Ecological plasticity of the secondary meristem

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17 **Abstract:**

18 Long-lived plants need to continuously adjust their structure to fit the changing environmental
19 constraints. Xylem and phloem growth represent both the means used to achieve these structural
20 adjustments and a good indicator of plant success and performance. This chapter reviews the growth
21 dynamics of the xylem and phloem and explores how resource availability and environmental variation
22 provides important context for understanding the impacts of global change. We first illustrate the intra-
23 annual patterns of xylem and phloem growth in different areas of the world to highlight the variations
24 caused by the environment. Then, the components of the growth process, from timing (phenology) to
25 the rates and the characteristics of xylem anatomy are presented to explain how these components are
26 marking valuable indications of the way plants growth respond to changing environmental conditions.
27 Finally we discuss how wood formation can contribute to advancements in ecophysiology and
28 dendroecology.

29

30 **Keywords:** Cambium activity, xylem, phloem, anatomy, growth pattern, plasticity, climate.

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Introduction:

Tree growth – defined here as biomass production – is principally related to the activity of the secondary meristem, the cambium. This meristem is responsible for the radial increase of stem, branches and roots, with cell division producing both phloem and xylem cells. While the phloem is responsible for the transport of assimilate, the xylem is a fundamental element of the hydraulic and mechanical architecture of plants [1], and represents an important pathway through which the water and carbon cycles are connected [2, 3]. The anatomical properties of the xylem influence the process of transpiration, which transfers water to the atmosphere, and carbon fixation, which is responsible for the tree's overall long-term carbon sequestration [4].

Terrestrial plants accumulate approximately 5×10^{10} t of atmospheric carbon in biomass each year [5] and release 4×10^4 km³ of water into the atmosphere [6], thus contributing significantly to the global water cycle and heat flux dynamics [7]. Variations in tree growth due to environmental changes can have important implications for the regional and global climates [8]. On the other hand, variations in climate require plants, as sedentary organisms, to be sufficiently flexible to acclimate to and endure the surrounding environment and its variability. Wood formation is one key process that plants need to adjust its conductive system to synchronize with a changing environment.

Cambium activity post cambial growth, the division and differentiation of cells that will form a distinctive layer of wood, has been studied and known for more than a century [9]. Early studies mainly focused on description of the process of wood formation [10, 11], while later studies explored how cambial activity shaped wood anatomy [12] and, more recently, how wood formation responds to the environment [13-15].

The formation of a new tree-ring is a complex process of cell division, growth and maturation. As a result, the annual resolution of tree ring widths is insufficient to infer intra-annual growth metrics such as the timing, duration, and the rates of growth within the growing season [16]. Such metrics supply relevant information and form a solid basis for the understanding of how the wood production responds to environmental changes [4]. With the growing awareness of the ongoing impact of climate change on forest ecosystems [17-19] knowledge of the phenology and physiology of water conduit formation is crucial to understand tree reaction to stress [20-23] and how trees adjust water transport to the new conditions. In particular, a more process-based understanding of plant responses to stress and changing environmental stimuli is required in order to understand the impact of xylem plasticity on the biogeochemical interactions of the terrestrial biosphere with the atmosphere [4, 24].

Wood formation only reveals one part of the story of cambial production as cambium is a bifacial lateral meristem that produces secondary xylem in the inside and secondary phloem towards the outside [25]. Compared with xylem formation, fewer studies on phloem formation and its structure can be partly explained by its relatively low economic value compared with the use of timber [26]. In addition, older phloem is exposed to relatively fast secondary changes (e.g., collapse, sclerification and inflation of parenchyma). Therefore, only the youngest phloem increments are available for histological observations. As older non-conducting bark tissues eventually collapse in a radial direction, deform and later often fall off the tree, the older phloem conduits are not suitable yet for dendrochronological studies [27]. Although their main functions differ, xylem and phloem are closely associated both spatially and functionally [3, 28]. Due to their tight coupling, any changes in water-carbon relations [29] have impact on xylem and phloem formation processes [30-32]. Therefore, carbon gain and whole-tree survival depend on the functioning and interplay between these two vascular subsystems [33]. Wood and phloem-anatomical features thus offer a direct link for understanding physiological processes in a tree [34].

