

Reading Climate in Wood: A Systematic Review of Dendro-Anatomical Proxies for Climate Reconstruction, Forest Health, and Sustainable Forest Management

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Systematic Review

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Reading Climate in Wood: A Systematic Review of Dendro-Anatomical Proxies for Climate Reconstruction, Forest Health, and Sustainable Forest Management

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Abstract. Dendrochronology is increasingly moving from measurements of ring width and density toward cellular-scale records of xylem formation. Wood anatomical elements—including tracheid dimensions, cell-wall characteristics, rays, resin canals, earlywood-latewood structure, and density profiles—can retain environmental information at annual and intra-annual scales. This systematic review synthesizes evidence on how dendro-anatomical proxies contribute to climate reconstruction, forest-health assessment, disturbance history, and sustainable forest management. Following the review protocol described in the supplied manuscript, literature published primarily between 1950 and 2026 was searched across Scopus, Web of Science, ScienceDirect, SpringerLink, Wiley Online Library, CAB Abstracts, JSTOR, and Google Scholar, supplemented by authoritative forestry sources and citation tracking. The selection process identified 3,274 records, removed 728 duplicates, screened 2,546 records, assessed 812 full texts, and retained 287 publications. The synthesis shows that ring width provides a broad annual growth signal, whereas anatomical traits can add information on water availability, temperature, hydraulic adjustment, defence investment, and disturbance timing. Quantitative wood anatomy (QWA) is particularly valuable because it links dated rings to cellular traits such as lumen area and cell-wall thickness, while densitometry and maximum latewood density provide established high-resolution temperature information in appropriate settings. Resin canals can preserve records of defence investment and disturbance but require careful attribution because multiple stressors can produce similar anatomical responses. The review identifies a central research opportunity: integrating anatomical, density, isotopic, remote-sensing, and computational evidence into standardized multi-proxy chronologies, with greater representation of tropical and African forests.

Keywords: dendrochronology; dendro-anatomy; quantitative wood anatomy; tree rings; tracheids; wood density; maximum latewood density; resin canals; climate reconstruction; forest health; sustainable forest management

Key Points

- Wood anatomical traits add cellular and intra-annual information that can complement conventional ring-width chronologies.
- Tracheid dimensions, cell-wall characteristics, density profiles, and resin canals encode different environmental and disturbance signals; no single proxy is universally dominant.
- Quantitative wood anatomy provides a reproducible pathway from dated rings to cellular measurements and climate-response analysis.
- Maximum latewood density remains a major temperature proxy, but its interpretation depends on species, site, calibration period, and measurement method.
- Resin canals can preserve defence and disturbance histories, although attribution requires independent ecological or climatic evidence.
- Future progress depends on standardized methods, open anatomical databases, multi-proxy integration, and stronger tropical and African chronologies.

Plain Language Summary

Trees record environmental conditions in the wood they produce. Traditional dendrochronology often measures how wide a growth ring is, but a ring also contains thousands of cells whose size, wall thickness, density, and arrangement can vary with water availability, temperature, disturbance, and tree physiology. This review brings these anatomical signals together and asks what they can add to conventional tree-ring studies. The evidence indicates that cellular measurements can improve the temporal detail of environmental reconstructions and can reveal stress or disturbance that is difficult to isolate from ring width alone. The review also highlights an important limitation: the evidence base is concentrated in Europe and North America, while tropical and African forests remain comparatively underrepresented. A next generation of dendrochronology should therefore combine wood anatomy with density measurements, stable isotopes, remote sensing, and automated image analysis to produce decision-ready records for climate science and forest management.

1. Introduction

1.1 Why wood anatomy matters in dendrochronology

Dendrochronology provides dated biological records of environmental variability and has applications in climatology, ecology, hydrology, disturbance ecology, archaeology, and forestry. Traditional chronologies commonly rely on ring width and density, but these measures integrate several physiological processes. Wood anatomy offers a complementary scale of observation because xylem cells are formed sequentially during the growing season and their dimensions and wall properties reflect the conditions experienced during formation (Fonti et al., 2010; von Arx et al., 2016).

