Project: Partnership for the development of training standards for tree assessors in Central and Eastern Europe
PROJECT NUMBER – 2019-1-PL01-KA202-065670

TREE ASSESSOR

Elementary tree biology, ecology and biomechanics

A manual for Tree Assessors and Arborists

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Author: Piotr Tyszko-Chmielowiec
Photos: Jakub Józefczuk, Piotr Tyszko-Chmielowiec (PTCh)
Graphic design: Paulina Sanecka
Editor of the series: Beata Pachnowska
Grapghic design for series: Marta Płonka

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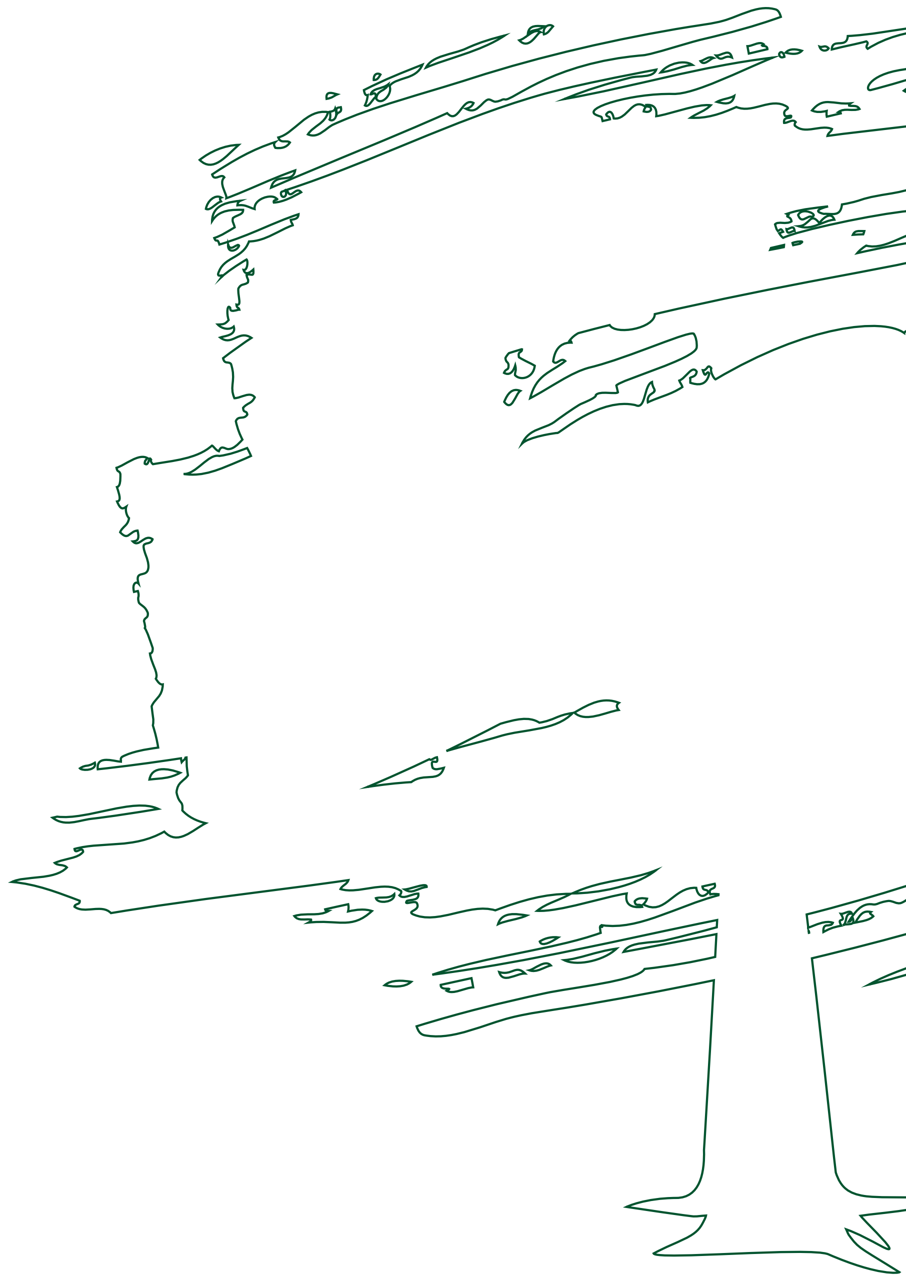