This chapter reviews the growth dynamics of the xylem and phloem and explores how resource availability and environmental variation provides important context for understanding the impacts of global change. The specific aims of this chapter are (1) to describe the general patterns of xylem and phloem growth, (2) to explain the *timing* and *growth rates* of the cambium and the resulting wood *anatomy*, and, (3) to present how wood formation can contribute to advancements in ecophysiology and dendroecology.

1-Patterns of growth in xylem and phloem over a growing season

The growth dynamics of the secondary meristems are dependent on the environment, as all metabolic and physiological processes involved in growth are limited by external factors [35, 36]. Under optimal conditions, the tree produces tracheid – also named xylem conduits– with structural characteristics that best fit the functional needs of transport, storage, defense, and mechanical support. However, to produce new cells, the cambium requires water to exert the necessary turgor pressure for cell expansion [3, 37], assimilates to build and thicken secondary cell walls, heat to allow the metabolic reactions to take place, and time enough to complete the maturation of the new conduits [24]. Cambium is a sink for carbon with low ranking priority for carbon allocation within a tree [38], and the amount and structure of the final xylem and phloem is the result of a trade-off between the available resources and structural and functional needs [39].

The ability to alter secondary vascular growth in response to external stimuli is highly adaptive but requires the coordination of the sequential developmental events during cell formation [40, 41] to produce appropriate tissues and physiological outcomes [42, 43]. Thus, as growth occurs and is modulated by the availability of resources (e.g., water and carbon) and environmental cues (e.g., temperature and photoperiod), the variability in the timing and dynamics of secondary growth the process represents a very sensitive bio-indicator of plant response to the environment. This variability is expressed in intra-annual patterns of xylem and phloem production, which also vary across vegetation types (Fig. 1).

Secondary growth patterns are sensitive to temporal variation in the environment during the growing season and differ among forests growing in different climates (Fig 1). In temperate and boreal climates with abundant soil moisture during the growing season and a dormant season in fall and winter, trees form a distinct annual ring. Growth occurs over one uninterrupted period of time, the growth rate forms a unimodal curve and cumulative growth over the growing season forms a sigmoidal curve (Pattern 1 in the top panel of Fig. 1) [44, 45]. In contrast, the growing season is longer in Mediterranean climates but summer drought limits moisture availability. When growth is uninterrupted, growth rates form a unimodal curve over a longer period but with a lower maximum rate (Pattern 1 in the bottom panel of Fig. 1) than in temperate and boreal climates. When drought limits water availability during the growing season, growth is temporarily suspended, but growth can resume following precipitation. Interrupted growth results in an intra-annual fluctuation (IADF) in wood density [46], commonly called a “false ring” (Pattern 2 in the bottom panel of Fig. 1). In this scenario, the growth rate forms a bimodal curve [21, 47, 48] and cumulative growth over the growing season forms an irregular sigmoidal curve. During severe drought, growth may be limited to a short period early in the growing season which is insufficient to form an annual ring, commonly called a “missing ring” (Pattern 3 in the bottom panel of Fig. 1). Similar to Mediterranean regions, different patterns of growth occur in subtropical and tropical climates. Unimodal wood production occurs in mesic and moderately wet forests in tropical and subtropical regions [49, 50]; however, without a dormant season distinguishing the rings formed in one calendar year from the next is difficult base on wood morphology alone. In some subtropical climates, the alternation of dry and rainy seasons or regular floods [51] can lead to multimodal growth patterns [52, 53].

All these informations are essential for dendrochronology as the formation of annual rings and their inter-annual variation are crucial for crossdating, which is the core principle of the discipline. Moreover, knowing when and how the tree-ring is formed will also help for properly understanding and inferring the causal agents of intra and inter-ring variation.

2- Xylem and phloem growth components

The physiological and environmental factors triggering and influencing the chain of cell division and differentiation define *timing* and *rates* of growth, and consequently the *anatomy* of the produced cells (xylem conduits, parenchyma cell, fibers, etc), their proportions and spatial distribution within the tree-ring. In this section, the importance of and environmental impacts on these three growth

components for *xylem* and *phloem* formation will be described. The three growth components provide a valuable indication of the way plants respond to changing environmental conditions.