The central premise of dendro-anatomy is therefore not that anatomy replaces ring width, but that it resolves components of the growth process that are otherwise aggregated. Cell lumen dimensions can provide information related to water availability and hydraulic adjustment, wall thickness can reflect carbon allocation and thermal conditions, density profiles can capture changes in cell-wall investment, and resin canals can archive defence responses. The environmental meaning of each trait is nevertheless context dependent and should be established through calibration and multi-proxy comparison.

1.2 Review gap and contribution

Existing literature has demonstrated the value of quantitative wood anatomy and dendro-anatomical approaches, while densitometry has a long history in high-resolution climate reconstruction (Fonti et al., 2010; Björklund et al., 2019). The supplied review identifies a broader gap: evidence is distributed across wood science, dendrochronology, plant physiology, climatology, disturbance ecology, and forest management. This review consequently organizes the evidence around a common pathway—environmental forcing → tree physiology → cambial activity → anatomical formation → dated proxy → environmental interpretation → management application.

This systems perspective is particularly relevant as climate change increases the need for records that resolve not only whether growth changed, but also how trees adjusted hydraulically, structurally, and defensively. Recent work using tracheid anatomy has shown that anatomical chronologies can refine long-term climate reconstructions, while methodological advances are making larger QWA datasets increasingly feasible (Björklund et al., 2023; Frigo et al., 2024).

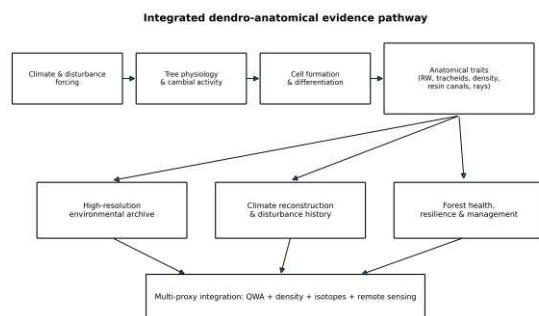


Figure 2. Integrated dendro-anatomical evidence pathway. Environmental forcing is translated through tree physiology and cell formation into measurable anatomical archives, which can

then support climate reconstruction, forest-health assessment, and management.

2. Methodology

2.1 Review design and search strategy

The study used a systematic literature review design following the PRISMA 2020 reporting framework (Page et al., 2021). The search was conducted between January and June 2026. Databases specified in the source manuscript were Scopus, Web of Science, ScienceDirect, SpringerLink, Wiley Online Library, CAB Abstracts, JSTOR, and Google Scholar. Additional material was identified from FAO and USDA Forest Service publications, the International Tree-Ring Data Bank, conference proceedings, university repositories, dissertations, and reference-list screening.

The principal search logic combined terms for dendrochronology or tree-ring analysis with wood anatomy or wood anatomical elements, climate or environmental reconstruction, and forest health or forest management. Additional terms covered quantitative wood anatomy, dendro-anatomy, tracheids, resin canals, density, earlywood, latewood, climate change, forest resilience, stable isotopes, tree physiology, and forest disturbances.

2.2 Eligibility and study selection

Studies were eligible when they addressed dendrochronology or dendro-anatomy and investigated anatomical elements as environmental or ecological proxies, climate–growth relationships, forest health, disturbance, or tree responses to environmental variability. The source manuscript included peer-reviewed articles, books, technical reports, dissertations, and conference proceedings published in English, provided sufficient methodological information. Studies without relevant dendrochronological or anatomical information, duplicates, inaccessible full texts, and studies outside the review objectives were excluded.

