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WOOD STRUCTURE AND FUNCTION (A KOUBAA, SECTION EDITOR)

Electrical Phenomena in Trees and Wood: A Review

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Abstract

Purpose of review This review covers electrical phenomena originating from the physical properties of wood, relevant to tree biology and timber industry applications. Membrane-associated cellular phenomena like action potentials are excluded. Trees exhibit diverse bioelectric processes of physical origin. The electrical properties of wood hold promise for advancing timber processing, and developing smart materials, while enhancing our understanding of tree-environment interactions.

Recent findings Streaming and piezoelectric potentials have long histories but are now reinterpreted based on our better understanding of plants. Streaming potentials from sap flow, discounted in the 2000s, have been reinstated through recent publications addressing past inconsistencies with current data on xylem structure. Electro-osmotic flow is gaining new applications in timber drying. Wood, previously considered weakly piezoelectric, shows much stronger activity after fungal degradation, spurring interest in practical applications and the underlying mechanism – now better understood through new findings on the structure, deposition and deformation of wood cellulose. Internal variation in the electric (conductive and dielectric) properties of green logs facilitates innovative timber quality mapping methods. Emerging research on perturbation of the atmospheric and soil electric fields by trees offers insights into inter-organism interactions.

Summary This review encompasses electrical measurement methods; electrokinetic phenomena, including streaming potentials and electro-osmotic timber drying; electric heating; mapping and technologies based on dielectric properties; wood-based electronics; electromechanical phenomena, including the piezoelectric effect and triboelectrification; atmospheric electricity around trees; and electrotaxis. Future research should explore electro-osmosis in wood and its applications. Electric potentials in green wood and living trees, generated through ion-transport mechanisms, need further exploration to elucidate charge separation processes.

Keywords Dielectric properties · Electrical signals · Electro-active wood · Piezoelectricity · Streaming potential · Wood conductivity

Introduction

Electrical signals in plants were first reported over 200 years ago, in the context of leaf movements [1]. In the twentieth century, electrical activity was implicated in almost every area of plant metabolism, including responses to environmental [2, 3] and ecological influences [4] with associated gene expression [5]. Most of these wide-ranging cellular responses of living plants depend on electrical potential differences across membranes, driven by transmembrane ion transport, as reviewed by Farmer et al. [6], and Klejchova et al. [7]. Wood cells are non-living, with a few exceptions, and do not have functioning cell membranes. This review is concerned with electrical phenomena that are *not* mediated by membrane potentials but derive directly from the physicochemical properties of wood.

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Engineers and materials scientists have studied the electrical properties of wood, i.e., dead xylem, in the context of its performance as an industrial construction material. Green, i.e., wet, never dried wood, is electrically conductive. Above fibre saturation point (FSP), the conduction of electric current is mostly determined by ionic composition and the distribution of free water in the wood cavities as well as temperature and grain orientation. Variability in these properties determines the vulnerability of trees to lightning strikes. On the other hand, dry wood can be used as a dielectric material for electrical insulation. The dielectric constant of wood increases continuously with the moisture content [8] and decreases with increasing frequency of the applied field. Most research has focused on dry wood below FSP, where electric properties are most sensitive to moisture content (Fig. 1) [8–11]. Wood can be used also as a dielectric material for electrical insulation (dry wood) [8]. The polarisation mechanism above FSP is dominated by ion mobility in water while below FSP dipole orientation becomes relevant. Detailed application of electrical properties above FSP and dielectric characteristics of wood have been discussed in [8].

The electrical properties of green wood have been studied much less, and the electrical properties of trees, less still. Engineering knowledge of the electrical behaviour of green wood therefore provides useful insights into the biology of trees.

The physical principles that govern electric phenomena in green wood and in whole, living trees are similar, but on the whole tree scale, or between trees, they have been studied much less than in the living cells or tissues of small plants. This paper reviews the electrical behaviour of both dry wood and wet wood, including trees, and is motivated in part by emerging interests in utilising electrical phenomena in wood commercially.

Measurement of Electrical Signals

Measuring Electric Properties of Wood

Electric properties of wood below FSP have been studied extensively in the context of moisture content determination, heating, gluing, drying and improving the quality of wood [8]. Less is known about electric properties above FSP. Spatial information on the electric pulse resistance along the radius of a tree stem can be investigated with a Shigometer [12]. Steel pin electrodes are inserted into predrilled holes while the electric resistance between them is continuously recorded. Characteristic variation in electrical pulse resistance along the radii, with lower resistance in the sapwood than in the heartwood and a decline towards the pith, has been observed [13]. However, this necessitates drilling one to several holes in the trunk to insert a coring bit, probe, or sensor, resulting in a wound that may compromise the tree's health for the rest of its lifespan [14]. Electric resistivity tomography has been developed as a minimally invasive method for identifying areas of internal decay, enabling arboricultural practitioners to make informed tree management decisions [15, 16]. Devices measure the resistance

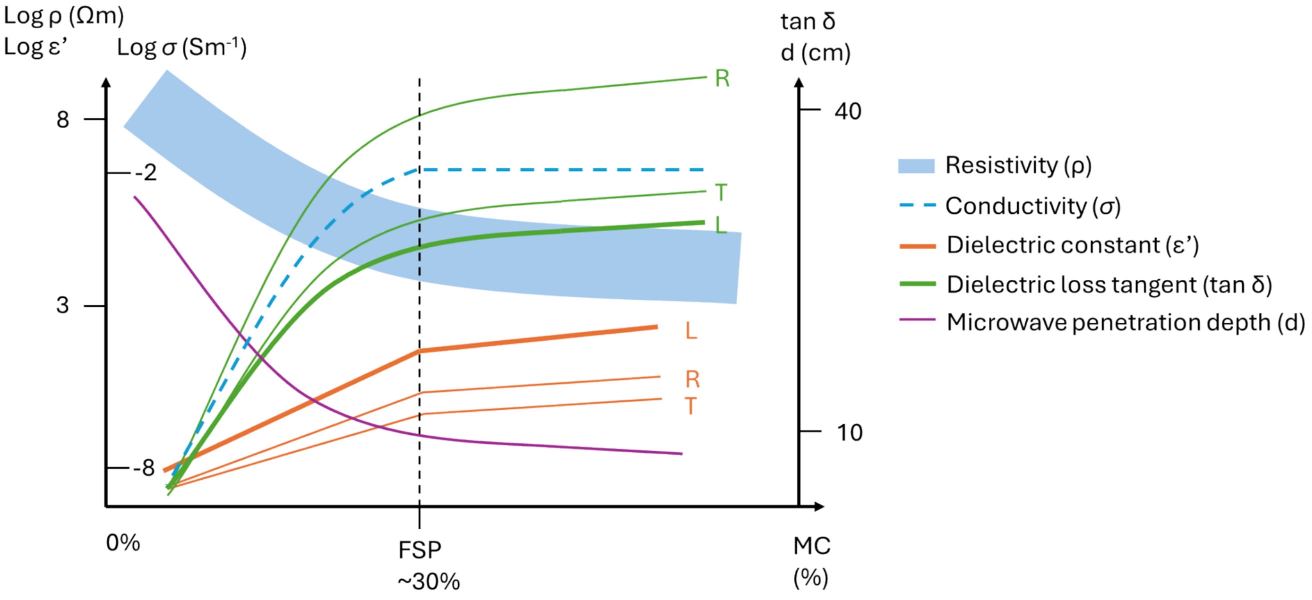

Fig. 1 Influence of moisture content (MC) on electrical properties of wood. Data collated from [9] (resistivity ρ), [10, 11] (conductivity σ), and [8] (dielectric constant ε', loss tangent tan δ and penetration depth d). Electric properties of wood are most sensitive to MC below fibre saturation point (FSP)

between pairs of electrodes placed around the circumference of a stem. Applying computer tomography algorithms, 2-dimensional images can be calculated from the acquired data. Such images can reveal the sapwood/heartwood interface in trees due to the different electric conductivity of heartwood and sapwood [17–19]. A segmented electrode for mapping the heartwood and sapwood extents of green logs has also been reported [20].

