The multiple functions of tree bark

Laura Ducatez-Boyer¹*, Pauline Majourau ²*

Abstract
Bark provides many functions for trees. Bark plays an essential role in transporting photosynthetic products in plant tissues. Bark is also crucial to the mechanics of the stem. Furthermore, bark is involved in defense against herbivory, protects against fire, and provides insulation in cold conditions. Other functions related to storage of water, metabolic regulation, or wound healing contribute as well to the life of trees. These functions of the bark are linked to its complex structure. Bark structure is well known and is defined as the whole tissue beginning from the vascular cambium and running until the rhytidome. A high variability of bark tissues morphology exists between species, which may indicate its importance in tree processes and highlights its role in plant ecological strategies.

Keywords
Bark, bark function, tree physiology, tree mechanics, tree protection.

1 Université de Guyane, UMR EcoFoG, BP 316, F-97310 Kourou, French Guiana.
2 Université des Antilles, UMR EcoFoG, BP 316, F-97310 Kourou, French Guiana.
* Corresponding author: Laura.Ducatez-Boyer@ecofog.gf, Pauline.Majourau@ecofog.gf

Introduction
A tree is an organism at least 7 meters high (as defined by the Food and Agriculture Organization of the United nations (FAO)). All trees have stems and branches composed of internal wood tissue. This wood is covered by bark with a percentage of 9 to 15% of the stem volume (Harkin and Rowe, 1971). Other organisms have barks (such as vines), however in this paper we refer only to the bark of trees.

Tree barks is morphologically diverse, which could be the result of specific ecological strategies. This diversity might also be the result of adaptation to environmental conditions, fire resistance, or insect attacks. This morphological diversity and its causes remains poorly understood (Paine et al., 2010).

First, bark anatomy will be described. Following this we shall discuss the physiological, mechanical and protective functions of the bark. These roles of the bark are covered in three parts. (1) Physiological aspects of the bark. Notably, bark contributes essentially to sap distribution in the plant. (2) The mechanic function of the bark, as a support for the tree for example, is dealt with in the second part. (3) Finally, the protective function of the bark discussed in the third part allows us to comprehend how bark can avoid damage to the tree. The final section is dedicated to discussing the idea of tradeoffs between the multiple functions.

1 Bark: diversity, anatomy, nomenclature and composition

1.1 The diversity of barks

Commonly, bark is viewed as the dead, touchable surface of trees that covers the trunk. In botanic terms, bark is actually a complex living tissue made of several layers. Bark tissues display a diversity of appearances and textures, thickness and shapes (Figure 1).
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1.2 Woody stem anatomy

In order to explain bark variation in different species of trees, the anatomy of woody stems must be understood. Stems of a tree, trunk included, are composed of wood and bark. Both wood and bark are associations of several kinds of tissues. Two radial meristems, called cambium, produce the different tissues inside the stems of a tree (Leite & Pereira, 2017).

The most inner cambium, the vascular cambium, synthesizes two different tissues, one in the inside flank and one in the outside flank of the cambium which are respectively: the xylem (heart wood) and the secondary phloem. The outer cambium, the cork cambium, also called the phellogen, produces the phelloderm towards the interior and the phellem (also called suber or cork) towards the exterior of the cork cambium.

Altogether, phellem, phellogen and phelloderm constitute the periderm (Leite & Pereira, 2017). The phloem is divided into functional parts (non-collapsed phloem), and non-functional parts (collapsed phloem). The successive layers of dead periderms associated with non-functional phloem layers constitute the rhytidome (also called the outer bark) (Angyalossy et al., 2016; Leite & Pereira, 2017), this is the outermost layer of bark.

Bark which represents approximately 10 percent of the log volume (Harkin and Rowe, 1971) is constituted of multiple layers which are, successively from the inside to the outside of the stem: phloem, periderm and rhytidome (Figure 2). The bark is also defined by the International Association of Wood Anatomists (Angyalossy et al., 2016) as all tissues outside of the vascular cambium.

1.3 Bark structure and composition

The potential functions of bark may also partially been explained by the specific cellular arrangement of bark and the chemical components included in its cells. Details about three tissues are given.