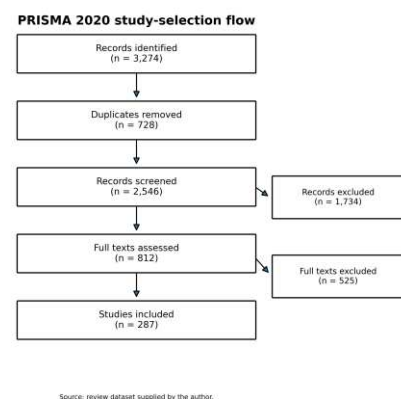


Figure 1. PRISMA-style study-selection flow reconstructed from the screening counts reported in the supplied manuscript. The arithmetic is internally consistent: 3,274 identified – 728 duplicates = 2,546 screened; 2,546 – 1,734 excluded = 812 full texts; 812 – 525 excluded = 287 included.

2.3 Data extraction, quality appraisal and synthesis

The extraction framework captured author, year, region, species, anatomical element, climatic variable, methodology, key findings, applications, and research gaps. The source manuscript classified studies as high, moderate, or low quality using criteria covering scientific rigor, methodological

transparency, sample size, statistical robustness, relevance, and data quality; only high- and moderate-quality studies were retained.

Because the included studies differed substantially in species, climates, anatomical traits, measurement protocols, chronology construction, and statistical approaches, formal meta-analysis was not attempted. Instead, the evidence was synthesized thematically. The synthesis was organized around growth rings, tracheid anatomy, density and MXD, resin canals, QWA, forest health, sustainable management, and emerging technologies. This approach follows the source manuscript while making the distinction between proxy capability and context-specific performance explicit.

2.4 Review limitations

The source review notes that dendro-anatomical research is concentrated in Europe and North America, leaving tropical regions comparatively underrepresented. Methodological heterogeneity also limits direct comparison among studies, while differences in imaging and anatomical resolution can affect trait estimates. These limitations mean that apparent proxy strength should not be interpreted as universally transferable across species or environments.

3. Results and Discussion

3.1 From ring width to cellular archives

The reviewed evidence supports a progression from conventional ring-width chronologies toward multi-dimensional tree-ring archives. Ring width remains a powerful annual indicator of integrated growth conditions, but it combines the effects of climate, competition, site conditions, disturbance, and tree physiology. Dendro-anatomical variables can separate some of these processes by recording cell-level attributes formed within the ring. This distinction is important for questions that require seasonal or physiological interpretation rather than annual growth alone (Fonti et al., 2010).

Table 1. Major dendro-anatomical proxies and their principal interpretive constraints.

Proxy	Primary information	Main caveat
Ring width	Integrated annual growth	Sensitive to multiple non-climatic controls
Tracheid lumen / conduit size	Water availability; hydraulic adjustment	Species- and site-specific response
Cell-wall thickness	Wall deposition; thermal and carbon signals	Method and developmental timing matter
Density / MXD	Warm-season temperature in suitable settings	Strong calibration and measurement dependence
Resin canals	Defence investment and disturbance	Different stressors can produce similar responses
Rays	Growth and storage/allocation processes	Less standardized than major tracheid/density proxies

Proxy	Primary environmental information
Ring width	Annual growth
Tracheid lumen	Water availability
Cell-wall thickness	Temperature / carbon allocation
Wood density / MXD	Warm-season temperature
Resin canals	Disturbance / defence
Rays	Growth & allocation

The signal is species-, site-, season- and method-dependent; proxies should therefore be interpreted jointly.

Figure 3. Proxy-signal matrix. The environmental interpretation of an anatomical trait is conditional rather than universal and should be calibrated against instrumental climate, ecological observations, or independent disturbance evidence.

3.2 Growth rings: the temporal backbone

Growth rings remain the chronological backbone of dendrochronology because they provide a dated sequence against which anatomical measurements can be aligned. Earlywood and latewood differ in cell dimensions and wall investment, and ring boundaries permit cross-dating among trees. The source review emphasizes that false rings, missing rings, frost damage, fire scars, abrupt growth suppression, and release events can preserve information on short-term stress and disturbance.