Timing and duration

The **timing** of xylem and phloem development corresponds to the period when environmental factors are favourable to growth. Thus, the cambium follows alternating periods of activity and rest, according to the annual cycles of temperature, photoperiod, and water availability. The phenological phases of onset and end, bounding the period of xylem development (green and black square, Fig 1.), are defined by both environmental constraints and resource availability such as carbon, nutrients and water. The time difference between the onset and the end of growth define the **duration** of the growing season which in cold ecosystems vary annually according to the temperature during the boundary of the growing season (horizontal arrows, Fig 1, [54]). Xylem forms and differentiate when the mean air temperature range between 6 and 8 °C [55]. However, in cold and semi-arid environments of the north-eastern Tibetan Plateau, the duration of xylem development can be also affected by the dry conditions occurring in spring and summer [56]. Cambial cell division normally starts on phloem and xylem sides simultaneously. However, prior to the first cambial division, the differentiation of one to two layers of phloem cells can occurs without previous divisions [57-59]. This is the reason why the onset of phloem formation begins earlier than xylem (see onset of phloem and xylem, Fig 1, temperate to boreal areas) [60-62]. Indeed, the onset of phloem formation precede xylem formation on average by 3–5 weeks in *Picea abies* [60, 61], by 5 weeks in *Larix decidua* and by 3 weeks in *Pinus sylvestris* [61].

In ecosystems at high latitudes or altitude, where the meristems are active during a short period of time, period of xylem development reflects a balance between avoidance of frost damage and maximization of growth and carbon assimilation [63, 64]. Under the coldest conditions, xylem requires 83 days to complete the maturation of all tracheids produced by cambium, which can be considered the minimum growing season of xylem in boreal and timberline regions [54]. Coniferous stands located at the lower distribution limit of larch, Norway spruce and silver fir exhibit a period of cambial activity, i.e. cell production, up to 134 days, and a period of xylem differentiation, i.e. cell enlargement and wall thickening, reaching 178 days [54]. The duration of the growing season is a key factor in xylem cell production in some species like black spruce where the growing season is short [40, 65], although such result is not confirmed in species of other environments, where the **rate** of growth exhibited a more relevant importance [66, 67].

Accordingly, in Mediterranean climates, xylem formation occurs from winter/spring until the severe summer drought and resuming after fall precipitation [68, 69]. Such an autumnal reactivation of xylem growth, which is observed in some trees of a stand, results in the formation of false rings or latewood intra-annual density fluctuations (pattern 2, figure 1). By contrast, the lack of a distinct phenology in the phloem production in conifers in Mediterranean (unknown onset and end, Fig 1.) regions suggests that variation in the timing of phloem formation is mainly defined by species and site in such area [70, 71]. Therefore, the observed differences in the phloem phenology among different areas suggest that phloem development is at least partly affected by local environmental conditions [72].

In tropical forests such as the Brazilian Cerrado, xylem formation lasts from October to June, when temperature is higher and precipitation events are frequent [50]. In some ecosystems, precipitation and soil water content can play an important role in defining the timings of xylem formation during spring [56, 73]. Tropical environments can show species with anomalous xylem growth. *Avicennia marina* is a mangrove species characterized by multiple-cambial layers, acclimatic growth rhythms of xylem growth, and a potentially continuous cambial activity throughout the year [53].

Rates of growth

Recent work on the **rates** of xylem cell differentiation (or rate of growth) have provided novel quantification and mechanistic models of wood formation kinetics that explain tree ring formation [24]. Xylem cell differentiation kinetics can be characterized by the duration the cells spend in the

different phases (i.e. cell enlargement and cell wall thickening) and the rate at which the different sub-processes (primary wall expansion, secondary cell wall deposition) occur [20, 74]. The duration and rate of the phase of cell enlargement determine its size, while the duration and rate of the thickening phase determine the quantity of deposited wall material (e.g., cell wall area). The relative proportion of cell wall to cell exterior dimensions are the basis for commonly used measures of tree-ring structure (e.g., cell wall thickness, tree-ring micro-density profile). At the beginning of the growing period, good growth conditions generally lead to high rates of enlargement and thickening. These rates then decrease towards the end of the season. This general pattern of variation in duration and rate of xylogenesis sub-processes is at the origin the universal tree-ring structure of light earlywood composed of wide cells followed by denser latewood composed of narrower cells [75]. Importantly, Cuny et al. [4] refute the long-standing assumption that the increase in wall thickness and wood density along the ring is driven by the fixation of more biomass during the wall-thickening process. Instead, they demonstrate that the amount of wall material per cell is almost constant along a ring except for the last few cells of the ring.