Nursultanov and co-workers measured anisotropic electrical conductivity of green wood [11, 21]. They connected 30 mm wide wood cubes via gold leaf to an AC electrical excitation and measurement system [21]. Set-ups utilising conductive gel were unsuccessful as the ions penetrated into the wood, changing the electrical properties of the cm-sized samples during the measurement [11]. The same research group further developed segmented electrodes which can be used to heat logs up to 0.5 m in diameter for phytosanitary or wood peeling purposes [20, 22, 23]. The segmented nature of the electrodes made it possible to locate heartwood and sapwood in the logs based on their different conductivity.

Dielectric properties of wood are measured using different techniques in accordance with the chosen frequency range. At low and high frequencies measurements with bridges are widely accepted, while measurements at super-high frequencies are carried out using waveguide and resonator techniques [8].

Measurements on Trees

Electrical measurements on intact, woody plants have proven to be challenging. Measurements on living plant tissues have to distinguish between intracellular and extracellular potentials. In the dead xylem of trees this difficulty does not arise, but there are still practical problems concerning ion distributions close to the electrode surface.

Electrical potentials must be amplified, and the recording device must have a high input impedance ($> 10^9\ \Omega$) as the potentials are weak [24, 25]. Surface contact electrodes and metal pin electrodes are most often used for extracellular measurements [24]. A typical surface contact electrode is the calomel electrode, which uses an ion solution to form a salt bridge between the electrode and the plant tissue. This is not damaging to plants: however, the ions penetrate into wood affecting its electrical properties [11]. This method is useful for measuring electrical potential over a short period of time (< 12 h) as the testing electrode may dry up, changing the ionic status and consequently affecting the measurement over longer durations. Metal electrodes that are inserted into plants cause some mechanical damage but can be used for long-term (> 24 h) monitoring of electrical potentials [26]. Koppán et al. [27] monitored electric potential differences constantly over four years using electrodes placed into the sapwood of *Quercus cerris* trees.

These methods can only detect potentials around the electrode and are therefore not suitable to distinguish spatial differences in the electrical potential in multiple cells or tissues. Optical recording methods using voltage-sensitive dyes overcome that limitation and allow monitoring of the bioelectrical activity at multiple sites, with high resolution [28]. These optical recording methods may well have potential for spatially resolved measurements on wood, but so far, they have only been applied to the study of membrane-mediated processes in plants [29].

Electrokinetic Phenomena

While electrical conduction in metals is due to electron transport, in biological materials it is commonly ions that are transported. Ions interact with associated water molecules, the same process that retards ion diffusion. In addition to ion transport within the solution, the solution itself can flow through whatever capillaries it occupies. The highly anisotropic capillary flow caused by the anatomy of wood [30] results in the electrical conductivity of green wood being highly dependent on grain orientation [21] and the diffusion coefficient [21, 31].

Electrokinetic phenomena are caused by coupling of electric potentials to the capillary flow of ion-containing solutions over charged surfaces (Fig. 2). This coupling can take two opposite forms: a streaming potential, i.e. an electric potential difference (voltage) driven by capillary flow; or conversely electro-osmotic flow, capillary flow driven by an electric potential difference. After an outline of electrokinetic theory in Sect. **3.1**, the streaming potentials that have been attributed to diurnally varying sap flow in trees are discussed in Sect. **3.2** and potential applications of electro-kinetic effects in Sect. **3.3**. A special case of electro-osmotic flow giving rise to shrinkage and swelling at the source and destination of the flow appears in Sect. **6**.

Electrokinetic Theory

Streaming potentials and electro-osmotic flow are well-understood physical phenomena with applications in geology, analytical electrophoresis and elsewhere [32]. Interaction between a charged solid surface and an aqueous solution creates a thin interfacial layer, the Debye layer, with an excess of mobile ions charged oppositely to the fixed charges at the surface. In the xylem of trees, the surface charges are negative [33, 34] and the net charge in the Debye layer is therefore positive. The excess charge in the Debye layer gives rise to the zeta potential ζ, a term adopted from colloid chemistry where it predicts the electrical repulsion that prevents aggregation of colloidal suspensions [33].

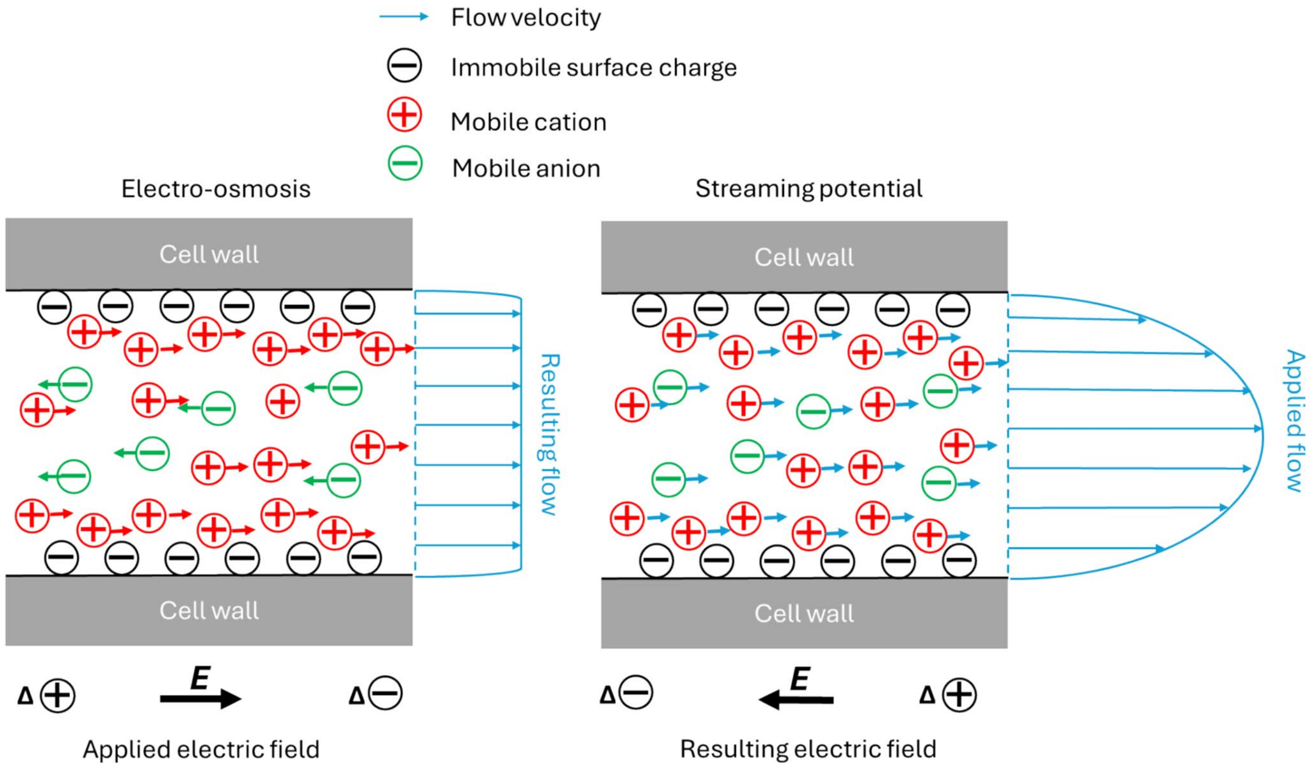

Fig. 2 Electrokinetic phenomena in moisture saturated wood. Immobile negative charges on wood cell wall surface attract positive charges from the sap, forming a Debye layer. An applied tangential electric field will result in fluid flow when the net positively charged solution migrates towards the cathode. Conversely, an applied fluid flow results in an electric field when mobile charged ions migrate towards the cathode

An applied electric field exerts a Coulomb force on the mobile charges, resulting in liquid flow; conversely, electric fields are generated by water movement in capillaries [32].