TREE
ASSESSOR

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Introduction

This manual is intended to be used by students of tree assessment and arboriculture, and those professionals who wish to deepen their understanding of trees. The tree science has made remarkable progress over last quarter of century, even though it still is lagging behind the knowledge about vertebrates (no surprise, as Homo sapiens is one of them). New scientific facts about plants, including trees, percolate not only to professionals, but also to the general public. Peter Wohlleben, a German author and forester („The Hidden Life of Trees" and other titles, 2016, 1019), was first to portray trees as beings which are, in many respects, like us. This helped him to reach not only readers' minds, but also hearts, and to awaken many to become friends with trees (even if some of Wohlleben's interpretations may seem a bit far-fetched). Another popular author to be recommended is Stefano Mancuso, a plant physiologist who personally performed many of the experiments that he reported on in „Brilliant Green: The Surprising History and Science of Plant Intelligence" (he calls his field „plant neurobiology", see below for explanation). I also appreciate the book „In Praise of Plants" (2002) written over two decades ago by professor Francis Hallé, an expert on tropical forests (French title „Éloge de la Plante, pour une Nouvelle Biologie"). Hallé explains the nature of being a plant through contrasting it with animals. Last, not least, it is necessary to mention Alex Shigo, a US forester and scientist, who could be arguably called a Copernicus of arboriculture (see below for substantiation of this judgement).

I have avoided referencing specialist research journals that are not easily accessible and not always transparent for an unprepared reader. The popular sources, including those from Internet, were verified and commented on, if needed. If searching the Internet, one needs to exercise criticism and look for sources that are supported by renowned scholars and scientific institutions.

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The text consists of three parts, different in style. In the first part, I attempt to subjectively explain „What does it mean to be a tree?". In the second part, I systematically review „The structure and function of a tree", focusing on these aspects that are relevant to tree assessment and care. The third part is subjective again – I discuss „Trees as a social being". I admit that some of my conclusions and generalisations may not find (yet) confirmation in hard data, however, they can be deduced from general knowledge and observations of practitioners.

I am indebted to reviewers of the draft. Dr. Urszula Zajączkowska of Warsaw University of Life Sciences helped to weed out some errors and mobilised me to give the text a more disciplined structure. We still remain at variance as to whether a professional manual should contain general comments on the nature of trees that go beyond science based on hard data. I greatly appreciate insightful comments by Beata Pachnowska and Julia Kończak to the Polish version and by John Parker to the English version.

Piotr Tyszko-Chmielowiec, Ph.D.
Photo by Arkadiusz Wierzba

I.

What does it mean to be a tree?

Are trees like us? Or entirely different?

Maybe both? In the first chapter, I will attempt to grasp the nature of trees, bringing up similarities or differences where applicable. This approach helps us to illustrate aspects that are relevant to tree assessment and care.

Since Aristotle, people have tended to consider plants as inferior forms of life (Mancuso i Viola 2017). We cannot see them communicating, we do not notice organs of movement and senses. Aren't animals, with humans at the top, more perfect, with their abilities to move, communicate, co-operate, conduct social life? And then the paramount of evolution comes: the central nervous system – plants have no brains. Additionally, animals – to whom we belong – evoke in us a sense of affinity and solidarity easier than plants, who are so distinct, so different and so harder to understand.

However, plants are not a kind of lesser cousins of animals. They have existed on the Earth for longer than animals have. Without photosynthesis, the atmosphere that makes the Planet liveable would not have been created. As recent research findings confirm, plants are functionally as perfect as we are. They have a wide palette of senses and conduct complex social lives (Mancuso 2017, Wohlleben 2016). The earliest trees were found to live on Earth 380 million years ago. It is hardly possible that organisms who are phylogenetically so old (and keep prospering today) could be „inferior". For trees are perfectly adapted to sedentary style of life – so different from our mobility.

Trees are special plants – for their longevity and huge dimensions. Most species live for between several decades and several centuries and can grow to become up to several dozen meters tall. Record breakers grow over 100 meters and live for thousands of years. The oldest trees that conserve their original form are the bristlecone pines growing in White Mountains in Southwest United States. However, if we account for trees that regenerated vegetatively, then a quacking aspen grove in Rocky Mountains holds the record. It has been some 80 thousand years since the first tree germinated. Over that period, the aspens (*Populus tremuloides*) kept sprouting from roots of older trees, growing, maturing, giving "birth" to new vegetative offspring and then dying. The grove, or maybe one tree, covers 43 ha and weighs 6 600 tons, which is 33 times the mass of the biggest animal – the blue whale (Wikipedia: Pando (tree) [1]). In this game, the oldest tree of Europe is a Norway spruce named The Old Tjikko, growing in Sweden and regenerating vegetatively since the end of the Ice Age – that is 11 thousand years (Wohlleben 2019, Wikipedia: Old Tjikko [2]). Needless to say, pace of their life is much slower than ours and strictly follows the rhythm of seasons (where they occur).