Consequently, changes in wall thickness and wood density are principally driven by changes in cell size. The reduction of the cell size along the ring is mainly due to decreasing duration of cell enlargement, whereas decreasing rate of cell enlargement only contributes marginally. Recent works [20, 76] show a very interesting mechanism of coupling between the rates and duration of cell wall deposition: as the season progresses and the rate of cell wall deposition is declining, the duration increase in such proportion that it perfectly counter balance the decrease of the rate, stabilising the production of the amount of cell wall material per cell. However, at the very end of the growing season when temperature drops [76], or when water conditions deteriorates too much [20], durations increase level off, breaking the coupling between rate and duration, and climatic conditions are directly written into tree-ring structure.

The highest *rate* of phloem cell production of *P. abies* was detected 2–6 weeks earlier than that of xylem [72] because the formation of the annual phloem increment is crucial for tree survival. The translocation pathways for photosynthates and biomolecules must be maintained because sieve cells function for only one to two growing seasons [3, 28]. While missing or discontinuous rings in xylem have been regularly reported, particularly in trees from extreme environments [77, 78], or in trees with reduced vitality [79], phloem rings are formed every year, even if very narrow [80]. The narrower phloem rings are caused by an asynchrony between the production of xylem and phloem derivative: cambium divides more frequently on the xylem side than on the phloem side and, consequently, xylem accumulates at a faster rate than phloem (e.g., Panshin and de Zeeuw [81], Jyske and Hölttä [31]). However, in the case of reduced radial growth, a tree's preference is for phloem formation, leading to a progressively smaller ratio between xylem and phloem widths [80, 82]. The pattern of phloem formation has a S-shaped growth pattern (pattern 1 in black, figure 1) in coniferous and deciduous tree species in temperate to boreal regions resulting in the typical bell shaped rates of growth (in blue, figure 1).

Anatomy

The environmental influence on the process of wood formation results in xylem *anatomy* changes that can also have functional implications [2]. The xylem structure determine the functional balance between efficient water transport to achieve optimal growth, minimum investment of construction costs to secure the xylem plumbing system, mechanical support for the assimilating leaves, and storage of water and nonstructural carbohydrates for defense and resistance to stress [42]. So for example, the capacity to transport water, which is an important functional trait connected with water use and net primary productivity, can be modulated by modifying the arrangement and structure of the wooden cells (**Figure 2**). Unmistakable examples of altered structure and functions are frost rings [83], light rings [84], blue rings [85] or even the intra-annual density fluctuations [86]. However, any environmental factors that alter the normal course of formation of the wooden cells can leave a characteristic signature within the anatomical characteristic of the annual ring (**Figure 2**). Indeed, each wooden cell first needs to enlarge before thickening the wall [87]. Thus, both the cell size and

the wall thickness of each cell in the ring can provide important information related to the environmental drivers influencing both these processes [88]. Several studies based on tree-ring anatomical methods [89] have already demonstrated the possibility to use time-series of cell anatomical features for a deeper insight on the factors affecting xylogenesis [90-93] and how these changes might affect future xylem functioning [94, 95].

Variations in the phloem conduits anatomy exhibit much less plasticity than that of xylem. Variations in the anatomy of phloem rings in temperate tree species are mainly observed at the site level rather than on a temporal scale [72, 96]. Intra- and inter-species structural variation in secondary tissues exists because of local adaptations and environmental conditions [97]. Jyske and Hölttä [31] found that phloem conduits are slightly narrower than xylem conduits in *P. abies*. Gricar *et al.* [30] further confirmed this trend but only for the early part of the annual rings, whereas in the increments formed in the second part of the growing season, it is just the opposite. Thus, tracheids in earlywood are on average 12–30 % wider and in latewood 30–50 % narrower than sieve cells in early and late phloem, respectively. The variation in the structure of annual xylem and phloem increments in *P. abies* clearly demonstrates that plasticity in the seasonal dynamics of cambial cell production and cell differentiation exists on both xylem and phloem sides. At the tissue and cell levels, wood anatomical traits have largely been studied in this respect (e.g. Fonti *et al.* [89] and previous section on xylem anatomy), whereas the proxy potential of phloem-anatomical traits still needs to be exploited [30, 31]. Intra-annual xylem and phloem formation analyses are therefore crucial for a better understanding of the mechanisms underlying the environmental response of xylem and phloem anatomy of different tree species.