Streaming potentials and electro-osmotic flow are mirror-image phenomena in electrical terms. They are not, however, equivalent hydrodynamically. Pressure-driven flow in a capillary is normally considered to follow a Poiseuille distribution with the fastest flow in the centre, and much slower than the average flow rate in the thin Debye layer at the edges [32]. This differs from electro-osmotic flow, which is driven from the edges of the capillary and therefore corresponds to ‘plug’ flow, where the flow rate is constant across the diameter. Therefore, the efficiency of conversion between pressure-driven energy and electrical energy is lower for streaming potentials than for electro-osmotic flow [35].

$$E = \frac{e_0 e_g}{sh} \zeta \Delta P \tag{1}$$

where;

E_0 is the vacuum dielectric permeability = 8.85×10^{-12} F m.$^{-1}$

e_g is the xylem dielectric constant ≈ 80.

s is the conductivity ≈ 0.01 S m.$^{-1}$

η is the viscosity ≈ 10^{-3} Pa s.

ζ is the zeta potential ≈ 0.01 V.

ΔP is the pressure difference ≈ 1 MPa.

It may seem surprising that Eq. 1 does not include the flow rate, nor the length or diameter of the capillary, but these terms are included in the end-to-end pressure difference ΔP. An alternate form of Eq. 1 [34] applies for a Poiseuille flow distribution, which is assumed for the occurrence of a streaming potential:

$$E = 8 v e_0 e_g \zeta L r^{-2} s^{-1} \tag{2}$$

where;

V is the linear flow rate.

L is the length of the capillary.

r is the radius of the capillary.

The zeta potential ζ is a key term in Eqs. 1 and 2, and depends on the surface charge of the xylem cell walls [32, 33]. The surface chemistry of wood is complex and is not the same as the bulk chemistry of the xylem cell wall. Lignin appears to dominate the surfaces and bears negative charges on free phenolic groups, whereas the carboxylate groups of glucuronoarabinoxylans are not generally reported to be exposed on these surfaces [36]. It has also been observed that surfactants and lipids are adsorbed on the inner face of wood xylem [37]. Hydrophobicity may influence radial ion distribution in capillaries in ways that depend on water structure and are not well understood [38].

Xylem flow is restricted where it passes through pit membranes, which have different surface chemistry from the secondary cell walls of the lumina of the xylem cells [39]. Like the xylem surface, the hydrated pit membranes are negatively charged, so the Debye layer has an excess of cations and the streaming potential has the same sign as in the xylem. In the pit membranes the negative charges can be on carboxylate groups with lower pKa than the phenolic groups on the xylem surface. There has been uncertainty about the relative contributions of pit membranes and the main part of the xylem vessels to electrokinetic phenomena, but Eqs. 1 and 2 show that they depend on the relative pressure drop, ΔP, and the zeta potential, ζ, at each location. The pores of the pit membranes are tens to hundreds of nm wide so their influence on pressure drop and streaming potentials is not negligible, even though most of the length of a xylem conduit is taken up by the wide vessel elements themselves. Both pit membranes and the xylem between them, therefore, are likely to be significant [40]. Conifer tracheids, being narrower than xylem vessels, should cause more pressure drop. The bordered pits joining them contribute to pressure drop and thus streaming potentials, but less than the pit membranes of angiosperms [40].

In wood with negatively charged surfaces and corresponding mobile cations, the generation of positive charge at the outflow is expected. This has been reported for *Salix alba* stems purged with 1 mM KCl and 0.1 mM $CaCl_2$ [34] similarly to most rocks in common natural conditions. Recent observations on *E. nitens* logs [41] revealed a negative potential for 20 mM KCl, ionic strength, comparable with in vivo conditions although higher and lower salinities led to a positive charge accumulation at the outflow. These data are generally consistent with the streaming potential mechanism outlined above.

Diurnal Variation in Electric Potential in Trees

Sap flows upward in the xylem of living trees during the day when open stomata are needed for photosynthesis. Diurnal variation in streaming potential would thus be expected to accompany the diurnal variation in sap flow. A series of early measurements of tree-to-ground potentials showed this pattern [42].

However, several studies in the 2000s highlighted anomalies in the measurement of diurnal patterns [35, 36, 43]. The diurnal variation in electric potentials lagged behind sap flow [44, 45], and was different at separate measurement points [46]. Such anomalies led Gibert et al. [43] and Love et al. [35] to discount streaming potentials altogether and suggest a variety of other mechanisms, including root potentials and local ion movements close to the measurement electrodes. These apparently negative findings led to some loss of interest in the topic of streaming potentials in trees.

Recently, however, Guha et al. [47] pointed out that the lag between sap flow and measured electrical potential could be explained by independent diurnal variation in the xylem pressure drop as root aquaporins alter the sap flow rate under the metabolic control of the plant's circadian clock. They also pointed out that the Zeta potential, ζ, is not necessarily constant throughout the day but is sensitive to variation in sap pH and to the binding equilibration of counterions with the inner surface of the xylem [47]. These insights negate key objections to streaming potentials as a partial explanation, at least, for diurnally varying electrical potentials.

Other evidence supports this view. Gindl et al. [34] avoided complications at the root-soil interface by using two electrodes 3 m apart in the xylem of a willow tree, observing diurnal amplitudes of about 20–30 mV m^{-1}. They also showed that the electric potential was proportionate to the flow rate in a 0.5 m willow stem section with electrodes in liquid reservoirs between which the stem was pressurised, avoiding any complications from electrode potentials. The minimum requirements for streaming potential in response to sap flow are a significant zeta potential, ζ, for the xylem as a whole [33], including both vessel or tracheid walls and pit membranes; and a significant vertical pressure gradient (Eqs. 1 and 2). Streaming potentials should therefore exist. A study on electrical phenomena during water evaporation through microchannels of natural wood showed that this process allowed the continuous harvesting of direct current [48].

Streaming potentials may of course be distorted or obscured in whole trees by electric potentials with other origins, including membrane and Nernst potentials in the roots or elsewhere and local potentials close to the electrodes [35, 43–45]. Atmospheric potential gradients (see below) might make a further contribution to measured xylem potentials

[49]. Early observations that are still unexplained include the short-period oscillations in electrical potential observed by Fensom [42] and occasionally hinted at by others; perturbation of diurnal potentials by mechanical displacement; and the presence of radial as well as vertical potential gradients [50].

