Bark: Its anatomy, function and diversity

Morris, Hugh; Jansen, Steven

Published in:
International Dendrology Society

Print publication: 05/07/2017

Document Version
Publisher's PDF, also known as Version of record

Bark

HUGH MORRIS and **STEVEN JANSEN** of Ulm University, Germany, discuss bark, its anatomy, function and diversity.

Introduction

Plants do not move, but remain *in situ*, with perhaps the exception of the walking palm *Socratea exhorrhiza*, where with the aid of stilt roots it can shift from the place of germination. Plants do not have a brain, an organ of soft nervous tissue located mostly inside the skull of vertebrates. This sounds like an obvious fact based on the appearance of a plant alone, but a lack of mobility may go some way towards an explanation. In fact, a species may only require a brain for controlled movement according to Daniel Wolpert, professor of Engineering at Oxford University. This theory was proposed from the Prof. Wolpert study by the phenomenon of the sea squirt, a water-dwelling invertebrate member of the Phylum Chordata, the classification that also houses fish, reptiles, birds and mammals, with the latter including humans. The sea squirt spends its early developmental life searching for a suitable place to attach itself, where once secured, it quickly devours its own brain. From that point onwards, the brain is not considered a requirement: the navigational work is done. Of course, vertebrates use their brains for far more than just movement; even a polar bear while in a slumber is registering myriad details such as temperature and small changes in light levels. So what does the interesting but unrelated fact about the sea squirt have to do with bark? Bark provides the protection or a kind of barrier to outside interferences, thus preserving the internal system of the tree, allowing continued optimum function.

Through natural selection, trees, the longest lived and largest organisms on our planet, have evolved to compensate for lack of movement by the development of a non-conductive tough, often rugged, outer skin referred to commonly as bark. To be scientifically accurate, what you see is only the dead portion of the outer bark, botanically referred to as the rhytidome, which replaces the epidermis and cortex cells of more juvenile growth, as observed in twigs. There are crucial differences: the outer bark is mostly comprised of a fat, suberin rich, dead tissue, called Borke in the German language (Borkr in Old Norse), while the inner bark is composed of mostly living cells referred to collectively as the phloem, a remarkable system that operates mainly in storage and transport of carbohydrates. Of interest is the derivation of the word 'Borke', as the German for birch (*Betula*) is Birke with the Gaelic for birch being Beithe, all possessing similar sounds. Furthermore, the old Sanskrit 'Bhurga' refers to 'a tree whose bark is used to write upon', in reference to birch. From this, it is safe to assume that the origin of bark is from birch.

The function and purpose of bark

The key functions of bark include: **protection of plant stems**, both through the