Achieving such dimensions was made possible by the sedentary lifestyle, which in turn follows from autotrophy. Tree's food is sunlight, carbon dioxide, and water. As the first two of them are ubiquitous, trees grow wherever liquid water is available, at least part of the year. To maximise absorption of light, a tree needs possibly large leaf area, preferably elevated on a high trunk above competing neighbours. For effective absorption of water, an extensive root system is needed. Can we imagine putting down roots every day in a new spot? This is difficult even for humans (not literally, of course).

The sedentary lifestyle has many consequences, for example, it makes it impossible to escape predators (we call them herbivores – another animal-centric bias).

This challenge is addressed mainly in two ways. First, a tree **produces substances that discourage consumers of leaves or bark**. Unless they are constantly present in the tissues, the tree launches their generation when an attack is perceived or when other trees notify it of the imminent danger via air, root grafts, or mycorrhizal network. The latter network was named by a Canadian researcher Suzanne Simard the wood-wide-web (WWW, see Part III). There are many interesting materials on the Internet, including TED lectures by Dr. Simard and a concise interview with her (Simard and Toomey 2016).

Second, **trees have evolved a considerable (but not unlimited) tolerance to the loss of parts of their body.** The champions in this sport are grasses, who hide their growing parts in soil, out of reach of herbivores. Trees also have learned to endure damage, due to **colonial structure** – meaning that they are composed of partly independent modules. After loss of a part (a limb or a root), the remaining body can continue performing all functions. Animals demonstrate unitary structure, meaning that every organ has its own function and is basically irreplaceable. Another adaptation of trees to sustaining damage is presence of flexible energy reserves. They make it possible to restore body parts lost to herbivory or wind and to heal wounds. These reserves are by no means unlimited and in trees growing under adverse conditions or otherwise stressed (like in urban trees), they are depleted.

1. https://en.wikipedia.org/wiki/Pando_(tree), 10.05.2021
2. https://en.wikipedia.org/wiki/Old_Tjikko, 10.05.2021

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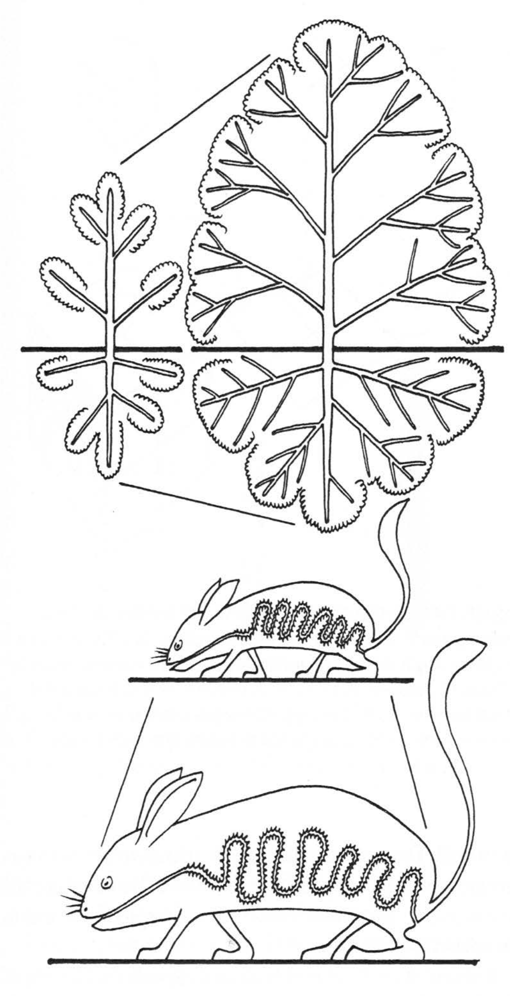

Fig. 1. The drawing by Francis Hallé (2002) presents modularity of tree growth in contrast with unitarity of animal growth. It also points out that food-absorbing surfaces in most animals are hidden inside their bodies, while in trees and other plants they are exposed outside. This follows from the obvious fact that plants are immersed in their food – sunlight and carbon dioxide.

Modularity/coloniality/segmentality demonstrates itself over whole ontogeny (development of an individual) of a tree (Fig. 1.). While a human is born as a miniature of an adult, a germinating tree expresses certain pattern of growth, then being replicated through decades, centuries, maybe millennia of tree's life. Humans grow in their entire bodies, every organ increases in size. In trees, growth happens only in specialised tissues – meristems. They are located in tips of shoots and roots (elongation) and as a cylinder under the bark of shoots and roots (lateral increment). That is why the hook that the grandfather drove into a cherry trunk to hang a hammock is still at the same height, even, if it became overgrown by wood.