Utilisation of the Electro-Kinetic Effect in Wood

Electro-osmosis has been used to remove copper preservatives from recycled wood by applying a DC electric field [51]. Conversely, electrochemical impregnation of wood with copper was investigated by [52]. This process was speculated to be the reason for copper found in wooden props located in Roman mines, having entered naturally when the timber ends were placed in copper-containing soils [53]. Silicification to strengthen archaeological wood using electro-osmosis was also explored [54].

Utilising the electroosmosis effect for dewatering timber has been suggested [55]. While that process has minimal energy requirements [56] it stops when capillaries at the anode become dehydrated, which happens at a high average moisture content.

More recent investigations revealed variation in streaming potential of *Eucalyptus nitens* logs purged with KCl solutions, attributed to electrokinetic effects in microscopic pores [41]. It was argued that this phenomenon could be used for reducing drying collapse in wood.

The electric energy generated by mobile charges moving through wood during water evaporation, and causing a streaming potential, can be harvested [48]. This process is also known as hydro-voltaic energy harvesting. Increasing the surface area by delignification [57] and doping with Fe_3O_4 nanoparticles [58] increased the power density by ~ 3 orders of magnitude.

Electrical Heating of Green Wood

Joule heating, also known as ohmic heating, is where an electric current flowing through a conductive medium generates heat. Green wood, being an electrically conductive material, can be Joule-heated causing a fast temperature rise [23]. The heating rate is considerably higher than that of conventional heating such as in kilns or soaking in hot water and could reduce the heating time by a factor of ten [59] if employed in industrial processes such as veneer peeling [60] or phytosanitary treatment [22, 61]. Recently, Joule heating has been employed as a pre-drying treatment for reducing drying collapse in *E. nitens* wood (Fig. 3, Table 1) [62].

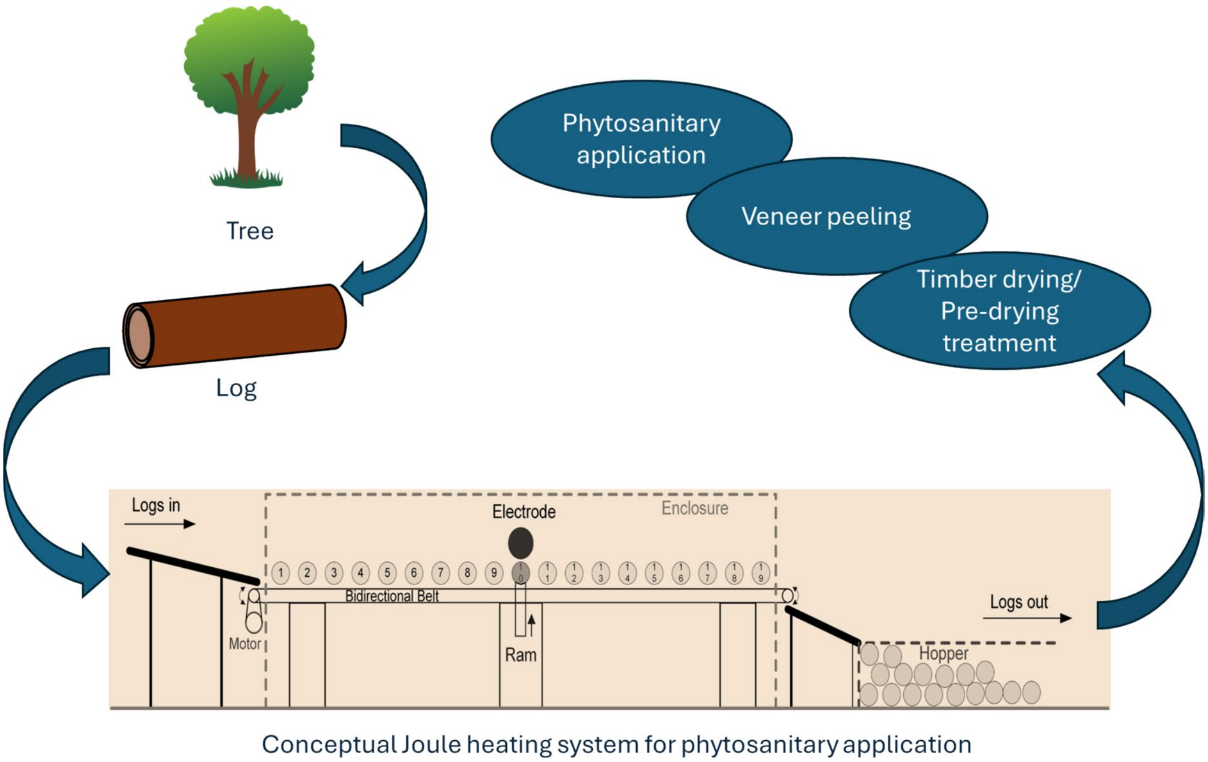

Fig. 3 Schematic illustration for ohmic or Joule heating applications in the wood processing industry [62]

Table 1 Summary of electrical phenomena and their application, with description, in the wood processing industry

Applications	Description
Wood moisture measurements	Electrical resistance: Assessing moisture content (below FSP) by measuring the electrical resistance between two electrodes in the wood Capacitance sensing: Used in portable devices to measure wood moisture content
Non-destructive testing (NDT)	Capacitance sensing: Density estimation and detecting defects like cracks or voids Electrical impedance tomography: Enable imaging of internal structures of standing trees by measuring electrical impedance, revealing features like knots or decay Piezoelectric phenomenon: Measure local mechanical forces in structural timber
Heating	Electromagnetic radiation: Electromagnetic fields interact with water and wood by different physical phenomena depending on the frequency. Energy losses heat timber fast preferentially in moist regions, reducing internal moisture gradients and consequently improves drying quality by reducing drying stresses. Also used to cure adhesives Joule heating/ohmic heating: Heating rate is considerably higher than that of conventional heating and could reduce the heating time by a factor of ten if employed in industrial processes such as phytosanitation or veneer peeling; pre-drying treatment for reducing drying collapse in wood
Wood modification	Electrochemical: Remove copper preservatives from recycled wood by applying a DC electric field,
Dewatering of wood	Electro kinetic phenomena: Free water can be removed from timber by applying an electric potential
Increasing permeability	Pulsed electric field: Applying short, high-voltage electric pulses can rupture pit membranes, facilitating drying and impregnation of chemicals or resins
Electro active materials	Electrochemical: Electromechanical transduction by movement of an ionic solution leading to local swelling and shrinkage. Delignification, high-temperature carbonization, or physical/chemical activation enhance the electrical conductivity and surface area
Energy harvesting	Piezoelectric energy harvesting: Large-scale wooden floors could generate electricity from human activity Electro kinetic phenomena: Evaporation of water through wood induces an electric potential which can be harvested Triboelectric effect: Triboelectric nanogenerators can be used as self-powered sensors
Wood-based electronics	Dielectric properties: Wood used as substrate for electronic circuit boards

A limited amount of work has been published concerning conduction of electricity in green timber [21], in contrast to wood below the fibre saturation point (FSP). Below FSP, i.e. in wood where unbound water is absent and typically below 30% moisture content, conductivity is linearly related to MC (Fig. 1) and electrical moisture meters are based on this correlation [13]. However, over the full range of moisture content the relationship between moisture content and electrical conductivity is nonlinear. A recent investigation on green wood's electrical conductivity [21] has shown that above FSP, electrical conductivity is determined less by moisture content than by other factors; the ionic composition of the sample, temperature [21] and the distribution of free water in the wood cavities become dominating effects, as described by Skaar [9].