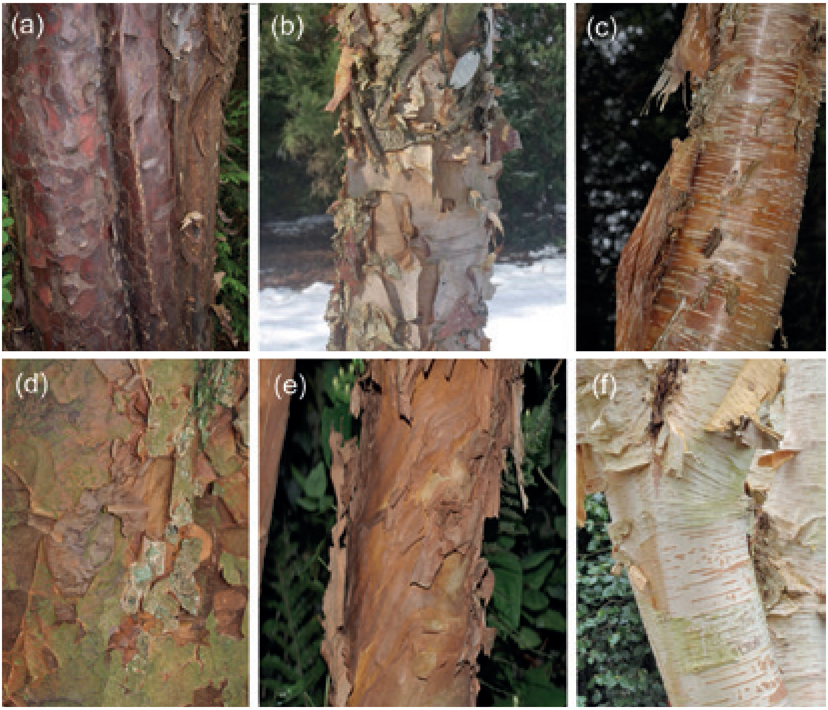


Figure 1 A range of tree species with spectacular barks, displaying many shades of colour as they exfoliate their outer layers to reveal new periderm forming underneath. The ecological reasons behind this phenomenon is not entirely known, though the ability of a tree to rid itself of fungal and bacterial agents is quite commonly speculated, while certainly the high flammability of such paper-thin, chemically-coated, outer layers in fire-prone areas is a strategy of many.

a. *Cupressus guadalupensis*, a native conifer of Mexico displaying light and dark red textures, where the outer peeling layers attract fire and release the seeds from the cones to recolonise the bare earth, now nutriment rich.

b. *Betula nigra* of North America has the densest, most multi-layered outer bark of any birch species, while in its youth, an unmistakable feature. The bark, when fallen, contains essential oils in varying concentrations that act to inhibit competition from neighbouring plants through its phytotoxic nature.

c. *Prunus maackii* 'Amber Beauty' with its wonderful amber bark and long horizontal white lenticels uniformly arranged between peels.

d. *Acer griseum* or commonly known as the paperbark maple was one of the greatest tree introductions to Kew Gardens and Great Britain in general during the Empire; introduced by the famous plant hunter Ernest Wilson mostly on account of its extraordinary bark of chestnut brown, orange-red hues.

e. *Fuchsia exocorticata* or the tree fuchsia is a native of New Zealand and a rarity in the British Isles and Ireland, where its thin red papery bark hangs in strips revealing a green periderm almost hidden underneath.

f. *Betula utilis*, a particularly stunning tree located in the grounds of the house of the late John Gallagher, Dorset, which was grown from seed collected by Roy Lancaster on the Himalayas at around 4,000 m ASL.