3-Contributions to dendroecology

Monitoring xylogenesis is contributing important mechanistic insights to disciplines that have strong ties with plant performance and survival, paleo-environmental reconstruction, and biogeochemical feed-back. In this chapter, the contribution of the studies on xylogenesis to the questions on global change and other ecophysiological fields are explained and discussed.

Plant performances, distribution and community composition

The ecological amplitude, and consequently the distribution of the individuals, are partly regulated by the plasticity of the species in response to spatio-temporal variability of the environmental conditions [98]. For example, the hydraulic structure of the xylem network and its plasticity is determinant, not only for the water balance of plants, but also for attaining maximal photosynthetic rates and optimal adaptations to specific microclimates. A limited capacity for phenotypic adjustment to changing conditions might have detrimental consequences for plant carbon budget, tree productivity and mortality [99]. Repeated and lengthy droughts, for example, can affect the delicate safety-efficiency trade-off in the water conduction system and trigger detrimental consequences in plant carbon allocation, which finally induces the death of the plant [19, 100, 101].

The effect of climatic factors on xylem anatomy has been extensively described [102], but particular focus has been placed to xylem anatomical responses in relation to water stress and/or plant mortality [103-110]. Many morphological characteristics of the xylem hydraulic architecture, such as the arrangement, frequency, size, wall thickness, pit characteristics of conduits and tissue proportion such as ray parenchyma, can be modified to regulate both the efficiency of water transport and the margins of safety against hydraulic system failures [111-114]. An example of such adjustments is shown in **Figure 2**. Nevertheless, the strategies of adjustment are diversified and depend on species and conditions. The observations of wood formation can thus be used to identify the drivers (which factor), timings (when) and environmental threshold (what intensity) behind the formation of specific anatomical characteristics, as it has been performed for the intra-annual density fluctuation observed in the dry Mediterranean regions [48, 115]. In this case, xylogenesis represents an indispensable basis of understanding the link environment-structure necessary for evaluating the range of plasticity and resilience of trees growing under defined environmental conditions and for predicting plant performances, distribution and community composition under future climates [116-118]

283 *Paleo-environmental reconstructions by mean of tree-ring proxy*

284 Dendrochronology usually date the formation of tree rings to the exact calendar years to extract
285 relevant paleo-environmental information integrating the whole growing season [119, 120] by means
286 of transfer functions. Similarly, the cell characteristics fixed in the datable tree rings represent an
287 archive of past conditions but at a much higher time resolution [89]. Thus, the assignment of a time
288 of formation of each cell in the ring will not only allow to increase the resolution of the paleo-
289 environmental proxies, but also put the basis for a better process-based understanding of the growth-
290 climate interactions. The increased resolution will allow to better relate intra-ring features, as the
291 appreciated environmental-sensitive maximum latewood density or other more novel data-types such
292 as stable isotopes ratios (usually C, H and O) and cell anatomical features, to the physiological state
293 of the plant at the time of cell formation. Assigning a time of formation to intra-annual wood
294 anatomical or isotopic measurements performed in cells within tree rings will specifically allow
295 causes and effects to be better linked and understood [48, 88, 91, 107, 121-123]. Questions related to
296 the mobilisation and storage of carbon assimilates in relation to the properties of secondary growth
297 might be finally better understood [22, 36, 124, 125] thus significantly improving the interpretation
298 of the paleo-environmental reconstructions.