Cross-dating is essential when anatomical traits are used as proxies. A cellular signal is only climatically meaningful when it is assigned to the correct year and, where possible, the correct intra-annual position. This is particularly important in tropical and subtropical environments where ring boundaries may be less visually distinct and annual periodicity may require additional evidence.

Table 2. Information preserved by growth-ring structure.

Ring feature	Potential information
Ring width	Integrated annual growth response
Earlywood structure	Early-season moisture and temperature conditions
Latewood structure	Late-season climate and growth termination
False rings	Short-term environmental interruption
Missing rings	Severe growth limitation
Frost-related anatomy	Freezing injury during active growth
Fire scars / growth release	Disturbance timing and subsequent recovery

3.3 Tracheid anatomy: cellular evidence of climate and drought

Tracheid-based proxies are among the most developed applications of dendro-anatomy in conifers. Measurements include radial and tangential dimensions, lumen area, cell-wall thickness, hydraulic diameter, and related wall-to-lumen metrics. QWA practical guidelines emphasize standardized sample preparation, imaging, measurement, and quality control because methodological choices can affect the resulting chronologies (von Arx et al., 2016).

The literature synthesized in the source manuscript consistently links smaller lumen dimensions and altered wall-lumen relationships with water limitation in many contexts, while cell-wall characteristics can contain temperature-related information. However, these relationships are not universal. A

review of climatic influences on wood anatomy documents contrasting species responses to drought and emphasizes that anatomical signals are shaped by species traits, phenology, and site conditions. □cite□turn0search3□

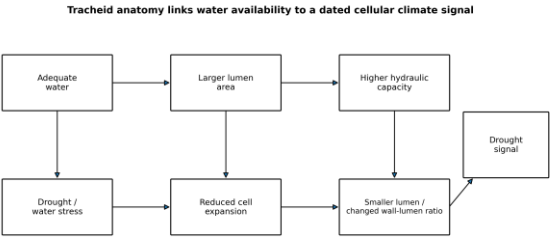


Figure 5. Schematic tracheid drought pathway. Water limitation can reduce cell expansion and alter lumen dimensions, producing a dated anatomical signal. The direction and magnitude of the response remain species- and site-dependent.

A major advance is the ability to resolve intra-annual climate information. Rather than treating the annual ring as a single observation, QWA preserves the sequence of cells across earlywood and latewood. This can reveal shifts in water availability, temperature, or physiological constraints within the growing season (Fonti et al., 2010; von Arx et al., 2016). Recent methodological work comparing embedded and non-embedded sample preparation further demonstrates that standardization can support larger datasets while reducing resource demands (Frigo et al., 2024).

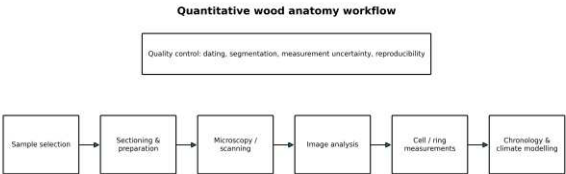


Figure 4. Quantitative wood anatomy workflow. Reproducible dendro-anatomical datasets require careful sampling, section preparation, imaging, automated or semi-automated measurement, chronology alignment, and statistical validation.

3.4 Wood density and maximum latewood density

Wood density integrates cell-wall deposition, lumen dimensions, tissue proportions, and xylem development. Among density variables, maximum latewood density (MXD) has a long-established role in dendroclimatology, particularly for warm-season temperature reconstruction in suitable conifer species and environments. The major methodological review by Björklund et al. (2019) highlights both the scientific value of densitometry and the analytical challenges associated with measurement and standardization.