photographs © Hugh Morris

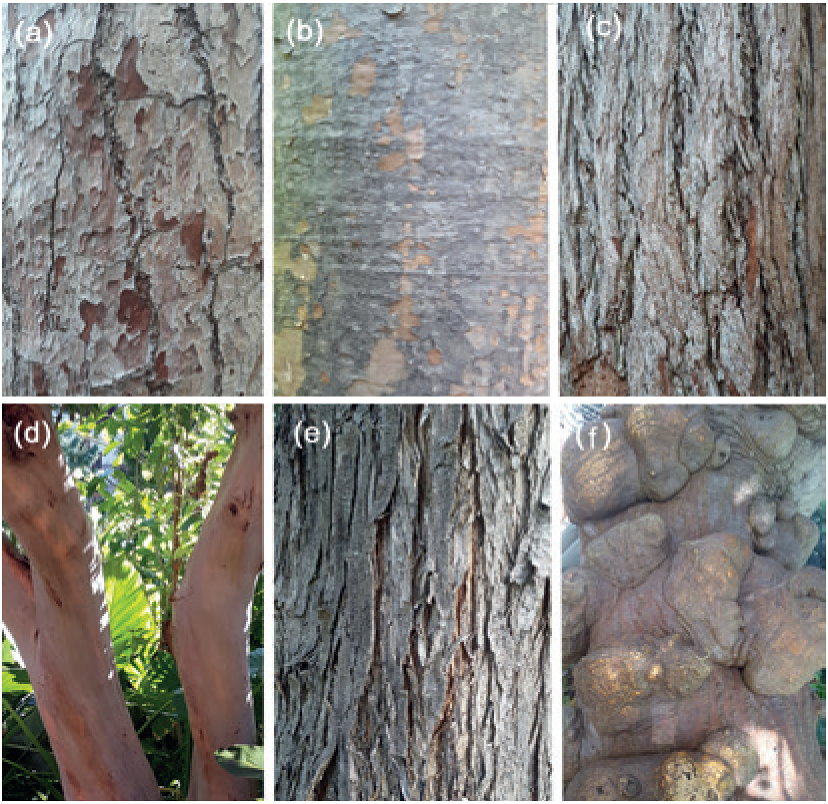


Figure 2 A range of subtropical trees with a diverse array of barks, all present on Tenerife Island, including La Hijuela del Botánico of La Orotava, with a range of native and introduced tree species.

a. *Pinus canariensis*, a native to the Canary Islands, with a plated bark typical of the species. Interestingly, while adapted to fire, the species has also evolved to sustain damage from rock throw via volcanic activity, where the high parenchyma levels of the inner bark and xylem results in faster wound closure.

b. *Agathis dammara*, a spectacular although exploited large conifer native to the Philippines and the source of copal from its inner bark, has an exfoliating rhytidome that is mottled, with a range of colours demonstrating that bark is as interesting in conifers as the flowering plants.

c. *Eucalyptus robusta* is part of a group referred to as the red mahoganies due to its thick red spongy bark and timber very untypical of the species.

d. *Arbutus canariensis* or commonly known as the Canary madrone, is an endemic to the Islands and boasts a very attractive red-pink peeling bark.

e. *Schinus terebinthifolius*, a member of the cashew family and known as the Brazilian pepper tree, has, in mature trees, a furrowed bark with brownish-grey strips. The inner bark houses antimicrobial chemicals that are toxic not just to bacteria and pathogenic fungi, but people also, where contact with the sap can cause a range of ailments.

f. *Erythrina americana* or commonly called the American coral tree often exhibits unusual growth abnormalities on the bark in old specimens, giving them a gnarled appearance; this particular example can be seen in the Botanic Gardens, Tenerife.

physical and chemical nature of the rhytidome, and the responsive activity of the parenchyma (living cells) located in the inner bark; **aeration**, where lenticels or pores, commonly seen on the bark of birch and cherry trees as horizontal protrusions with slit-like openings, in which gases can permeate through and from the stem; **water storage**, where the bark acts as an important source for both daily and seasonal water transport in the xylem; **photosynthesis**, as evidenced by the green bark of many tree species, which have the capacity to make their own food locally, harbouring carbon directly from the sunlight, for example in the snake-bark maple group (e.g. *Acer tegmentosum*) and acting as a hugely important microhabitat for various organisms, particularly in barks with crevasses, such as in *Quercus* species.

There is also a **mechanical purpose** to bark, as studied by a world leading authority on plant mechanics Karl Niklas of Cornell University. Professor Niklas states that bark provides a mechanical stiffness helping the tree to counteract bending forces from external stimuli, such as wind and snow. However, this mostly applies to young branches, where eventually the burden of mechanical support shifts to the wood of trees, scientifically known as the xylem. So, bark is multifunctional, with different functions being more or less prominent depending on the environment in which the species grows.

This article will focus primarily on the bark as a defence system after a brief background in bark evolution, diversity and anatomy. To understand how bark functions though, one must master the anatomy first. Plant anatomical terminology can be off-putting, even for the most ardent of plant enthusiasts, so a great deal of patience is needed as well as a penchant for difficult words; however, if one persists, it unlocks the key to an intimate understanding of the life of plants. It is also important to understand that bark is not an entity unto itself. It forms a morphological continuum with xylem (wood), which is developed to the interior of the cambium. The ray parenchyma act as a bridge between phloem and xylem, a living cell type appearing like the 'spokes of a wheel' and formed in a bifacial manner via the cambium.