Dielectric Properties of Wood

Dielectric properties of a material are relevant when, in contrast to direct current (DC), or relatively low frequency alternating current (AC) such as the power frequencies (e.g., 50 to 400 Hz) considered above, higher frequency AC (typically in the MHz range) is applied. The dielectric behaviour of wood in an alternating electric field is governed by moisture content (Fig. 1), frequency, temperature, density and grain direction [8]. Dielectric properties of wood are used to measure the moisture of solid and chipped wood even above FSP [8].

As thermal energy is generated when electromagnetic waves penetrate green wood, this phenomenon is used on an industrial scale for wood drying, generally referred to as radio frequency (RF) or microwave heating. Compared to conventional kiln drying where heat is transferred by convection and conduction, heating with electromagnetic waves is rapid and is accelerated in moist regions, potentially resulting in uniform drying and fewer drying defects [63].

Differences in the dielectric properties of wood can be used for non-destructive diagnostic purposes [64]. Various technologies differing in the frequency of the electromagnetic radiation have been developed. A non-destructive and fast method called high-frequency (HF) densitometry has been used for measuring relative density variations along wood surfaces utilizing the dielectric properties of wood. The method is based on the propagation of continuous electromagnetic waves through the HF transmitter–receiver link of a small electrode system, which is in direct contact with the wood surface [65]. Dielectric properties also influence microwaves [66]. As dielectric properties of wood differ with moisture and density, microwaves can be used in microwave tomography to produce a cross-sectional image of wood to detect knots, decay and cavities in tree trunks and timber [67–69]. In a similar frequency range, radar scanning, which also utilises the differences in dielectric permittivity of wood, can generate images to detect internal features of green logs such as knots and timber [70]. Applications of still higher, terahertz-frequency radiation have been recently reviewed [71] and include measurement of moisture content, detection of defects and dendrochronology (Table 1).

Wood as an Electroactive Material

Electro-active polymers (EAP) change in size and shape when stimulated by an electric field, and have been explored for applications such as soft actuators or built-in sensors [72]. The best-known mechanism is the piezoelectric effect described below. Electromechanical transduction can also be mediated in other ways, such as by the movement of an ionic solution in a hydrated porous material, leading to local, moisture-driven swelling and shrinkage [72].

Sometimes electromechanical coupling is observed but the mechanism is uncertain, especially when the moisture content is too high for the piezoelectric effect to operate. For example, 'electro-active paper' (cellulose acetate film) was shown to exhibit a remarkable bending performance, which might be connected to electrokinetic solution transport across the film, with consequent asymmetric swelling [73]. Many biobased EAPs are ion-conducting materials, with their ionic conductivity depending on the polymer matrix, ionic species and strength of complexation [74]. The ion transport behaviour of wood can be significantly influenced by altering its surface properties (zeta potential, ζ), and/or pore size. For instance, surface functionalisation, such as grafting a cationic functional group (e.g., $(CH_3)_3N^+Cl^-$) to the cellulose backbone through an etherification process, modifies the zeta potential, ζ, of natural wood from a negative (-27.9 mV) to a positive ($+37.7$ mV) value [75]. Furthermore, pore size can be modified by various methods, including delignification and densification [76], stretching and ion-swelling [33], all of which modulate the ion transport mechanism.

Recent advances in the use of wood as an electroactive material have focused on multifunctional modifications for energy storage devices and filtration membranes [75]. Techniques such as delignification, high-temperature carbonization, or physical/chemical activation have been employed to enhance the electrical conductivity and provide a larger specific surface area for loading electroactive materials [77].

Wood-Based Electronics

The high electric resistivity of wood allows it to be used as an environmentally friendly substrate for electronic circuits. The challenge is to create resilient, electrically conductive surface layers, for which laser induced graphitization with and without a catalyst [78], applying conductive ink [79] and impregnation [80] or coating [81] with metals have been tested. Impregnation of wood with a mixed electron–ion conducting polymer allowed the construction of a transistor [82].

Piezoelectricity of Dry Wood

Dry wood exhibits an observable piezoelectric effect, converting mechanical energy into electrical energy and vice versa. The piezoelectric properties of wood and cellulose have been known for a century, and were the subject of a classic series of experiments by Fukada and others (reviewed by Fukada [83] and more recently by Smith and Kar-Narayan [84]). Piezoelectric potentials are not observed at the high moisture content of green wood or living trees, because conduction dissipates piezoelectric potentials as fast as they arise [85].

Piezoelectric potentials in wood are generally quite small, particularly in response to the axial tensile stresses to which wood is predominantly adapted [86] (Fig. 4a). It was a surprise, therefore, when Sun et al. [87, 88] and Ram et al. [89] reported a piezoelectric response nearly two orders of magnitude greater when wood that had been delignified or degraded by fungal action was compressed across the grain. There has since been resurgent interest in the possibilities of wood-derived materials and synthetic cellulosic analogues for energy harvesting and as strain sensors, for example in wearable medical devices [84]. The reasons for the exceptionally large piezoelectric response of degraded wood [88] are a puzzle, encouraging us to review the underlying physics, below, with the aim of encouraging new developments in functional wood-based materials.

The piezoelectric effect depends on structure. It originates from the reorientation of polar groups, such as the hydroxyl groups in cellulose, when the structure deforms under stress [84]. With six possible stress orientations (tension and shear, each in three dimensions) and three possible electric field orientations, there are potentially 18 combinations of force and electric response. When there is a mirror plane within the structure, piezoelectric effects on either side cancel out to zero. For single crystals, the orientations of stresses giving non-zero piezoelectric responses can therefore be predicted from the symmetry of the crystal structure as expressed in the space group [84]. Centrosymmetric