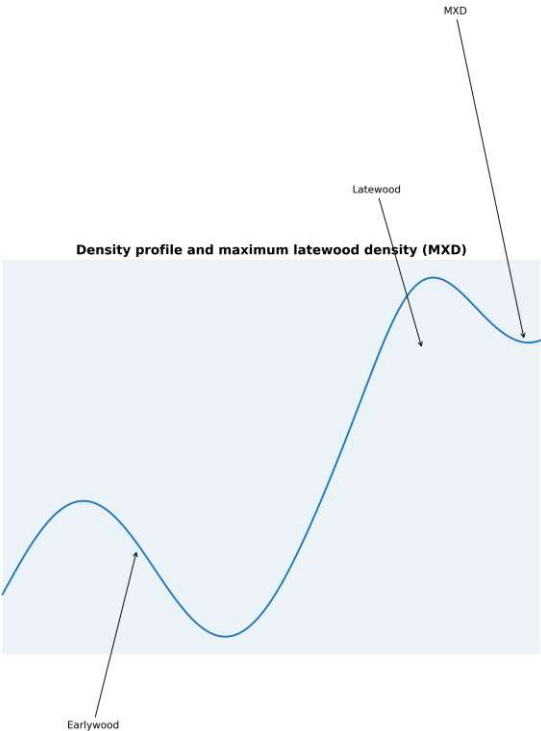


Figure 6. Schematic density profile across a growth ring. Maximum latewood density is the highest density value within the latewood portion and can carry a strong warm-season temperature signal in appropriate settings.

Recent evidence illustrates both the power and the context dependence of MXD. Björklund et al. (2023) reconstructed warm-season temperature using annually resolved tracheid anatomical measurements over 1,170 years in Scots pine, demonstrating how cellular measurements can address uncertainties in historical climate reconstructions. De Mil et al. (2024) further showed that X-ray computed tomography can extend MXD-based reconstruction to challenging bristlecone pine material. These studies support the broader conclusion that high-resolution anatomical and density measurements can expand the temporal reach of dendroclimatic archives, but they do not justify treating MXD as a universal temperature proxy.

Table 3. Density measures and interpretation.

Density-related measure	Typical use in the review	Interpretive caution
Mean/ring density	Integrated wood-formation response	Affected by anatomy and measurement method
Earlywood density	Moisture or early-season conditions in some settings	Site and species dependence
Latewood density	Late-season climatic and physiological signal	Developmental timing matters
MXD	Warm-season temperature in many high-latitude settings	Requires calibration and standardized measurement

3.5 Resin canals: disturbance and defence archives

Resin canals provide a different type of dendro-anatomical information because they can reflect defence investment as well as environmental stress. Normal resin canals are part of the anatomical architecture of many conifers, whereas traumatic resin canals can form following disturbance. A review by Vázquez-González et al. (2020) describes annual resin-duct characteristics as a potential archive of defensive

investment and emphasizes the need to account for genetic and environmental sources of variation.

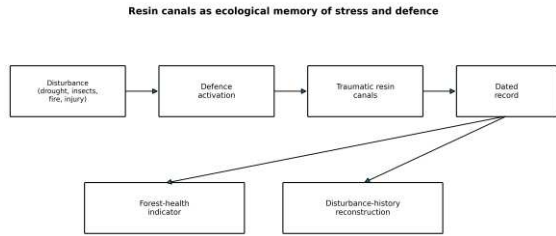


Figure 7. Resin canals as ecological memory. Disturbance can activate defence responses and leave traumatic resin canals that are subsequently dated within the annual-ring sequence. Independent evidence is needed to attribute the cause of a canal response.

The review evidence supports applications in insect-outbreak analysis, fire and mechanical disturbance studies, and forest-health assessment. At the same time, resin canals are not diagnostic of a single stressor. Drought, insects, pathogens, fire, and mechanical injury can all affect defence investment. Therefore, resin-canals chronologies should be interpreted alongside climate records, field observations, ring-width changes, and other anatomical or isotopic indicators.

Table 4. Resin-canal indicators and attribution requirements.