The diversity of bark morphology due to selective pressures encountered by tree species is huge, and can provide a very important identification feature, particularly at the family level in the tropics, but also at the species level. A keen dendrologist from temperate regions of the world could identify with ease, Tibetan cherry (*Prunus serrula*), Chinese red birch (*Betula albosinensis* var. *septentrionalis*) (sometimes confused with forms of *Betula utilis*), paperbark maple (*Acer griseum*; figure 1), or species that may provide more of a challenge, such as the lacebark pine (*Pinus bungeana*) the rainbow eucalyptus (*Eucalyptus deglupta*), *Prunus maackii* 'Amber Beauty' (figure 1) and the shagbark hickory (*Carya ovata*).

Each tree has a designated name for its own type of bark, with common terms such as smooth (e.g. *Fagus* spp., *Ficus* spp.), shaggy, flaky, dappled, stringy, tessellated, rugose, rough, and so on. Such terms as well as being important for identification are strongly tied to ecological adaptation. For instance, the smooth barks of the lowland wet tropics repel climbing plants (lianas), while the oil containing exfoliating bark of many eucalypti encourages fire and is therefore easily ignited. Fire promotion in the latter, a common strategy among many tree species, is in conflict with our deeply ingrained views of life. The evolutionary concept of ecological succession (reproduction) presents itself as a ruthless priority over individual survival: the survival of the species takes precedence over the survival of the individual.

How bark evolved into the diversity we have today goes back to the transition of plants from water to land. Land plants had to develop a thin outer layer referred to as a cuticle to keep the internals from drying out. The plant's insides, once composed of parenchyma only (living cells with primary cell walls) like that of their aquatic algal ancestors, slowly evolved in line with the water-tight outer skin during the early Silurian (*ca.* 440 Mya). A robust internal system of narrow, dead, and chemically reinforced channels for conducting water gradually replaced parenchyma, and served to allow land plants to advance and radiate. Bark formed later during the Devonian period (earliest records from 400 Mya), alongside 'true' wood and the lignification of tracheids for long-distance water transport. With these new traits in place, plants could conquer the world above them (grow taller) as well as the world around them.

The sequence of tissues from the vascular cambium outwards begins with the phloem (inner bark), commonly referred to as bast owing to the presence of 'bast' fibres, which support the conductive tissues of the phloem. An example of a North American tree named after this tissue is the American basswood (*Tilia americana*), due to its economic importance for making thread for sewing, or a fine yarn for making bags and cordage. The outer bark, or collectively the periderm is made up of three distinct interconnected layers, with each deriving from the Greek word *phellos*, commonly referred to as cork. At its core is the phellogen (*Phel + gen*, 'to produce'), otherwise known as the cork cambium, a cellular active region that produces a layer or two of living cells to its interior, which mature into parenchyma (living at maturity), and termed the phelloderm. Produced to the exterior by the phellogen is the outermost layer, termed the phellem. The cork cells that make up phellem are dead, light in weight, and provide protection by way of insulation. Often visible on the phellem are the lenticels, small air channels through which gas can flow in and out. It was the Austrian plant anatomist Gottlieb Haberlandt who, in 1914, linked the lenticels with function by demonstrating that blocking them affected their gas exchange.