The phellem, or cork, is a foam, made of dead parenchymatous cells with empty lumens. This tissue is mainly composed of very regularly closed arranged hexagonal prisms cells which represent 90 to 95% of the total volume of cork. These cells are the earlycork cells (Pereira, 2015). The tightly-packed organization of these cells forms a compact structure without any intercellular spaces. The apparent regularity of the cork’s structure made by the earlycork cells is broken off by the yearly growth of latecork cells. These few latecork cells, which are smaller prisms with a thicker cell wall than the earlycork cells, lead to the formation of seasonal rings.

Moreover, in function of the species, numerous and sometimes large lenticular channels can also be visible in the middle of cork tissue and interrupt its regularity (Leite & Pereira, 2017).
The phellem is also characterized by the two main components of its cell wall: suberin and lignin. Cell walls of the phellem contain 53% suberin. Suberin gives impermeability, resistance and compressibility properties to the cells. And Lignin, the other important component of the phellem cell wall represents 26% of the whole cork. Lignin is an aromatic polymer with a remarkable three-dimension molecular structure which confers strength to the cell wall (Pereira, 2007, 2015).

The phloem, another tissue of the bark, is composed of different specialized cells: the companion cells, the sieve-tube elements and the parenchyma cells. All these cells are interconnected through plasmodesmata and each of them carries out a distinctive function. The parenchyma cells produce nutritive resources. The companion cells are specialized parenchyma cells, necessary for the maintenance of the enucleate sieve elements. And the sieve-tube elements form the path for sap flow (Angyalossy et al., 2016; Rennie & Turgeon, 2009).

Phelloderm tissues are mostly composed of parenchymatous cells, these cells are rarely specialized and usually not suberized. These cells differ from cortical cells (phellem) by their radial alignment and may perform the storage of photosynthetic products (Angyalossy et al., 2016).

2 The role of bark in tree physiology

As we saw, bark has a complex structure. This structure permits many functions for tree functioning and we first interest to physiological benefits for tree from the bark. These functions are manifold and comprise the sap flow in the inner part of bark and the water storage in the outer part of bark. But bark also plays a role in the exchanges of water and gases, and permit sometimes photosynthesis.

2.1 Sap flow: sugar transport and tissue communication

Phloem is the path of circulation for phloem sap. This substance contains sugars, mainly saccharose (Zimmermann & Milburn, 1975), but also many ions, metabolites, RNAs, proteins and hormones (Dinant, 2008), transported from photosynthetic organs through all the living tissue. Sap is the essential energetic source for the plant’s metabolism. In the goal to measure it, Helfter, Shephard, Martínez-vilalta, Mencuccini, & Hand (2017) developed a non-invasive system allowing the direct detection of sap movements and velocity by a thermal method.

The presence of such molecules, like RNAs or proteins in phloem sap could explain its role in physiological regulation and responses (Ruiz-medrano, Xoconostle-cázares, & Lucas, 1999). For example, proteins such as jasmonic acid are essential for leaf recovery and are found in the sieve tubes (Zhang & Baldwin, 1997).

Phloem may allow essential communication between plant tissues in defense processes, growth mechanisms and probably other important pathways like environmental adaptation (Divol, Thibivilliers, Kusiai, & Dinant, 2005).

2.2 Water storage

Water storage capacity is defined as the amount of water that can be withdrawn from a compartment to another in case of water potential changes (Scholz et al., 2007). Bark wettability or bark water storage exists and allows water to be released to the rest of the tree when water needs increase. This water storage capacity (principally in outer parenchyma (Scholz et al., 2007) appears to be crucial to prevent drought damage and reduce loss of water from evapotranspiration (Levia & Herwitz, 2005).

This water storage is an important factor in plant–water relations, this mechanism differs significantly among tree species and is linked to bark morphology and branching architecture, and to the geocology of trees (Scholz et al., 2007). For example, increased bark thickness contributes significantly to greater water storage (Rosell et al., 2013).

2.3 Exchanges of water and gases

Lateral water and gas exchanges can occur in bark. Phellem tissues are involved in these transports.