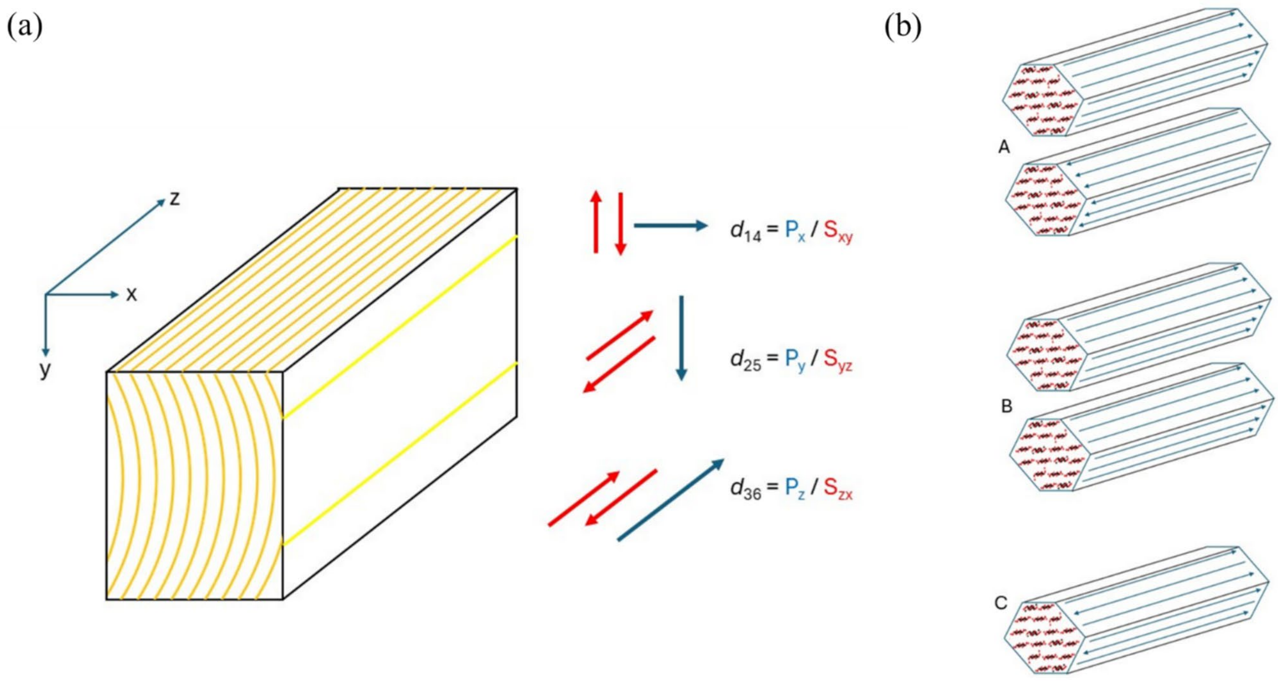

Fig. 4 (**a**): The three predominant piezoelectric responses of wood to shear stress, in the co-ordinate system of Hirai et al. [86] (x: radial, y: tangential, z: axial/longitudinal; yellow lines: annual rings); (**b**): Cellulose chain orientation in microfibrils (arrows) (A), two cellulose microfibrils each with parallel chains, but arrayed antiparallel as normally found in wood (B), two cellulose microfibrils each with parallel chains, in a parallel array as in oriented nanocellulose films or in spiral xylem thickenings (C), Cellulose microfibril with antiparallel chains, as in regenerated cellulose II or as formerly, but incorrectly, assumed for native cellulose I

structures, with mirror planes in all three dimensions, are not piezoelectric. Nor are disordered structures comprising randomly oriented domains.

Fukada [83] stated that in native cellulose I, only two non-zero directional combinations associated with shear would remain, due to rotational averaging around the fibre axis and the axial centrosymmetry resulting from the antiparallel chain arrangement then assumed (space group C2: Fig. 4b, Panel C). Axial tension, to which cellulose microfibrils are particularly adapted, would have net zero piezoelectric effect. The tensor matrix expressing these relations is still sometimes used, but is based on a cellulose structure accepted then but now known to be wrong.

Wood cellulose [90] like other native forms of cellulose [91], does not have the antiparallel chains assumed by Fukada [92]. Plant cellulose microfibrils have parallel chains [93, 94] (Fig. 4b Panels A and B) and are therefore intrinsically capable of axial piezoelectric activity.

However, it is necessary to consider not only the structural symmetry of individual cellulose microfibrils but also how the microfibrils are arrayed in the cell walls of wood. Bidirectional movement of the cellulose synthase complexes [94] gives rise to antiparallel microfibrils [93] (Fig. 4b, Panel A). Piezoelectric fields generated by microfibrils so arranged, in axial tension, would partially or wholly cancel out to zero.

Consistent with these observations, macroscopic axial piezoelectric coefficients are observable, but very small, in wood from a range of tree species [86] (Fig. 4a). However, in thin films of unidirectional cellulose nanocrystals with the chain direction aligned in parallel across the film thickness (Fig. 4b, Panel B), much larger piezoelectric responses have been observed than in wood [95, 96].

It may be inferred that bidirectional synthesis of cellulose, leading to approximately antiparallel microfibril arrays with small or zero axial piezoelectric behaviour, is not automatic but is actively maintained and in some way adaptive for the normal functioning of wood cells. Cell-wall domains in which bidirectional synthesis of cellulose is incomplete, for whatever functional reason, do occasionally exist—an example is the spiral thickenings of immature xylem vessels [97]—and can be expected to show enhanced axial piezoelectric behaviour.

There are further intrinsic reasons why wood cellulose does not behave like a simple piezoelectric material such as a single quartz crystal. The microfibrils of wood cellulose are only partly crystalline, with about seven distinct kinds of glucosyl residues [98], all of which differ from the two glucosyl residues in the cellulose Iβ crystal structures but share the parallel orientation of the chains. Piezoelectric theory assumes that a crystal deforms monotonically [72]. Cellulose, even a single cellulose Iβ crystallite, does not deform in such a simple way under tensile stress [90, 99, 100]. The electrostatic free energy change on stretching has large contributions from interplane multipolar interactions as well as hydrogen bonds [100, 101]. Changes in polarisation at the molecular level would certainly be expected under tension or longitudinal shear but might not be well described by a tensor matrix derived simply from the crystallographic space group of cellulose Iβ.

A further complication is that the nanoscale deformation of cellulose microfibrils that results from any macroscopic deformation of wood is complex, different in each layer of the wood cell wall and dependent on the thickness of the wood sample [102]. Macroscopic axial tension leads to shear stresses between, and consequently shear within, the microfibrils, depending on the microfibril angle [90]. Gindl et al. [103] perceptively used X-ray diffraction to monitor how the internal structure of cellulose deformed on application of an electric potential to pine wood (converse piezoelectricity). They observed zero axial deformation, consistent with the discussion above, but unexpectedly they found that a transverse potential increased the intersheet *a* dimension of the cellulose unit cell, even when the potential was reversed. They did not observe intersheet shear, but shear would be difficult to detect in the diffuse X-ray diffraction patterns from wood. Shear between sheets, in both directions, is now known to increase the intersheet spacing [104], explaining why this dimension was increased by transverse electric potentials of either sign.

We can now return to the puzzling question, why does degraded wood show much larger piezoelectric activity? Fungal decay cleaves microfibrils into shorter lengths, so that macroscopic tension is resisted by shear between microfibril surfaces. Shear loading between microfibrils leads inevitably to shear within their structure. Both fungal decay and delignification also remove lignin and hemicelluloses, augmenting the cellulose-cellulose contacts that are subject to shear [85]. Wood that has been decayed by fungi or by chemical delignification is more flexible and can deform to much greater overall strain, in which shear inside microfibrils is a significant component that can contribute to piezoelectric potentials [87, 88, 92].

Recent innovations include degradation of wood by thermal [105] or solvent treatment [106] leading to large piezoelectric effects. The piezoelectric phenomenon in wood has been used to measure local mechanical forces in structural timber [92] and to monitor movement [87] and vibration [89]. Piezoelectric energy harvesting is also receiving increased interest (Table 1), [107]. It was suggested that large-scale wooden floors could generate electricity from human activity [108]. Piezoelectric materials prepared by impregnation or chemical modification of wood, but retaining its anisotropic, porous anatomy, have been designed for sensing, biomedical and energy harvesting applications, as reviewed in [109–111]. Further practical developments may be expected.

It is worth noting that mechanical energy can be also converted into usable electric energy based on triboelectrification, i.e. friction-induced charge separation [112]. Wood-based triboelectric nanogenerators can be used as biodegradable self-powered sensors.

Capturing Atmospheric Electricity

Air is a good insulator, except in the ionosphere where the charge built up by thunderstorms is globally integrated. There is therefore a vertical gradient of electrical potential from the ionosphere to the earth, typically of the order of 100 V/m and varying diurnally, seasonally and with the weather [113]. A 50 m tree would then span a 5000 V atmospheric potential difference. Because trees are much poorer insulators than air, almost all the voltage drop is in the layer of air surrounding the crown of the tree [114] rather than within the tree's stem. The influence of a tree on a surrounding electric field can be felt at distances up to 100 m [114].