Proliferation of trees can be effected in both generative and vegetative ways. Some individuals are monoecious, meaning that male and female flowers are born on one tree (as in beech or birch), others are dioecious – individuals are either male or female (as in poplars, yew, gingko). Some species, as the common ash, can become monoecious or dioecious, and even are able to change sex during their lifetime. Pollination is

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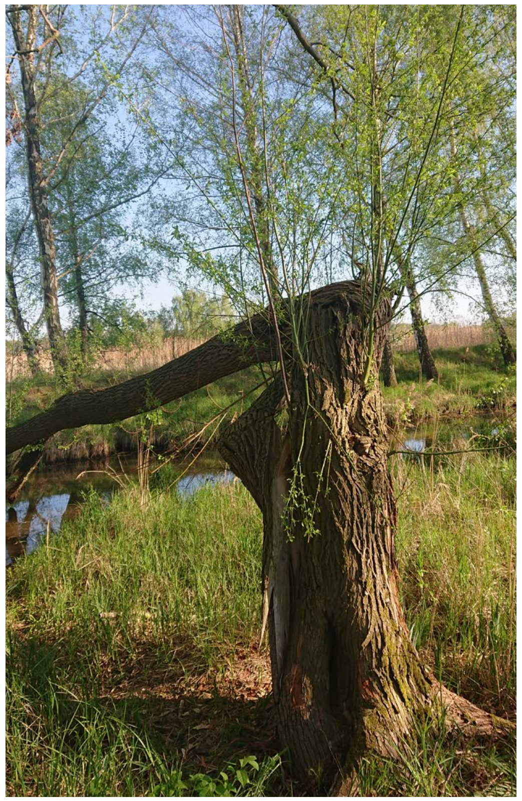
effected either by wind (e.g. pines, poplars) or by animals (e.g. willows, apples).

Poplars and willows are especially capable of vegetative proliferation. For example, the former can create whole groves from root sprouts, while the latter can put down roots from broken branches and grow new individuals from them. Willows, not being resistant to wood decay by fungi, often lose their branches and trunks due to wind damage (Fig. 2, 3). Unabashed by the loss, they sprout profusely from the damaged parts and keep growing as natural pollards. Some broken limbs resting on ground can even put down roots, thus initiating a new tree. Such capabilities allow some trees to become practically immortal (see also chapter III.2).

Fig. 2 & 3. Naturally pollarded willows: after decayed trunk failed, adventitious branches took over the role of the lost crowns. (PTCh)



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II.

The structure and function of a tree

1. HOW DOES A TREE WORK?

CROWN AND LEAVES

The tree crown is a sugar "factory", composed of countless leaves – bioreactors, converting the energy of sunlight into the energy of chemical bounds (Fig. 4.). In the process of photosynthesis, molecules of glucose are made of carbon dioxide from the air and water from the soil (via roots, see also the Box 1. "Products of photosynthesis"). The oxygen contained in water is discarded into the air as a by-product of photosynthesis.

A leaf of a land plant is protected from excessive loss of water by epidermis (an impregnated layer of cells). The lower side of the leaf is dotted by small openings, called stomata, that make gas exchange possible. A stoma can be opened and closed, when needed, thanks to action by neighbouring cells. It stays shut in the night and under water stress, e.g. on a hot day. Land plants grow mainly during the night, when closed stomata allow to generate adequate pressure in young green tissues.

The interior of a typical leaf is filled with cells containing chlorophyll, the green pigment that captures the sunlight energy to drive carbon dioxide assimilation. They are loosely packed to allow for good contact with the air, allowing efficient gas exchange through cell membranes. Carbon dioxides diffuses into the cell, while oxygen and water vapour moves outside (see the box "Role of water in tree's life"). At night, when the plant gets energy from respiration only, these directions are reversed.