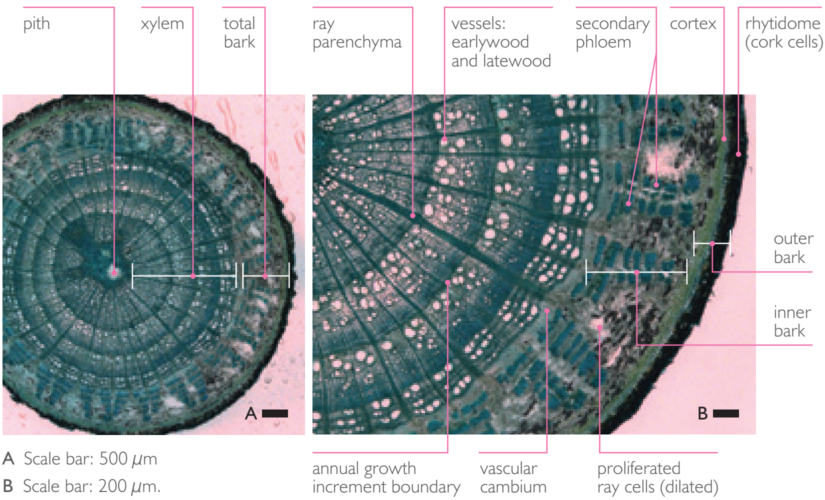
The general process by which bark is formed involves an intense pressure coming from xylem (wood) being built to the interior of the cambium layer (cell dividing zone). This pressure causes both the cambium and phloem to be pushed outwards and evidence of it can be seen when one witnesses photographs © Hugh Morris

Figure 3 Tree species with striking and unusual barks from around the world in the Botanic Gardens of Tenerife (Jardín de Aclimatación de la Orotava in Puerto De La Cruz, where the photos were taken) initially starting out as a hobby by King Carlos III of Spain during the Enlightenment.

a. *Aleurites moluccanus*, the candlenut tree of the spurge family showing uncharacteristic bumps along the trunk called burrs. Similar to warts on a hand, these peculiar benign outgrowths are caused by viruses or fungi and are generally of little harm to the tree.
b. *Ficus superba* is a strangler fig known as a hemi-epiphyte, with this specimen displaying flowering from the trunk, a phenomenon known as cauliflory. Cauliflory allows terrestrial animals to pollinate the flowers, giving such trees an adaptive advantage.
c. *Casimiroa edulis* or the white sapote of the citrus family is native to Central America. Very prominent creamy wart-like lenticels, which allow for gas exchange, can also be a nice identifying feature of a tree species.
d. *Erythrina poeppigiana* displaying a striated greyish bark with prominent thorn-like protuberances that are conical in shape
e. *Ceiba pubiflora*, a member of the mallow family, has a spectacular bark with green photo-synthetic bark and a strong defensive system in the form of sharp thorns. Although traces of rhyidome can be seen in mature specimens, the green parts are not rhytidome (dead), as only living cells can store chlorophyll, the green pigment responsible for capturing light.
f. *Hura crepitans*, also known as, owing to its large threatening woody thorns, the monkey no-climb tree. The tree is a native to tropical regions of Central and South America.

outer layers exfoliating in lateral or longitudinal papery peels, as in birch or the Killarney strawberry tree (*Arbutus unedo*) or in patches, as in sycamore maple (*Acer pseudoplatanus*) and London plane (*Platanus* × *hispanica*). To avoid complete rupture of the entire tree stem, growth must occur on the periphery of the plant in parallel sequence to the xylem. The establishment of a continuous cover of rhytidome is what keeps the lenticel channels functioning and the insects, fungi and bacteria from entering. However, a kink in the armour can lie with the lenticels. Similar to the brain-eating amoeba (*Naegleria fowleri*) entering your nostrils and infecting the brain, usually resulting in death, the lenticels, while allowing for gas exchange, also present opportunities for bacteria to enter and cause serious internal harm.

Selective pressures exerted on bark from the environment determines its appearance, its overall thickness, and the thickness ratio between outer and inner bark. As shown in a recent study by Julieta Rosell of the National Autonomous University of Mexico, some species have very thick outer bark



A Scale bar: 500 *μ*m
B Scale bar: 200 *μ*m.