There has been recent exploration of these potential gradients in the air surrounding plants, including electrical perception by pollinating insects [4] and consequences for redox processes in the ground under trees [114]. What happens within the tree has not been the focus. Some studies on tree to ground potential differences have suggested an irregular contribution from captured atmospheric potentials, confusing or obscuring the measurement of streaming potential [43, 49, 115].

Irregularity would be expected from the nature of short-term variation in the atmospheric potential gradient, but also from the influence of the tree's foliage. Each leaf may be assumed to perturb the atmospheric electric field around it. Since the field perturbations of nearby leaves overlap, the electrical potential at the surface of each leaf is a function of how other leaves are spaced around it. Each leaf makes its own contribution to the basipetal potential gradient, and these individual contributions will change as wind moves the leaves. The information content of the resulting internal potential gradients should be sufficient to provide feedback control of the spacing of leaves in the canopy, even those on branches originating from widely separated places on the trunk or from nearby trees. However, it would be unwise to conclude that such mechanisms do indeed operate in the morphogenesis of

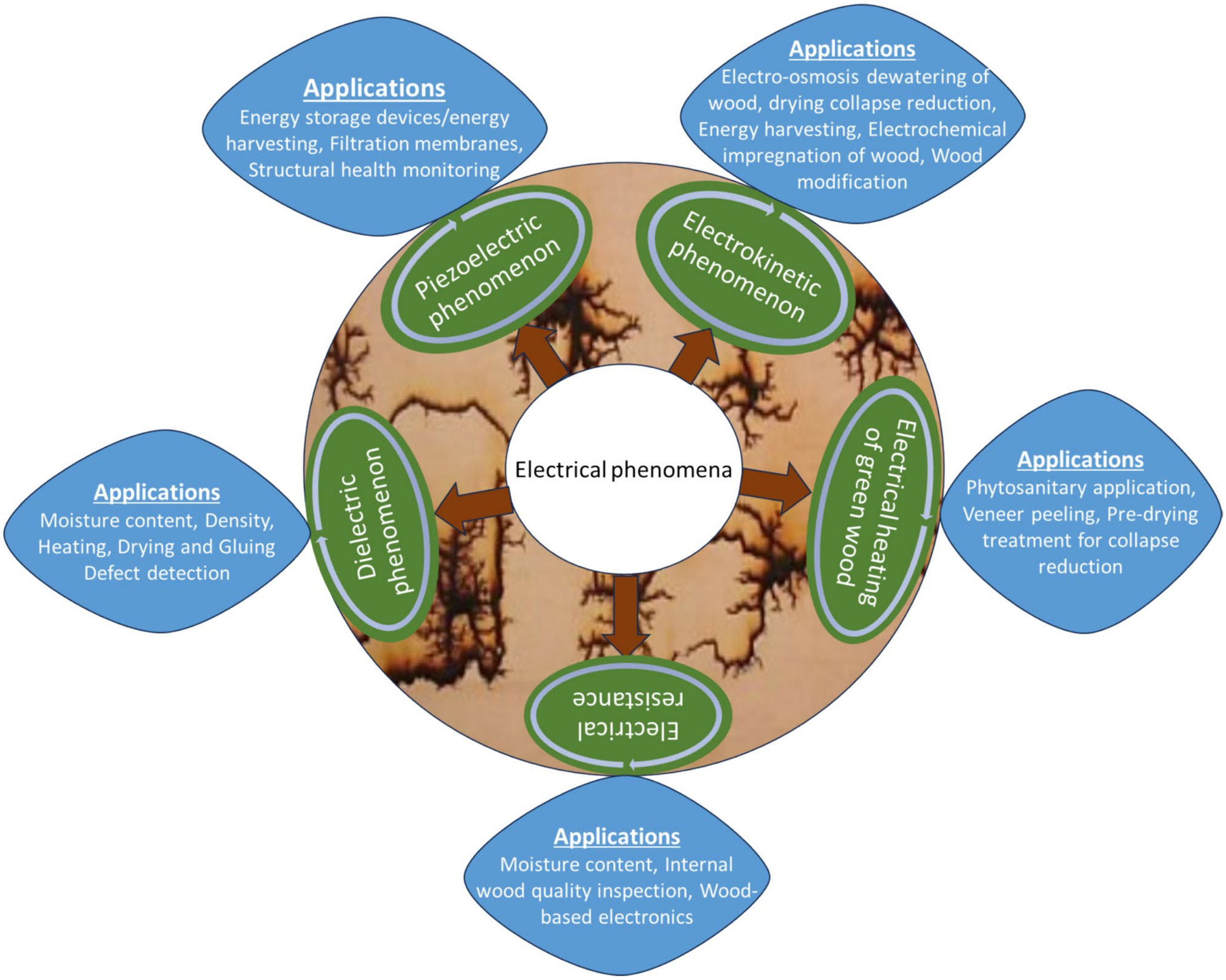

Fig. 5 Graphical illustration for key electrical phenomena in green and dry wood and their application in the wood processing industry

trees: other influences such as shading and perhaps gas exchange may well be sufficient.

Electric Phenomena Relating to Tree Associated Microorganisms

Conduction of atmospheric potentials ends at the root-soil interface. The soil being conductive, growing roots are surrounded by small electric fields originating from atmospheric gradients but also from the transfer of ions between the soil and the root and from sap flow [114]. It has long been known that zoospores of *Phytophthora* spp. and other tree pathogens use electrotaxis (electric field attraction) to locate roots [116]. Lab-on-a-chip devices have been developed to study electrotaxis [117]. It is thought that the flagellate shape and relative electrical charge on the front and back flagella of the zoospores determines their electrotactic response. Interfering with root-zone electric fields could help protect trees from disease infection [116]. Electrotactic attraction has also been demonstrated for rhizobia and suggested for mycorrhizal symbionts [116]. Roots themselves respond to electric field gradients [118].

It has been shown that electric fields can slow down the growth of wood decaying fungi [119]. The exact mechanism is unknown, but wood has been shown to increase in electrical conductivity in the early stages of fungal colonisation [120].

Conclusions and Future Directions

The electrical conductivity of wood, as well as the range of physical bioelectric phenomena that it exhibits independently of membrane processes, is dependent on its moisture content. Piezoelectric and dielectric phenomena are conspicuous in dry wood and have practical applications. For instance, moisture meters employing electrical resistance or capacitance measurements are frequently used to assess the moisture content of timber, a critical parameter in drying processes, quality control, and decay risk. The piezoelectric phenomenon in wood has been harnessed to measure local mechanical forces in structural timber, while the application of piezoelectric energy harvesting by generating electricity is also gathering increased researcher attention. In contrast, in green wood and in living trees, electrical potentials are generated through various mechanisms involving ion transport, with sap flow being an example in vivo, while converse effects could be utilised in heating, drying, energy harvesting and protection of wood (Fig. 5).

Moreover, techniques such as electrical resistance tomography facilitate the detection of internal defects in standing trees, including decay, voids, and cracks. The modification of wood with conductive materials, such as metal nanoparticles, can yield electrically conductive wood-based composites suitable for applications in electromagnetic shielding, smart textiles, and energy storage devices such as supercapacitors. Additionally, the incorporation of conductive polymers or nanomaterials can significantly change the electrical properties of wood composites for targeted applications. These modified materials hold potential for use in electronics, bioengineering, and advanced construction materials (Fig. 5).