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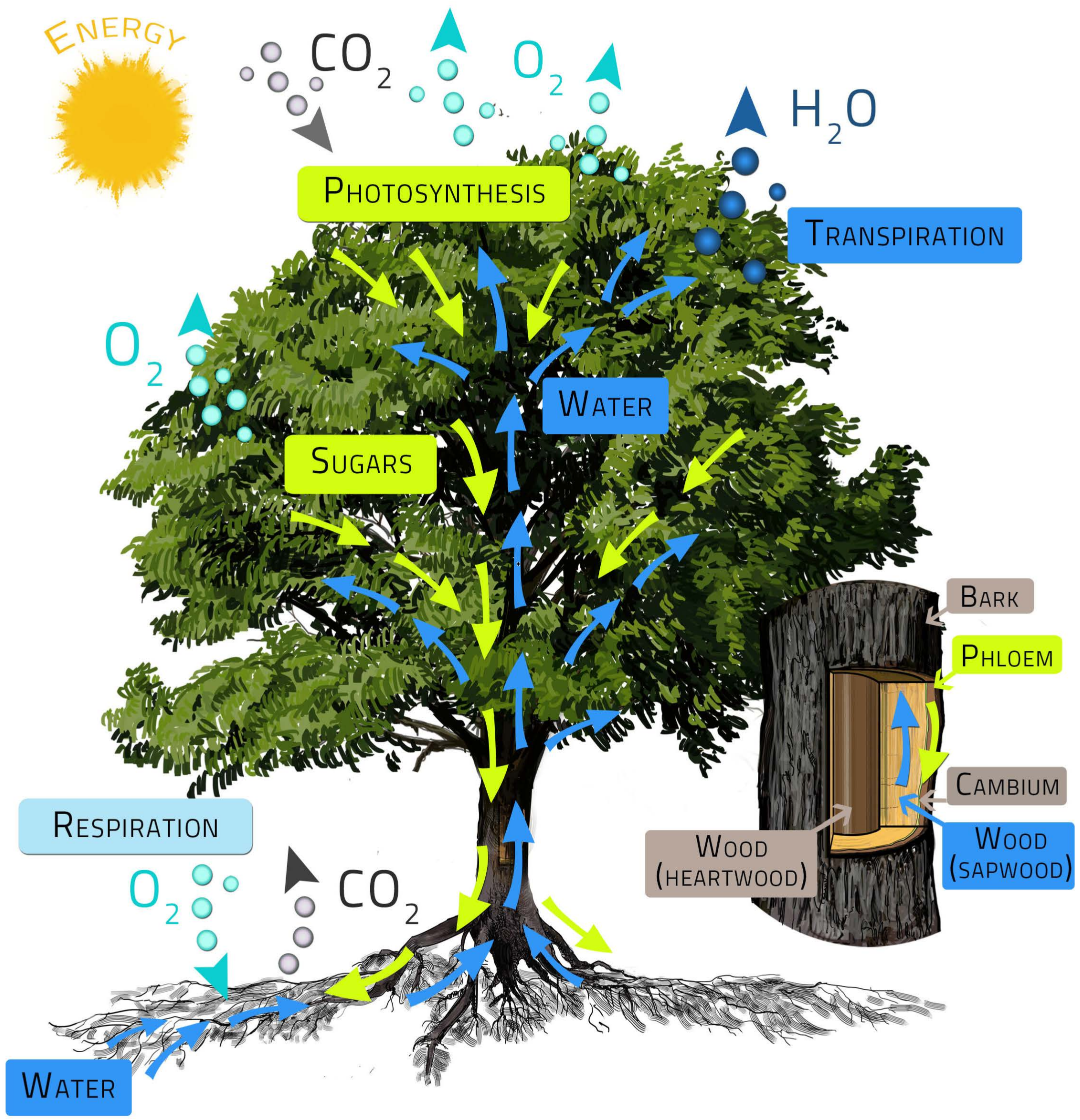

Fig. 4. Movements of water, energy, and elements in a tree.
Drawing by Jakub Józefczuk

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Box 1.

PRODUCTS OF PHOTOSYNTHESIS

The glucose molecules are used by the plant to build all other needed compounds, in particular:

SUGARS

delivering energy to other parts of the body, particularly saccharose (used by humans to sweeten coffee and tea);

POLYSACCHARIDES

storing energy in the trunk, branches, roots and seeds – such as starch;

CONSTRUCTION POLYSACCHARIDES

cellulose and hemicellulose, that reinforce cell walls;

LIGNIN

serving as filling of lignified cell walls in wood;

LIPIDS (FATS) AND PROTEINS

building blocks of cell membranes and intracellular structures;

ENZYMES

proteins that run cell metabolism

ENERGY RESERVES IN SEEDS

sugars, polysaccharides, proteins or fats

SUBSTANCES CARRYING INFORMATION

to enable the plant to communicate within its body and with other individuals – hormones and pheromones

DEFENCE SUBSTANCES

including phenolic compounds and resins serving to control spread of decay caused by fungi;