The phellem is made up of multiple layers of dead cells and waxes, and provides the barrier for water and gas transfer (Lendzian, 2006) but in certain species, the phellem is interspersed with lenticels, aerenchymatous cork areas which are paths for the exchange of water vapor, oxygen, and carbon dioxide between the tree and the atmosphere (Lendzian, 2006). These lenticels are multicellular structures and functionally analogous to stomata permitting the transport of vital gasses (Lendzian, 2006). It is these lenticels which are responsible for the porosity of cork (Pereira 1996).

However, diffusion rates are related to lenticel density and size, which vary substantially among species. For example, in turkey cork oak, the lenticular channels are rare and not required for gas exchanges (Leite & Pereira, 2017; Şen, Miranda, Santos, Graça, & Pereira, 2010).
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The resistance to efflux may depend on bark thickness, but also to the degree to which bark tissues are impregnated with suberins, lignins and waxes (Lendzian, 2006). Suberins, which represent 53% of the cell wall of phellem can reduce the permeability of bark to water and gases (Leite & Pereira, 2017; Pereira, 2015). Furthermore, the periderm at the surface of the bark can reduce water evaporation and have a negative consequence on gas exchange between the tree and the atmosphere (Groh, Hübner, & Lendzian, 2002).

3  Stem mechanical support

The physiological function of the bark is important to ensure nutrition of the tree and it allows to the tree to synthesize its stems and leaves. The whole leaves and stems form the canopy which is a massive and heavy structure. Mechanical support is necessary to resist against rupture of its stems and trunk. Bark has an essential role in the mechanical support of the tree (C. Romero, 2013).

The different proportions of bark thickness are observed in old and young stems: more bark covers the trunk at the tips and consequently less wood is produced in these areas (K J Niklas, 1999; Rosell et al., 2014). In young stems, bark stiffness is associated to bark thickness. In the opposite of what can happen in the young stems, the contribution of bark to mechanical support in later tree development steadily decreases. In conclusion, it seems that the contribution of bark to branch stiffness is mainly related to bark quality (Rosell et al., 2014). However, along the ontogeny, bark’s contribution to mechanical support comes mostly from higher quantities of bark rather than tissue quality (Rosell et al., 2014).

Moreover, wood, of course, plays an important role in mechanical support, and it is not clear if both bark and wood participate equally to this function (Karl J. Niklas, 1992; Rosell et al., 2014). The contribution of wood may surpass the one of bark in the mechanical support of the tree (Rosell et al., 2014).

In the same time, particular environmental conditions may lead to favor bark contribution in the mechanical support. For example, in moister forest, where trees can be taller, the bark appears stiffer (Rosell et al., 2014). Or in the African Baobab, the secondary phloem occupies 75% of the bark volume (Kotina & Oskolski, 2017). In these two cases, mechanical role of the bark is important, but it is not expressed in the same way. In the moist forest, rigidity of the bark is prioritized. In the dry forest, the important volume of the bark which is involved in droughtness solutions, plays also an important role in the mechanical support.

Mechanical properties attributed to the bark are complex and difficult to understand. Further study should clarify these previous results.

4  Protective function of bark

4.1  Protective mechanisms and adaptations of bark

Many animals globally specialize in herbivory of trees (all parts, e.g. LIST), such as vertebrates and insects (principal beetles (Tavakilian, Berkov, Meurer-Grimles, & Mori, 1997)), which significantly impact tree health (Paine et al., 2010).

The bark is first to be impacted and thereby has an important role to play in protecting the entire tree. More specifically, given that the cutinized epidermis or suberized periderms of trees are the first tissues that potential pathogens and predators encounter (Kolattukudy and Koller 1983), and given that the majority of tree species can live for centuries, the protection bark is effective (Biggs, 1992).

Trees adapt to tolerate the kinds of pressures and damage to which they are habitually exposed. The adaptations can be morphologic (such as spines (Campbell, 1986; Cooper & Ginnett, 1998), metabolic (such as secretions (Langenheim 2003), or toxic secondary compounds (Coley, Bryant, & F. Stuart Chapin, 1985; Reichardt et al., 1990)), or behavioral (establishment of relationships with herbivore-repelling ants (Janzen, 1973)) (from Romero & Bolker, 2008).