The possibility of interaction between physical and membrane-dependent potentials suggests that physical mechanisms could influence tree metabolism, although that possibility remains to be investigated. Electric potentials observed in green wood and in living trees, which arise from ion-transport mechanisms, need further exploration to elucidate the underlying charge separation processes. The phenomenon of electro-osmosis in wood and its potential applications in timber processing require thorough exploration, alongside anticipated advancements in the practical development of piezoelectric energy harvesting from wood. Also the precise mechanism responsible for the growth inhibition of wood-decaying fungi in electric fields remains poorly understood and deserves further research.

Key References

[3]• Li J-H, Fan L-F, Zhao D-J, Zhou Q, Yao J-P, Wang Z-Y, et al. Plant electrical signals: A multidisciplinary challenge. J Plant Physiol. 2021;261:153418.

This paper summarizes recent research on plant electrical signals from an interdisciplinary approach, mainly focused on biological functions of plants, which is required to improve the effective aggregation and utilization of plant electrical signal data.

[21]•• Nursultanov N, Heffernan W, Altaner C, Pang S. Anisotropic electrical conductivity of green timber within 20-90 °C temperature range. Wood Sci Technol. 2020;54:1181–96.

This work proposes plausible explanations for electrical conductivity variation in young wood and proposes that electrical conductivity variation between trees and wood zones might be attributed to ionic content change within sap, which has been corroborated by current research.

[37]•• Schenk HJ, Michaud JM, Mocko K, Espino S, Melendres T, Roth MR, et al. Lipids in xylem sap of woody plants across the angiosperm phylogeny. Plant J. 2021;105:1477–94. https://doi.org/10.1111/tpj.15125.

This work provides convincing proof for the presence of significant amounts of phospho- and galactolipids in xylem conduits, which can impact the surface charge of xylem cell walls and thus zeta potential.

[41]•• Ghildiyal V, Altaner C, Heffernan WJ. Managing ion concentration in sap to control drying collapse, permeability, and streaming potential in plantation-grown eucalyptus timber. Sustain Mater Technol. 2024;41:e01048, ISSN 2214–9937. https://doi.org/10.1016/j.susmat.2024.e01048.

This study found that the variation in streaming potential of Eucalyptus logs purged with KCl solutions was caused by electrokinetic effects in tiny pores. This phenomenon has potential implications for timber drying and improving the quality of plantation timber.

[47]•• Guha A, Bandyopadhyay S, Bakli C, Chakraborty S. How does the diurnal biological clock influence electrokinetics in a living plant? Physics of Fluids. 2024;36(5). https://doi.org/10.1063/5.0195088.

This paper unravelled the electrokinetics in response to the diurnal variations of a plant as the authors pointed out that the lag between sap flow and measured electrical potential could be explained by independent diurnal variation in the xylem pressure drop.

[60]• Ghildiyal V, Herel Rv, Heffernan B, Altaner C. The effect of Joule heating on collapse and water absorption of wood. Wood Mater Sci Eng. 2022;18:1228–36.

This study investigated the use of ohmic heating, also known as Joule heating, to enhance wood's drying quality. While this technology has previously been applied to the peeling of veneer and the application

of phytosanitation, this paper opens up new possibilities for the advancement of this technique in the wood processing industry.

[67]• Tosti F, Gennarelli G, Lantini L, Catapano I, Soldovieri F, Giannakis I, et al. The use of GPR and microwave tomography for the assessment of the internal structure of hollow trees. IEEE Trans Geosci Remote Sens. 2021;60:1–14.

This recent paper provided the efficacy of GPR enhanced by a microwave tomography inversion approach in the assessment of hollow trees in order to detect internal structure and decay.

[69]•• Wang Y, Gao R, Ma L, Kang K, Wang C, Guo Y, et al. Analysis of the application status of terahertz technology in forestry. Eur J Wood Wood Products. 2024:1–18.

This recent review summarized the application of Terhertz technology in forestry, in order to provide new solutions for scientific researchers in forestry sciences.

[72]•• Gebeyehu EK, Sui X, Adamu BF, Beyene KA, Tadesse MG. Cellulosic-bsed conductive hydrogels for electro-active tissues: a review summary. Gels. 2022;8. https://doi.org/10.3390/gels8030140.

This recent paper provides a current state-of-the-art related to the complete process of utilising cellulosic materials for manufactring conductive hydrogel for tissue engineering.

[75]•• Shan X, Wu J, Zhang X, Wang L, Yang J, Chen Z, et al. Wood for application in electrochemical energy storage devices. Cell Reports Phys Sci. 2021;2:100654. https://doi.org/10.1016/j.xcrp.2021.100654.

This paper provides the most recent research advances in the use of wood materials for electrochemical energy storage, primarily in supercapacitors and various types of batteries, and then discusses the current issues and future prospects for developing wood-based energy storage materials.

[83]•• Jarvis MC. Forces on and in the cell walls of living plants. Plant Physiol. 2023;194:8–14. https://doi.org/10.1093/plphys/kiad387.

The mechanical forces acting on plants, their transmission through various cell wall types, and the network of polymers that make up the cell wall were all examined in this paper, which reviewed recent developments in this field and also discussed piezoelectric signalling.

[91]• Makarem M, Nishiyama Y, Xin X, Durachko DM, Gu Y, Cosgrove DJ, et al. Distinguishing mesoscale polar order (unidirectional vs bidirectional) of cellulose microfibrils in plant cell walls using sum frequency generation spectroscopy. J Phys Chem B. 2020;124:8071–81. https://doi.org/10.1021/acs.jpcb.0c07076.

This paper demonstrated the antiparallel (bidirectional) arrangement of microfibrils within the cell wall, providing an explanation for the common lack of piezoelectric activity along the microfibril axis.

[106]•• Sun J, Guo H, Schädli GN, Tu K, Schär S, Schwarze FWMR, et al. Enhanced mechanical energy conversion with selectively decayed wood. Science Advances. 2021;7:eabd9138. https://doi.org/10.1126/sciadv.abd9138.

In order to effectively produce electricity from mechanical energy input, this paper offered a simple, nontoxic, economical, and environmentally friendly method of functionalizing wood. The capacity to generate a building's own electricity through a variety of indoor human activities creates new opportunities for the use of sustainable and renewable materials in the design of future buildings with higher energy efficiency.

[114]•• Moratto E, Sena G. The bioelectricity of plant-biotic interactions. Bioelectricity. 2023;5:47–54. https://doi.org/10.1089/bioe.2023.0001.

This recent review draws together current research on the responses of a range of organisms to electric fields, shaped by plants, in the atmosphere and the rhizosphere.

[115]• Sarkar D, Sun Y, Tayagui A, Adams R, Garrill A, Nock V. Microfluidic platform to study electric field based root targeting by pathogenic zoospores. 2022 IEEE 35th International Conference on Micro Electro Mechanical Systems Conference (MEMS): IEEE; 2022. p. 884–7.

This work describes the development and use of a microfluidic Lab-on-a-Chip platform for the investigation of pathogenic microorganisms' electrotactic movements. With this framework, researchers have a unique chance to evaluate to the electrotactic movements that may enable pathogens to find and invade host tissue.

Author Contributions V.G. conducted the literature search, drafted the initial manuscript, revised the manuscript and prepared figures; C.A. conceptualised the work, drafted and revised the manuscript and prepared figures; B.H. drafted and revised the manuscript; M.J. conducted the literature search, drafted and revised the manuscript and prepared

figures. All the authors have critically reviewed the manuscript and agreed to the published version.

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Declarations

Conflict of interest The authors declare no competing interests.

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