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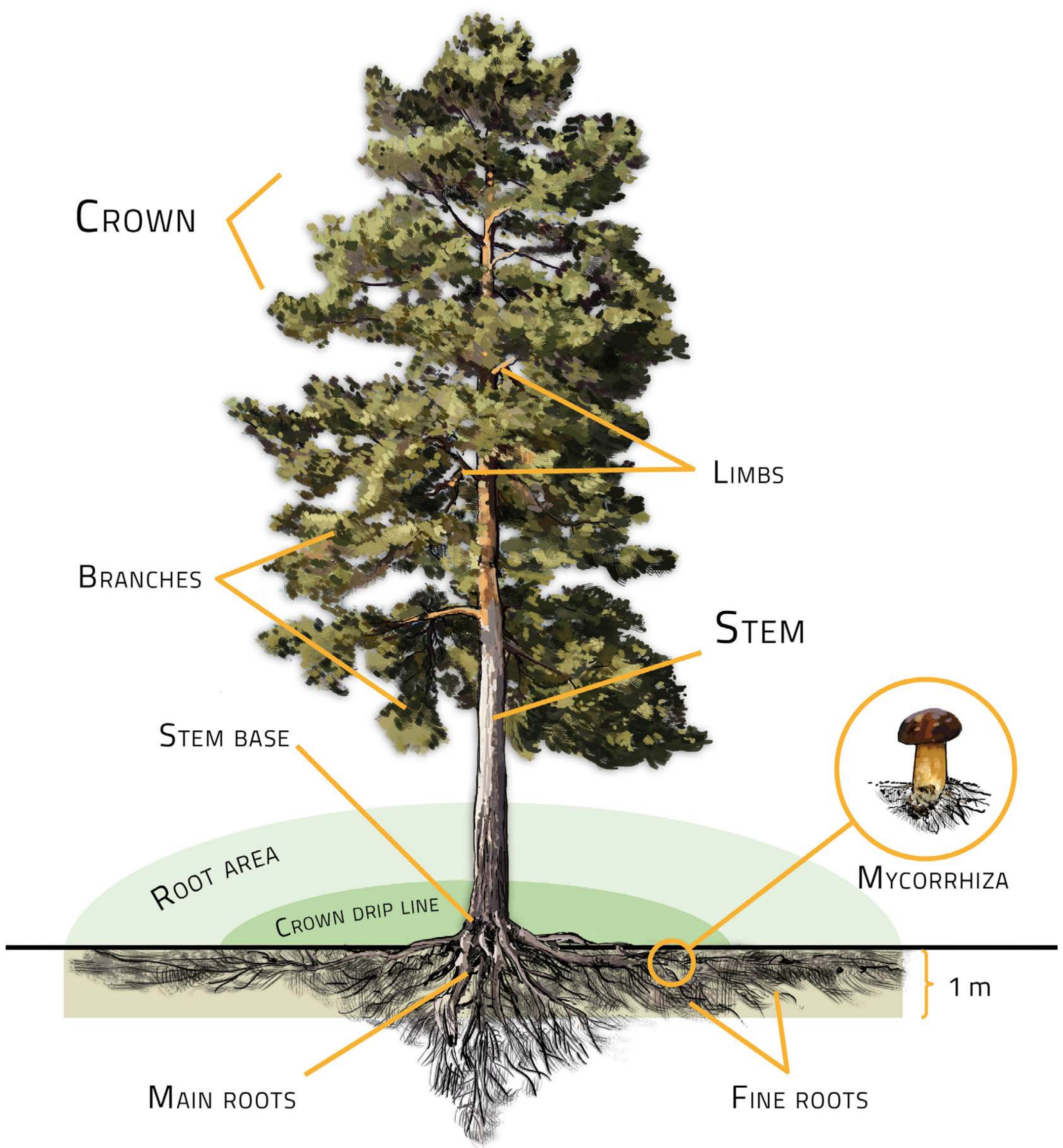

Fig. 5. Parts of a tree in the environment.
Drawing by Jakub Józefczuk

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TRUNK

The trunk supports the crown and assures a good position in the race for light. Importantly, it is a pipeline that supplies water from roots to leaves and photosynthates from leaves to roots. These currents also carry with them hormones and bioelectric impulses to assure communication between parts of the tree and coordination of growth.

