevity and stem anatomical plasticity is only possible if different specimens from the same species among different sizes and sites are considered (Poschlod et al. 2011).

Annual increments of 1466 samples range from 0.05 to 1.0 mm (Fig. 2d), 662 samples had increments between 1.0 to 3.0 mm, 61 species showed wider rings, and growth rates of 332 species with indistinct ring boundaries remained undefined. The average annual increment of all tree species in Switzerland is 1.5 mm (Brändli 2010). In this regard, it is important to note that no changes in ring width occur after cell formation, which includes the process of cell enlargement, the formation of secondary walls and their lignification.

Anatomical classification (Wheeler et al. 1989), supplemented with herb-specific structures (Schweingruber et al. 2012), defined the number of xylem characteristics for each individual specimen, ranging from one to 92 possible traits. Equal proportions of principal xylem anatomical characteristics are found in the collection of 2521 (smaller) dwarf shrub and herb species, as well as in the subset of 826 (larger) tree, shrub and liana species (Fig. 3). The fraction of cells with lignified walls in the xylem of annual and perennial plants ranges from ca. 2 to 95% (Fig. 4). Stem and root formation of almost all terrestrial dicotyledons, including small annual and big centennial plants, follow the universal principle of secondary radial growth, with their anatomical structures mainly fulfilling hydraulic and mechanical functions. Anatomical adjustment to environmental variation is found within and between different taxonomic groups (Spicer & Groover 2010). The xylem of herbs suggests a clear tendency for small vessel diameters and large amounts of parenchyma in comparison with trees. Fibres, apotracheal parenchyma and procumbent ray cells are scarce or absent in herbs. A certain level of trait-specific dependency however implies some degree of uncertainty that should be considered while interpreting our results.

Comparison of the frequency of anatomical traits in trees, shrubs and dwarf shrubs that are summarized in the Inside wood databank (http://insidewood.lib.ncsu.edu/) with those of the present study revealed several differences, which mainly depend on the larger number of dwarf shrub species and several characterization features resulting from the double staining technique, such as the presence of parenchyma (Table 1). Newly defined xylem anatomical traits that were so far not included in the IAWA list (Wheeler et al. 1989) are, for instance: ring boundaries...
marked by tangential splits (ring shake), extremely small (<20 μm) and frequent (>200 mm⁻²) vessels (Fig. 5h; Diapensia lapponica L.), as well as very thick (>2 μm) vessel walls and reticular inter-vessel pits. Fibres can be totally absent (Fig. 5b; Cerastium semidecandrum L.), often only occur at the periphery of the stems or in intra-annual tangential bands (Fig. 5d; Saxifraga moschata L.), and may also not be lignified (Fig. 5h; Diapensia lapponica L.). So-called pervasive axial parenchyma can be very dominant, which may appear dark under polarized light. Primary vascular bundles are frequently separated by large rays and keep their form over many years (Fig. 5c, e; Pedicularis foliosa L. and Clematis alpina (L.) Miller). Rays that are...
commonly not well separated from axial parenchyma are called confluent rays.

A combination of IAWA (Wheeler et al. 1989) and newly defined (see also Schweingruber et al. 2012) characteristics further highlights the main wood anatomical differences between trees, shrubs and herbs (Table 1, Fig. 4). While most features occur in all life forms and vary considerably in their frequency, i.e. the distribution of vessels (3), the wall structures of vessels (14, 20, 20.1, 36, 39.1) and vessel diameters (40.1, 42), as well as the absence of fibres (60.1 70.3) and fibre wall structures (65, 68, 70); the distribution of axial parenchyma (76, 79.1) and the absence of rays (117), ray width (96, 99), ray composition (100.1) and ray cell walls (100.2), as well as the persistence of vascular bundles (99.1) and the presence of prismatic crystals (136). Some of these differences might be explained as different plant sizes and the corresponding mechanical and hydrological demands. Although the detection and interpretation of relationships between wood anatomical traits of trees and shrubs and ecologically defined floral regions from the tropics to the boreal forests have been the subject of many studies (Baas & Schweingruber 1987; Wheeler et al. 2007), only very few anatomical studies have defined specific functional traits that

---

**Fig. 5.** Visual examples of differently lignified herbaceous plants. (a) An intensively lignified Mediterranean herb (therophyte) with one annual ring. Most of the xylem is lignified (red) except for some ray cells and a few gelatinous fibres (blue) (photo Guenther-Blaich). (b) A weakly lignified Mediterranean herb (therophyte) with one annual ring. Fibres and rays are absent, and only a few vessels are lignified. (c) A partially lignified subalpine herb (hemicryptophyte) with eight annual rings. Vessels and tangential groups of fibres are lignified. Large rays and major parts of latewood are non-lignified (photo Oechslin). (d) A weakly lignified alpine herb (hemicryptophyte) with eight annual rings. Fibres and rays are absent (photo Oechslin). (e) A partially lignified subalpine liana with 16 annual rings. Vessels and thin-walled fibres are lignified. Vessels and the axial parenchyma cells are non-lignified. (f) A weakly lignified subtropical shrub with 12 annual rings. Vessels and primary fibre walls are lignified; ray cells and secondary fibre walls are non-lignified. (g) An intensively lignified tree of the temperate zone, which may reach ages up to 500 yrs. Vessels, fibres and rays are lignified; apotracheal parenchyma cells are non-lignified. (h) A poorly lignified stem of a cushion plant from the arctic zone with 22 annual rings. Only vessel walls are lignified, whereas all other cells are non-lignified (photo Oechslin).
differentiate the xylem of Mediterranean and temperate European tree species from those in the tropics. Schweingruber et al. (2013a) discuss the ecological significance of anatomical features in plants of all life forms in relation to selected communities.