Figure 4 Juvenile wood of *Asimina triloba* of the Annonaceae, the only ring-porous tree within the family, a feature found in temperate regions (large earlywood vessels followed by an abrupt decline in size of the latewood vessels). Due to its juvenility (some four years old), the cortex is still visible, a region of living parenchyma cells that store water and carbohydrates similarly to the pith, both regions being linked via the ray cells (also living parenchyma). Eventually the cortex region is destroyed and crushed against the outer suberised region composed of cork cells (dead at maturity). The inner bark here is particularly thick, especially when compared to the outer bark. This is likely to make a strong mechanical contribution until the xylem is of an age where it can take over the mechanical burden, and for water storage, where a wider inner bark can store a greater quantity. However, there is a third reason why the inner bark is thick: the pawpaw, as it is commonly known, stores chemicals in this region called acetogenins, which are powerful natural insecticides. Aside from insects, acetogenins have also proven to be unpalatable to a range of herbivores.

and thin inner bark (e.g. *Allocasuarina torulosa*; native to Queensland and New South Wales), while others show the opposite trend (e.g. *Eucalyptus punctata;* also native to Queenland and New South Wales). To understand this balance is pertinent to understanding what selective pressures are at play. For instance, a thick outer and thin inner bark shifts the balance in favour of a more passive kind of defence, as dead tissue cannot react against threats, but relies solely on its constitution — texture and chemical makeup.

On the other hand, a thick inner and thin outer bark suggests a more dynamic strategy, where the living cells of the phloem (inner bark) may play a greater role in defence by actively responding to the threat or / and in a greater capacity to store water.

A thick outer bark may be key to protection of inner tissues from fire or large vertebrates, such as mammals. A tree whose thick spongy bark you will all be aware of is that of the giant redwood *Sequoiadendron giganteum*, where in parks across the Northern Hemisphere, fist-like impressions circumvent the tree at breast height, giving the bark a glossy sheen! The redwoods can survive the most intense of fires through their often over a half metre thick fibrous bark (mostly rhytidome), where the flames can open up cones, releasing seeds en masse once the ground is suitably cooled. Thin smooth outer bark, often observed in tropical lowland trees where fires seldom occur, rely on the dynamic response from the living inner bark to seal wounds inflicted on the outer bark rapidly and prevent entrance of air / pathogens into the xylem, with the latter tissue found to be defensively fragile in a range of tropical species when compared to trees of more temperate origin. Since bark is the first line of defence, it makes sense to reinforce this area where possible, allowing the xylem to carry out its function in water transport unimpeded. Also, by keeping air out of the system, a function of the fat-rich outer bark, fungi are discouraged. This important group, which houses many important parasitic pathogens and saprotrophs (fungal decay types that live solely off of dead tissue) require oxygen to establish.

The inner bark, from a defence perspective, also differs considerably between conifers and angiosperms (the flowering plants), where crystal-containing cells (referred to as idioblasts) and specialised polyphenolic parenchyma cells (abbrev, PP cells) are found most predominantly in conifers, while laticifers (produces latex) are a common feature of many hardwood trees. The oxalate crystals of inner conifer bark (and a number of broadleaved trees) destroy the mouth parts of over-eager mammals or insects, while also acting as a toxin once broken down. However, an interesting exception may lie in a number of temperate deciduous broadleaved trees, where calcium oxalate crystals might not be a deterrent but rather the opposite. A recent idea is the calcium hypothesis, where grey squirrels gnaw at bark to release the calcium stored in the phloem in order to balance a calcium deficiency (Nichols et al., 2016), which might explain their erratic behaviour at times.

The crystal-bearing parenchyma cells and other specialised axial parenchyma of the secondary phloem work in unison, especially in cases where beetles are vectors for deadly pathogens, devastating entire conifer forests, such as in the case of the European spruce bark beetle (*Ips typographis*) harbouring the deadly fungal pathogen *Ceratocystis polonica* of Norway spruce (*Picea abies*). Here, the specialised parenchyma cells are triggered into a chemical defence by the fungus, where the cell's phenolic compounds deactivate fungal enzymes rendering them ineffective. *Ceratocystis* (different species) also causes oak wilt disease and canker stain of plane (*Platanus* spp.). Similar to the function of resin ducts in conifers, are the aerenchymatous (living and vessel-like with air cavities) latex cells of many tropical angiosperms. One such tree is the rubber tree *Hevea brasiliensis*, a species whose latex fuelled the economy of Manaus in the heart of the 'tall tree' Amazon rainforest for years, even affording it its own opera house during the Belle Époque, a token of the town's wealth at the time.