Resin-canal signal	Possible interpretation	Required corroboration
Increased canal frequency	Elevated defence investment	Climate or biotic disturbance evidence
Traumatic canal rows	Discrete disturbance episode	Event chronology / field context
Persistent elevated production	Repeated or prolonged stress	Multi-year environmental record
Canal size/area changes	Variation in defence response	Species-specific calibration

3.6 Quantitative wood anatomy as the integration platform

QWA is best understood as an analytical platform rather than a single proxy. It enables large numbers of cells to be measured and positioned within dated growth rings, allowing anatomical traits to be converted into time series. The method therefore connects microscopy and wood formation biology with dendrochronological chronology building and statistical climate analysis (von Arx et al., 2016).

Methodological standardization is an emerging priority. Frigo et al. (2024) compared embedding and non-embedding approaches and found broadly similar measurements for several commonly used xylem traits, while noting methodological differences for some parameters. The implication for systematic synthesis is important: future networks will benefit from explicit protocols, uncertainty reporting, shared metadata, and open data structures that allow measurements from different laboratories to be compared.

Automation is another major development. Image segmentation, cell detection, feature extraction, and machine-learning classification can reduce manual measurement burdens. The source review identifies AI, machine learning, high-resolution imaging, and automated anatomical analysis as major future directions. These technologies should, however, be treated as measurement tools that require

validation rather than as substitutes for biological interpretation.

3.7 Forest health and disturbance assessment

Dendro-anatomical proxies can contribute to forest-health assessment by detecting changes in growth, hydraulic structure, density, and defence. Growth suppression may indicate drought, competition, defoliation, or other stress, while growth release can indicate recovery after disturbance. Anatomical traits can add physiological context to these annual patterns. Insect outbreaks illustrate why this matters: non-climatic disturbances can distort climate reconstructions if their signatures are interpreted solely as climate responses. Recent work on larch budmoth effects demonstrates that accounting for insect outbreaks can materially change the inferred climate signal from ring-width chronologies.

For forest management, the most useful interpretation is therefore diagnostic rather than purely descriptive: a combination of proxies can identify whether a tree or stand is responding primarily to water stress, temperature, disturbance, or a combination of pressures. Such information can support resilience monitoring, restoration prioritization, and climate adaptation.

3.8 Sustainable forest management applications

The source review identifies several management applications for wood anatomical information: growth assessment, site evaluation, species selection, timber-quality interpretation, carbon assessment, climate adaptation, restoration, fire management, and pest monitoring. These applications are strongest when dendro-anatomical records are integrated with stand-level observations and spatial data rather than used in isolation.

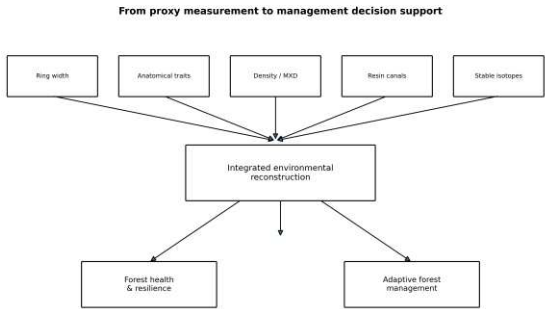


Figure 8. Multi-proxy pathway from anatomical measurements to management decisions. Integration of conventional tree-ring variables, QWA, density, resin-canal information, and stable isotopes can strengthen environmental interpretation and decision support.

Table 5. Applications of dendro-anatomical evidence in forest management.

Management application	Relevant evidence	Potential decision use
Climate adaptation	Growth + tracheid/density response	Species/site selection and vulnerability assessment
Forest health	Suppression, anatomy, resin canals	Early warning and stress diagnosis
Disturbance history	Fire scars, resin canals, growth releases	Risk and disturbance planning
Carbon assessment	Density + growth + biomass context	Long-term carbon monitoring

Timber quality	Density and anatomical traits	Material characterization and utilization
Restoration	Growth response and site history	Targeting resilient species and sites

3.9 Tropical and African research gap

The source review identifies tropical and African forestry as a major evidence gap. This is scientifically important because tropical wood formation can differ markedly from the strongly seasonal systems in which much dendrochronological methodology was developed. A recent synthesis of tropical and subtropical American dendrochronology likewise emphasizes challenges in identifying annual boundaries and the value of complementary dating and visualization approaches. [cite turn0search7](#)

For African forestry, an especially useful research agenda would combine local species chronologies with anatomical descriptions, meteorological observations, drought indices, stable isotopes, remote sensing, and forest-inventory data. Such networks could help address questions that are highly relevant to Zambia and neighbouring countries: how drought alters wood formation, which anatomical traits provide stable climate signals, how plantation species respond to climate extremes, and whether anatomical indicators can support early-warning systems for forest decline.