299 *Quantifying biogeochemical cycles*

300 Quantifying the intensity of carbon and water exchanges between terrestrial ecosystems and
301 surrounding environments (atmosphere, hydrosphere, pedosphere-lithosphere) is a central challenge
302 for understanding the biogeochemical cycle and a prerequisite for reliable future scenarios of climate
303 change. In this complex climate system, the growth activity of plants plays a determinant role. The
304 timings of wood formation define the period when carbon fixation into wood is activated and for how
305 long. So, growth onset and cessation, which are usually controlled by temperature and photoperiod
306 [126], defines the period when growth can occur, while the environmental conditions determine the
307 speed of the process. These conditions do not only define the properties of the ring (e.g. the thickness
308 and the density of the wood) but also determine the future performance of the functional xylem via
309 the anatomical structure. These properties are important in determining how much carbon is
310 sequestered by plants in new and future growth, how much nitrogen and other nutrients are absorbed
311 from the soil and how much water is returned to the atmosphere via transpiration. Current models
312 estimating growth periods and intensity are usually calibrated using phenological observations from
313 satellite remote-sensing (e.g. Pettorelli *et la.* [127]), or from field observations (e.g. Menzel *et al.*
314 [128]). This monitoring is based on activity of the primary meristems and often assumes a direct link
315 between primary and secondary meristems functioning [45, 129]. To increase reliability and
316 resolution of the prediction of the impact of climate change on water and carbon cycles, more
317 observational description on how cambial activity affects the physiology of the plant on a short and
318 long-term perspective are necessary to improve the new generation of process-based models relying
319 on a description of the cambial activity to simulate radial growth and related physiological processes
320 at an intra-annual scales [24].

321 Monitoring xylogenesis shows that environmental factors substantially modulate the duration and
322 rate of growth processes of xylem and phloem cells. Several studies have revealed a high plasticity of
323 wood formation to various environmental conditions in many different environments [47, 130-136],
324 but also between species [44, 94, 137, 138], age and size classes [139-141] and social status [67].
325 Among the environmental factors studied, temperature seems to be the factor driving the onset of the
326 growing season in temperate and boreal environments. An inter-annual variation of up to one month
327 has been observed in the timing of wood formation across conifer species in Europe and Canada [16,
328 55, 136, 142] an altitudinal and latitudinal gradient [4, 54, 134, 143]. Stem heating during the
329 quiescent stage also demonstrated that cambium reactivation in temperate or boreal environments is
330 extremely sensitive to temperature and xylem differentiation was induced after two weeks of
331 continuous exposure independently of bud activity [144]. In the boreal forest, a model predicts longer
332 duration of xylogenesis at higher temperatures, with an increase of 8-11 days/°C, because of an
333 earlier onset and later ending of growth [145]. Insufficient water availability, like in a Mediterranean

climate, has also been related with the duration of the growing season. Effects of water deficit include earlier culminations of the maximum growth rate, shorter periods of growth and reductions in the number of tracheids produced [21, 105, 142, 146]. Shifts from the S-shaped pattern (pattern 1, figure 1) to bimodal radial growth (pattern 2, figure 1) can even be observed in non-Mediterranean species, depending on the timings of the drought events during the growing season and on plant strategy [23, 68].

There is now a consensus that the determination of the intra-annual growth pattern under different changing conditions yields important insights into the possible ecological response of trees by modulating how the trees can perform under current and future environment. Accounting for this more detailed information of the growth patterns and their variability is fundamental to significantly improve the process-based model of growth, with implications for up-scaled modelling of global flux changes within climate change scenarios.

Concluding remarks

Plant growth is inextricably linked to the environment. On the shortest and smallest scales, the environmental conditions directly influence physiological processes. On longer periods and wider spatial scales, environmental changes influence species performance, distribution and community composition, which eventually influence the regional and global climate. Understanding how the growth of plants responds to these changes is a critical requirement for simulating ecosystem dynamics under future climate. The study of xylem and phloem growth, through a highly resolved and detailed description of how the environment affects the *timing*, *rates* and the *anatomy* of the cell conduits, is providing important contributions to the major scientific challenges related to plant performance under climate change.

In the last decade, investigations on intra-annual dynamics of growth have gained in popularity and are supplying a greater and deeper understanding of the secondary growth processes with beneficial implications in many disciplines. Expanding the studies to more environments and species will provide a more complete basis for an up-scaled and up-dated process-oriented understanding of how cambium activity and secondary growth responds to and influences global and local environmental changes.