Application of knowledge

You may well ask why on earth all of this is important from a practical viewpoint. Well, knowledge of bark can help to inform your actions around trees that are under your supervision, particularly around young trees that have yet to develop a mature bark. Since the invention of mechanical tools and rotary machines, trees have never been more under threat, and ironically from people who might wonder why their newly planted young trees will not grace the landscape and great parks as their predecessors once did. Lacerations apparent at the base of so many young trees in urban parks, along streets, house gardens, and even places of education such as colleges and public arboreta, do not cause the death of the tree immediately; they linger stunted and unchanged in dimensions due to the reallocation of resources (carbohydrates) into tending the wounds instead of growth.

In this condition, they are also prone to a range of bacterial and fungal diseases owing to low energy levels and the creation of infection sites around the open wounds. Fungal target-shaped cankers are particularly deadly in young trees, where spore enter at the site of the damage. The open wounds coupled with the stress that ensues make the situation all-the-more precarious. Cankers are bark killing and can kill trees outright through girdling of the entire stem. They can also prevent complete healing, keeping wounds open to fresh re-establishment of fungi. Examples of fungal canker are *Nectria* spp. (on a range of hosts, including ash and pear), strumella canker (*Urnula craterium* on *Quercus* spp.) and *Eutypella* on maples.

Mature trees are a different matter, partly owing to the presence of heartwood, a substance which attracts a range of fungi that can be observed and identified through the presence of large fruiting bodies often seen around the root plate, at the base of the tree (figure 5), along the lower trunk, and


photograph © Hugh Morris

Figure 5 *Inonotus dryadeus* is a decay-causing fungus that is most commonly found on oak (in this case *Quercus petraea*) throughout Europe and is always positioned at or near the base of the trunk. The large basidiocarps or fruiting bodies are lumpy and irregular in appearance with a key feature being the formation of amber liquid droplets oozing from the surface when young. It can often be seen on oak trees growing alongside roadways and in built-up urban areas, as in the case with this example, where the wind-borne spores take advantage of open wounds caused by extensive and persistent damage to the roots. Its presence is of a serious concern regarding the stability of the infected tree, where the destruction of the roots and lower bole can result in a high likelihood of wind-throw.

seldom on large branches around old pruning wounds. Heartwood is the dead core of the tree and is generally rich is phenolic compounds, has a relatively low moisture content compared to the sapwood and is low in free oxygen, ideal for heart rot fungi, such as *Laetiporus sulphureus* (sulfur fungus; found on *Quercus* spp, *Robinia* spp. and *Taxus*). The fruiting body of the latter fungus appears through the bark only after advanced decay, indicating extensive damage. Other fungi of note are *Meripilus giganteus* (giant polypore) on beech and *Inonotus dryadeus* on oak (figure 5), both of which are very commonly found on urban park trees and along roadways and are linked with mechanical damage to roots.

Bark is a fascinating substance and is far from being fully understood. The range of functions associated with bark demonstrate its sheer complexity. It is also beautiful, through its many forms, textures and range of hues. Bark is the first line of defence against outside threats, and acts to protect the internal biological system, a combination of living and dead cells that are interconnected through a three-dimensional continuum. We can make simple adjustments to protect bark in both young and older trees, and an understanding of bark—its anatomy and functions—is a good place to begin. Our current mistreatment of trees is deeply ingrained in our culture. The aesthetic appearance of a neat lawn takes precedence over the health of a tree, and this entrenched view will only change through education and a cultural shift. The father of modern arboriculture Dr Alex Shigo once said, 'Trees are alive; they live all year round, and not just in summer'. Once we begin to comprehend this and gradually adapt our way of thinking, protection will naturally follow.