3.10 Emerging technologies and future directions

The field is moving toward digital dendrochronology in which anatomical measurements, climate data, remote sensing, genomics, and computational models are connected. AI-assisted image analysis can accelerate cell identification; remote sensing can extend tree-level observations to landscapes; stable isotopes can provide complementary information on water and carbon processes; and genomic approaches can help separate genetic control from environmental plasticity.

The most promising direction is therefore not a single technology but a standardized multi-proxy architecture. The review suggests five priorities: (1) expand tropical and African chronologies; (2) standardize QWA protocols and metadata; (3) build open anatomical databases; (4) validate automated measurement systems against expert datasets; and (5) develop integrated models that connect cellular traits with stand-level forest responses.

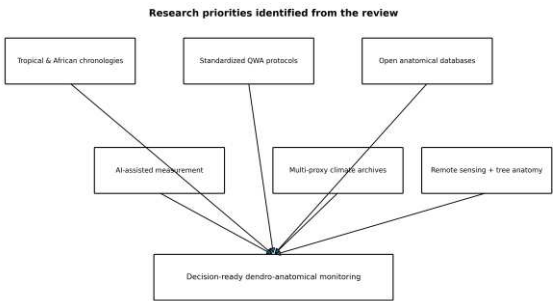


Figure 9. Research priorities emerging from the review. The strongest opportunity is to connect improved geographic coverage and methodological standardization with open data and multi-proxy integration.

4. Synthesis and Research Implications

Across the evidence base, the central contribution of dendro-anatomy is increased resolution. Ring width provides a dated annual growth signal; density adds information on wood formation and, in appropriate contexts, temperature; tracheid and conduit traits add hydraulic and physiological detail; resin canals add defence and disturbance information; and QWA provides the measurement architecture needed to integrate these signals. The resulting evidence is complementary rather than hierarchical.

Three implications follow. First, proxy selection should be hypothesis-driven. A study asking about drought should not automatically prioritize the same trait as a study reconstructing warm-season temperature. Second, anatomical signals should be calibrated against independent observations because similar anatomical outcomes can arise from different stressors. Third, the field needs geographic expansion and methodological harmonization if anatomical chronologies are to become broadly comparable across regions.

Table 6. Priority actions for the next generation of dendro-anatomical research.

Priority	Why it matters	Near-term research action
Tropical/African chronologies	Current evidence is geographically uneven	Establish replicated species-site networks
QWA standardization	Protocol differences limit comparability	Publish shared preparation and measurement metadata
Open databases	Large-scale synthesis requires interoperable data	Archive cell-level traits with chronology information
AI validation	Automation can increase throughput but introduce bias	Benchmark algorithms against expert-labelled images
Multi-proxy integration	Single traits rarely isolate one driver	Combine anatomy, density, isotopes, climate and remote sensing

5. Conclusion

This systematic review synthesized the role of wood anatomical elements as proxies in dendrochronology using the evidence base and screening process reported in the supplied manuscript. The review retained 287 publications after screening 3,274 records and demonstrates that wood anatomy can extend the information content of conventional tree-ring chronologies. Growth rings provide the temporal framework; tracheid and other cellular traits add physiological and seasonal resolution; density and MXD provide established high-resolution signals in appropriate settings; and resin canals can preserve evidence of defence and disturbance.