The ecological value of wood anatomical combinations has so far only been evaluated numerically for the component of plant age (Nobis & Schweingruber 2013). A visual comparison of anatomical features in finely demarcated plant associations, however, exhibits a large diversity that is typical for various vegetation units. The existence of functional traits has been demonstrated for communities across arctic and alpine steppes, tall herbaceous meadows, dry grass steppes and halophytic succulent (Chenopodiaceae) steppes, for instance. Stem anatomical structures may even open a new perspective on the classification of vegetation units. Of special interest will be questions about how anatomical traits allow plants to cope with various hydrological and thermal conditions, such as plants in snow beds in contrast to those specimens on windy ridges (Schweingruber et al. 2013a,b).

Small plants that form annual rings demonstrate the possibility of expanding current dendrochronological research, which so far almost exclusively considers trees and only marginally includes shrubs (Hallinger et al. 2010; Poschlod et al. 2011; Macias-Fauria et al. 2012). The subsequent spatial expansion of dendrochronology and wood anatomy would be huge, as the global landmass consists of ca. 20% forest (Friedl et al. 2010), but non-forest vegetation that includes grasslands, shrublands, savannas, wetlands, croplands and urban mosaics (App. S2; see Brändli 2010 for a detailed definition of the Central European vegetation cover) accounts for ca. 56% (Fig. 6) of the Earth’s land surface. While trees (and hence past dendroecological research) are not restricted to forests, the use of herbaceous plants will allow even greater expansion of wood anatomical research to non-forest regions. Complementarily, xylem characteristics of herbaceous plants in forest understories may help us to better understand climatic effects in entire forest ecosystems. Novel dendrochronological studies beyond forests should, however, be limited to conditions in which a seasonal climate induces annual rings (Fritts 1976). The seasonal tropics are perhaps also an ideal test bed for future case studies that aim to evaluate whether tropical vegetation dynamics ‘beyond forests’ are indeed driven by highly seasonal precipitation patterns and pronounced dormant periods.

Conclusions

By revealing an unexpectedly rich catalogue of xylem anatomical characteristics and dendrochronological features in dwarf shrubs and small herbs, this study demonstrates that annual ring formation in angiosperms occurs independently of plant size, life form and site ecology. Secondary growth, which is expressed as plants age, defines the main developmental principle of terrestrial dicots. These findings emphasize the potential to further gain annually resolved and species-specific insight on past dynamics of dry matter production and carbon allocation for many marginal areas that are particularly vulnerable to environmental change. Our results may also contribute to timely efforts in comparing plant morphological and wood anatomical characteristics with phylogenetic patterns, and thus ideally stimulate new research questions, such as how site ecology and evolution shape plants, and how changes in forest and non-forest vegetation affect the global carbon cycle.

We ultimately prioritize four partly interrelated research avenues in future wood science that include shrubs and herbs and move well beyond the geographical limits of forest growth: (1) recognition that xylem and phloem structures may help inform phylogenetic studies of herbaceous
as well as woody plants; (2) determination of plant ages to quantify spatiotemporal changes in species distribution, population turnover, production rates and associated carbon dynamics; (3) extension of stem anatomical and dendrochronological investigations from ca. 7500 tree and shrub species to >190 000 dicotyledon species; and (4) unification of the so far separated wood anatomical and dendrochronological communities to create methodological and conceptual cross-disciplinary synergy.

Acknowledgements

The Co-ordinating Editor Mike Palmer kindly provided valuable suggestions and recommendations to various earlier manuscript versions and vitally assisted in the complex review process. Comments from anonymous referees further improved our article. UB obtained financial support for the Czech project ‘Building up a multidisciplinary scientific team focused on drought’ (No. CZ.1.07/2.3.00/20.0248).

References


Greguss, P. 1945. *Holz anatomie der europäischen Laubhölzer und Sträucher*. Budapest akad, Klado, HU.


Whittaker, R.H. 1975. *Communities and ecosystems*. Macmillan, New York, NY, USA.


### Supporting Information

Additional supporting information may be found in the online version of this article:

**Appendix S1.** Whole plant and stem-specific examples of plants studied.

**Appendix S2.** Central European vegetation diversity aggregated into forest and non-forest areas.