Bibliography

Franceschi, V. R., Krokene P., Christiansen E., Krekling, T. (2005). Anatomical and chemical defenses of conifer bark against bark beetles and other pests. *New Phytologist* **167**: 353-375.

Haberlandt, G. (1884). Physiologische Pflanzenanatomie. Leipzig : W.Engelmann.

Lendzian, K. J. (2006). Survival strategies of plants during secondary growth: barrier properties of phellems and lenticels towards water, oxygen, and carbon dioxide. *Journal of Experimental Botany* **57**: 2535-2546.

Morris, H., Brodersen, C., Schwarze, F. W. M. R., Jansen, S. (2016). The parenchyma of secondary xylem and its critical role in tree defense against fungal decay in relation to the CODIT model. *Frontiers in Plant Science* **7** (1665). doi.org/10.3389/fpls.2016.01665

Nichols, C. P., Drewe, J. A., Gill, R., Goode, N., Gregory, N. (2016). A novel causal mechanism for grey squirrel bark stripping: The Calcium Hypothesis. *Forest Ecology and Management* **367**: 12-20.

Niklas, K. J. (1992). Plant biomechanics: an engineering approach to plant form and function. University of Chicago press.

Niklas, K. J. (1999). The mechanical role of bark. *American Journal of Botany* **86**: 465–469.

Paine, C. E. T., Stahl, C., Courtois, E. A., Patiňo, S., Sarmiento, C., Baraloto, C. (2010). Functional explanations for variation in bark thickness in tropical rain forest trees. *Functional Ecology* **24**: 1202–1210.

Pfautsch, S., Renard, J., Tjoelker, M. G., Salih, A. (2015). Phloem as capacitor: radial transfer of water into xylem of tree stems occurs via symplastic transport in ray parenchyma. *Plant Physiology* **167**: 963–971.

Poorter, L., McNeil, A., Hurtado, V. H., Prins, H., Putz, J. (2014). Bark traits and life history strategies of tropical dry- and moist forest trees. *Functional Ecology* **28**: 232–242.

Prance, G. T., Prance, A. E. (1993). Bark: The formation, characteristics, and uses of bark around the world. Timber Press, Oregon; Royal Botanic Gardens, Kew, UK.

Richardson, S. J., Laughlin, D. C., Lawes, M. J., Holdaway, R. J., Wilmshurst, J. M., Wright, M., Curran, T. J., Bellingham, P. J., McGlone, M. S. (2015). Functional and environmental determinants of bark thickness in fire-free temperate rain forest communities. *American Journal of Botany* **102**: 1590–1598.

Romero, C., Bolker, B. M. (2008). Effects of stem anatomical and structural traits on responses to stem damage: an experimental study in the Bolivian Amazon. *Canadian Journal of Forest Research* **38**: 611–618.

Romero, C. (2014). Bark structure and functional ecology. In: Cunningham AB, Campbell BM, Luckert MK, eds. Bark: use, management, and commerce in Africa. New York, NY, USA: The New York Botanical Garden Press, 5–25.

Rosell, J. A., Olson, M. E. (2014). The evolution of bark mechanics and storage across habitats in a clade of tropical trees. *American Journal of Botany* **101**: 764–777.

Rosell, J. A., Gleason, S., Méndez-Alonzo, R., Chang, Y. & Westoby, M. (2014). Bark functional ecology: evidence for tradeoffs, functional coordination, and environment producing bark diversity. *New Phytologist* 201: 486–497.

Rosell, J. A. (2016). Bark thickness across the angiosperms: more than just fire. *New Phytologist* **211**: 90–102.

Schwarze, F. W. M. R., Engels, J., Mattheck, C. (2000). Fungal strategies of wood decay in trees. Heidelberg: Springer, Germany.

Srivastava, L. M. (1964). Anatomy, chemistry and physiology of bark. *International Review of Forestry Research* 1: 203–277.

Wolpert, D. (2011). The Real Reason for Brains. https://www.ted.com/talks/daniel_wolpert_the_real_reason_for_brains [Accessed 28 May 2017].