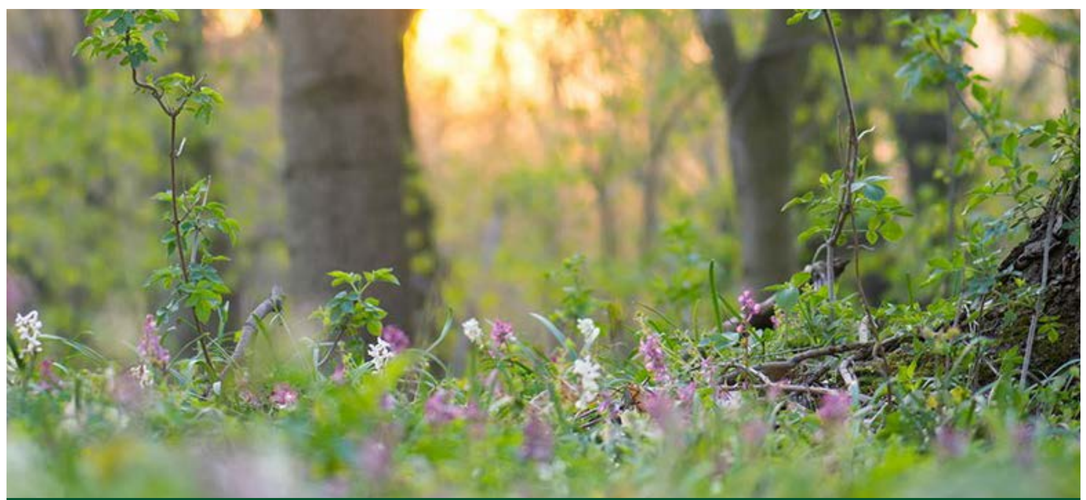
ROOTS AND MYCORRHIZA

Roots anchor the tree in the ground and provide water to its crown (Box. 2.). Their food are photosynthates produced in leaves and processed in roots through respiration, using oxygen from soil air. Roots generally occupy shallow layers of soils and most of their mass is concentrated above the depth of several dozen centimetres (Fig. 5.). This is the layer where precipitation water and air are easier available. The soil air contains oxygen and nitrogen, the latter assimilated by trees capable of that, thanks to symbiosis with bacteria (such as alder and robinia). Some trees grow deeper sinker roots, reaching the water table. Shapes of root systems depend on soil conditions, species and individual features. The central root, if present, later disappears when the tree reaches maturity (see below). In a freely growing tree, the root system reaches several times the crown radius. In urban trees, the shape of the root system is unpredictable, due to heterogeneity of the soil and abundance of artefacts.

MYCORRHIZA AND SOIL MICROORGANISMS

The fine roots take up water through root hairs, minute and short-lived structures protruding not far from the tip. The fine roots constantly grow and die off. To improve water supply, trees and other plants employ mycorrhizal fungi. **Mycorrhiza** improves water and nutrient uptake efficiency, as fungal hyphae are much finer than the finest roots and can penetrate much smaller soil pores. The hyphae surround and penetrate fine roots to make a more efficient connection. In addition to supplying water with dissolved minerals, mycorrhizal fungi serve trees as information and distribution network. Via the underground network of roots and fungal hyphae, photosynthates and molecules carrying information, are being sent to other trees, particularly to progeny (see below).

One tree can have several mycorrhizal partners at the same time, and it is possible for old alliances to be dissolved and new ones established. Both trees and fungi have been found to bargain with their partners for a better deal. Mycorrhizal services are not for free: some 20-30% of whole photosynthetic production of a tree is allocated to the fungal partners and other soil microorganisms. The tree supports also soil bacteria that are crucial in bedrock weathering and releasing biogenes.



Box 2.

THE ROLE OF WATER IN TREE'S LIFE

it is multifaceted and is not limited to being a substrate in photosynthesis:

Water is a **medium transporting** dissolved nutrients – elements necessary for sustaining metabolism and synthesis of diverse compounds, such as nitrogen, potassium, phosphorus, calcium, sulphur, and magnesium – the latter being a key component of chlorophyll.

Water serves as a **coolant**, as it transpires through stomata and evaporates from leaf epidermis surface, while absorbing heat in this process. This gives a tree the cooling power of several big air conditioners, although trees do not move heat from one place to another, as AC does. They convert it into energy powering the water cycling in atmosphere and make it come back as precipitation.

Water is a **construction material** for plants: kept under pressure, it maintains rigidity and allows for expansion of nonlignified shoots: leaves, shoot and root tips. Green parts of plants grow mostly at night, when stomata are closed and the plant is able to generate adequate pressure to allow for expansion of cells.

Intense loss of water in transpiration can be viewed as a cost of gaining carbon dioxide. In order to absorb the latter, stomata must be open, to allow for contact of the air with photosynthesising cells in leaf's interior. Meanwhile, water vaporises from their surface and transpires through stomata. This affects turgor (pressure) in the leaf. If water loss is faster than supply from the roots, stomata close and transpiration ceases – but photosynthesis stops as well, due to lack of carbon dioxide.