Most pathogens are unable to directly penetrate the corky suberized tissues of most outer bark (such as phellem which have 53% suberinised cell walls) and rhytidome. These outer layers represent defensive barriers to pathogen ingress (Biggs, 1992) and allow the inner tissues of the tree to be resistant to acid among other things (Leite & Pereira, 2017; Pereira, 2015).

Another well studied bark function is protection against fire damage. According to Brando, Nepstad, & Balch (2012), bark resistance to fire damage can be understood according to two major parameters: the heat transfer rates (which is the reverse of cambium insulation) and the density of bark and wood. These two parameters are influenced by tree size, bark thickness and water storage.

Moreover, phellem is very durable, it is flexible without fracturing under compression (Pereira, 2007). This property is important to avoid trunk damage from impacts such as from other trees.

4.2  Bark self-repair mechanisms

In contrast with leaves, tree stems need to persist and recover after damage. The sensitivity to damage varies considerably among tree species. Once damaged, the rate at which bark grows to close the wound varies widely between trees (Claudia Romero & Bolker, 2008).
The ability of parenchyma cells to recover is linked to the capacity of cells surrounding wounds to become meristematic (Claudia Romero & Bolker, 2008; Zimmerman & Brown, 1971). Rays also play a role in wound phellogen healing (Miller and Barnett 1983). The ability of bark to heal itself is often a trade-off between speed and efficiency. For example, Chorisia speciosa closes bark wounds rapidly, and this speed compensates for partial inefficient decay control. By contrast, Pseudodolmedia laevis closes wounds slowly, but compensates with efficient defenses against decay. The relationship between anatomical and/or structural traits and damage response variables reveals that species with favorable traits for rapid wound closure (e.g., widely dilating rays) have traits that favor xylem decay spread (e.g., low wood density) (Claudia Romero & Bolker, 2008).

Discussion and conclusion:
trade-offs of functions in bark

We saw that bark has a complex internal structure, with an important variability across species, reflecting the manifold functions of barks. The multiple functions we have mentioned are mostly studied using functional traits (barks functions being often more difficult to measure) such as bark density or thickness which permit to describe the bark diversity observed about structure, morphology, anatomy and physiology. And this is with these traits that we try to explain the huge functional diversity of bark (Rosell et al., 2013).

Figure 3 - Trade-offs between two functional traits (bark density and bark thickness), and some functions associated with bark (in blue). Arrows indicate enhancing or not of the traits and functions between them (complete arrow: positive link; dash dot: negative links). The link between water storage and photosynthesis (1) is due to the requirement for water stock in cells to realize photosynthesis; and the link between water storage and mechanics (2) is a physical relationship and this is a trade-off often found in wood between stiff walls (for mechanics) and open cells lumina (for water storage) (Inspired from Rosell, Olson, & Aguivre-hern, 2012).

The maximum of capacity for each bark function is never observed in the same individual tree. In one tree, some functions are expressed to their maximum capacity, some functions are neglected, and some have a medium expression. The priority of the tree leads to these trade-offs. Consequently, trade-offs and functional coordination are common in bark, and depend on environment conditions and constraints.

In order to enhance our understanding of bark functions and the variations observed in bark morphology and physiology, we should adopt a systematic approach. The study of one functional trait must be correlated with the simultaneous study of other functions. Further study is required which analyses one function in relation with several different functional traits. These overarching studies should enable us to have a better view of the trade-offs made by trees in function of environmental pressure, herbivory and other influencing factors. These kind of study, rarely made nowadays except by Rosell (Rosell, 2016; Rosell et al., 2013) could permit us to have a better understanding about the influence of morphology and anatomy on the operation of, and the functions performed by, bark.

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References


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Table I - Several denominations of bark. The different names used in the document are listed in the first column. The respective correspondences of these names with other English terms, but also with French terms are reviewed in the second and third column.