The strongest future opportunity is integration. Quantitative wood anatomy, densitometry, stable isotopes, remote sensing, genomics, and artificial intelligence can be combined into multi-proxy environmental archives that are more informative than any single measurement. However, the review also highlights the need for methodological transparency, careful attribution, uncertainty reporting, and broader geographic coverage. Tropical and African forests should receive particular attention because expanding chronologies in these regions would improve both scientific understanding and the practical value of dendro-anatomical monitoring for climate resilience and sustainable forest management.

Declarations

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Conflict of Interest

The author declares no competing interests.

Ethics

This study synthesizes previously published literature and involved no human participants, animals, or personal data; ethical approval was therefore not required.

Data Availability

No new primary dataset was generated. The evidence base was derived from published literature and the review-search process described in the manuscript.

Author Contributions

Mulenga Brian Nsofu: conceptualization; literature search; screening; data extraction; evidence synthesis; manuscript preparation; review and editing; and final approval.

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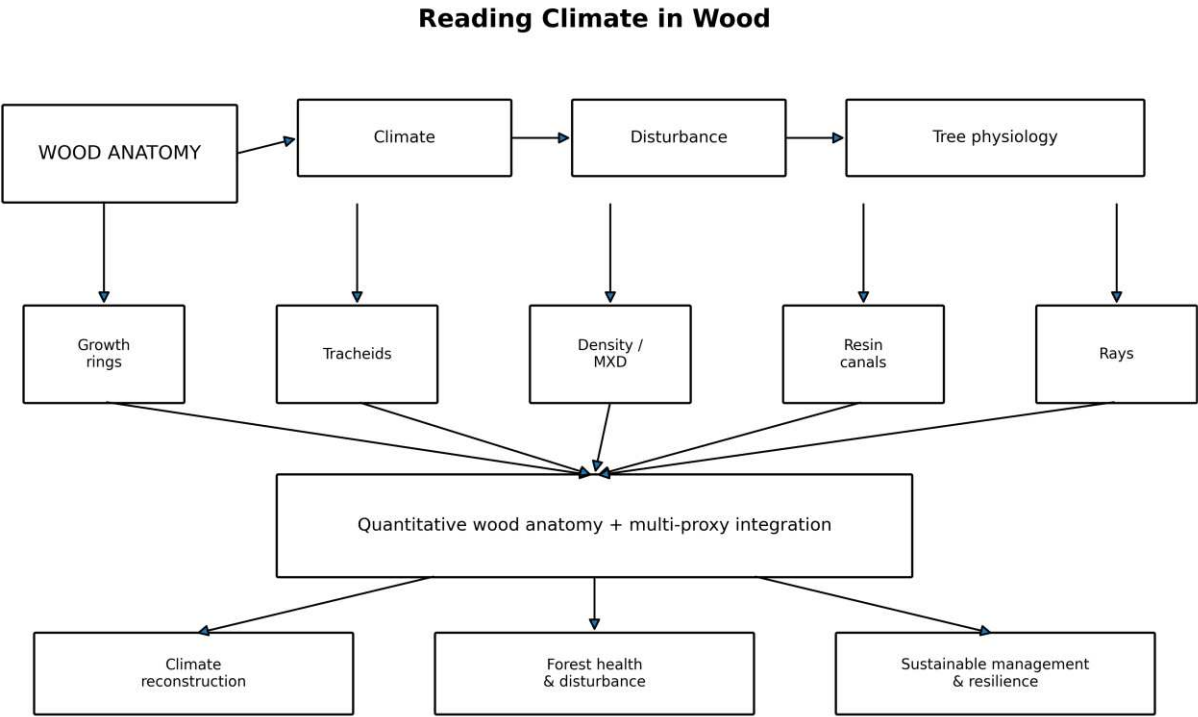
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Graphical Abstract



Graphical Abstract. Wood anatomical traits provide complementary records of climate, physiological stress, disturbance, and forest response. Their integration through QWA and multi-proxy analysis creates a pathway from cellular measurements to climate reconstruction and management decision support.