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696 **Figure 1. Plasticity of growth patterns in two contrasting biomes.** Xylem and phloem growth over
 697 one growing season resulting from cambium activity in boreal or temperate (top) and Mediterranean
 698 (bottom) forests. In each case, the period(s) of growth is defined by the *onset* (green squares) and
 699 *cessation* (black squares) while the arrow represents the time variability in the *onset* and *cessation*.
 700 For both xylem and phloem, the progress of *growth over time* (black lines), quantified either as the
 701 number of cells or amount of produced ring width along a year. A general *rate of growth* (blue lines),

702 which indicates how fast the process occurs in terms of the measured quantity per time unit, can be
703 represent as the first derivative of the progress of growth (black lines). Only one pattern of xylem and
704 phloem growth over time was represented for temperate-boreal areas illustrated as the S-shaped
705 (pattern 1) growth pattern (black line). The general *rate of growth* of this pattern is typically bell
706 shaped (blue line, in pattern 1). For Mediterranean areas, three patterns of growth over time were
707 represented: (pattern 1) S-shaped growth, such as for temperate-boreal conifers with its bell-shaped
708 rate of growth (solid black and blue lines); (pattern 2) Intra-annual density fluctuation (IADF, dotted
709 black line) with its bi-modal rate of growth (dotted blue line); (pattern 3) missing rings or dark rings
710 (illustrated as the *rate of growth* only, dotted blue line) where there is a local formation of few xylem
711 cells (less than five cells), which are slowly differentiating and can look like latewood cells. Phloem
712 growth rate (in red) is hypothetical and has been shown to be bi-modal (in orange) like the xylem.

713

a) Forming ring: at time zero when the new environmental constraint is occurring. The part of the forming annual ring to the left of the vertical arrow, is already terminated and thus its anatomical structure permanently fixed. The part on the right is “in construction” with cells under differentiation. The transition from light blue to red indicates the transition from cell with only primary cell wall (cellulose) to cells with different level of secondary wall formation and lignifications (red)

b) Efficiency and safety: The capacity to conduct sap is proportional to the fourth power of the radius of the vessel. However the risk of cavitation is proportional to the vessel size. By adjusting the size and density of vessels, the tree can so regulate the trade-off between safety and efficiency

c) Redundancy: A densely inter-connected network of pipes can reduce the negative effect of a local failure (cavitation, in grey) on the whole system. The more vessels are connected with each other (increasing vessel clustering), the more alternate paths for sap flow are available, and thus the risk of system failure is reduced.

d) Reparability: Embolism dysfunction is not always permanent. Parenchyma cells (wood rays and vasicentric cells) containing starch seems to be actively involved in the mechanisms of embolism repair. Increasing number of these cells guarantee higher capacity for repair.

Figure 2. Plasticity of the final product: The figure shows an example of how the structure of the xylem hydraulic architecture of a forming *Populus x canadensis* annual ring from temperate environments can be plastically adjusted to respond to a new environmental constraint, e.g., a long drought period. The example is based on micro-sections observations as they might appear when performed under a light microscope (magnification 100×, staining performed with safranin and astrablue). To guarantee the fulfilment of future needs (e.g., safe and efficient water transport and mechanical stability) trees have to adjust their growth by optimizing the available resources (e.g., carbon, warmth, water, and the time to perform the process). Figure (a) shows the situation of the

723 forming ring at the time the event is occurring. Figures (b) to (d) show examples that simulate possible
724 adjustments in vessel size and arrangement as they appear visible along a ring cross-section. Efficient
725 sap flow occurs when large and numerous vessels contribute to the transport, although large vessels
726 are susceptible to cavitation (in grey) under strong negative pressure. Drought and freezing can both
727 cause embolisms in plants, even leading to complete system failure if extended embolisms occur.
728 Strategies of modifications can be oriented towards increasing safety (at the cost of efficiency) (b),
729 redundancy (c) or reparability (d) of the system. Other anatomical characteristics which are not shown
730 in the figure, as for example the length of the vessels, the number, sizes and structure of pits of
731 connecting vessels, and the division of whole plants into independent hydraulic units, can also
732 influence these attributes. For simplicity, the responses described in the figure are shown to be rapid
733 and to have immediate effect on the anatomy of the new forming ring. However, depending on
734 frequency and magnitude of the events, induced modifications of the wood structure can last over the
735 formation of more annual rings.

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