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2. TREE ANATOMY

The drawing below (Fig. 6) presents a cross-section of a tree trunk or a branch:

BARK

the most obvious role of bark is to protect the trunk, branches and roots. Cork, the outermost layer of bark, consists of non-living cells, and is basically impermeable to water and air. The underlying meristem – phellogen or cork cambium – produces a new layer of cells every year: cork on the outside and phelloderm on the inside. Cork, phellogen and phelloderm constitute periderm, while periderm and phloem (see below) constitute bark, as botanists define it. In common usage, the term 'bark' may be narrowed down to periderm.

As the trunk thickens, external, older layers of the bark (born when the trunk was thinner) need either to stretch, crack, or peel off. In beech, a thin bark stretches, covering the trunk with a smooth, silver coating. In oaks and willows, the old bark cracks and stays in ridges. In sycamore and plane, the old bark is shed in smaller or larger flakes, uncovering brighter young bark.

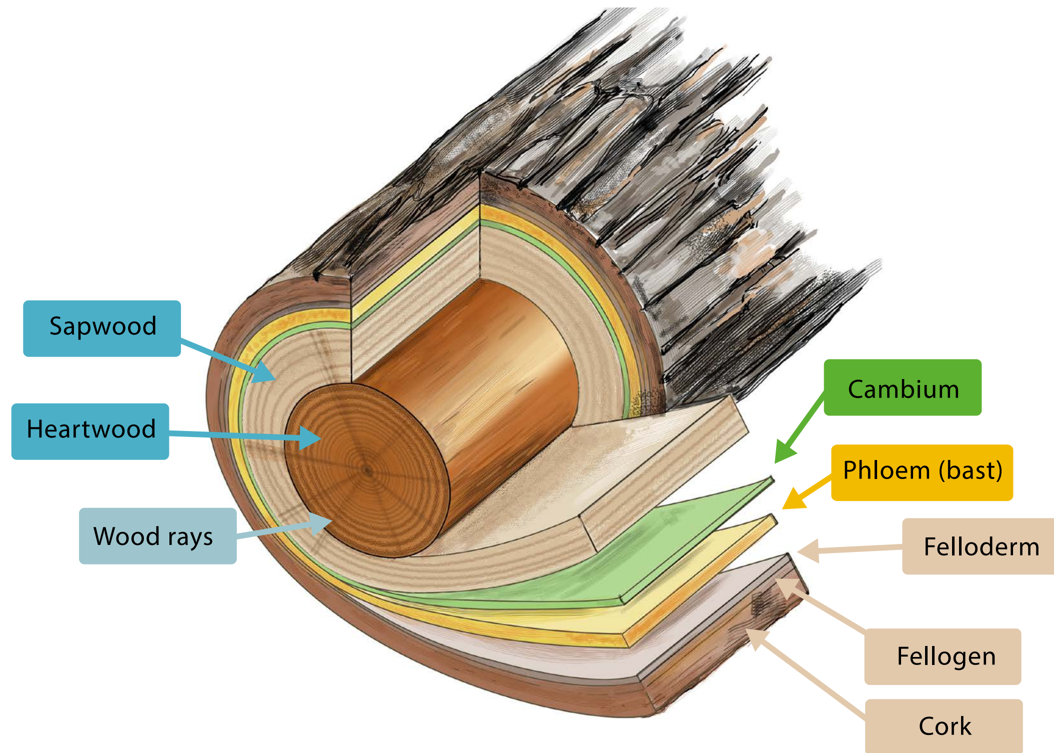

Fig 6. Cross-section of a trunk or a branch.
Drawing by Jakub Józefczuk

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In species with cracks, the brighter young bark can be seen between ridges in areas of intense growth. This is a symptom of tree's good condition and indicates which parts undergo active expansion.

PHLOEM (BAST)

guides photosynthates from leaves to the trunk, and further down to the roots. This flow can be reversed when the food is transported to buds, from winter storage in trunk. Transverse direction applies, when the photosynthates are moved to cambium, rays, and phellogen. The main component of the phloem are sieve tube elements – living cells, stacked one on another, and connected by strips of cytoplasm through pores in transverse walls (hence the name). Old tubes are crushed as new ones are generated by cambium, so older cells do not accumulate as in in the case of wood. Other kinds of cells observed here are parenchyma and fibers. The latter made bast a favourite material in traditional crafts to produce bags, shoes, and other artefacts.

CAMBIUM (VASCULAR CAMBIUM)

is a meristem that generates phloem cells on the outside and wood cells on the inside of the trunk. This is the most fragile tissue of the interior of a stem or a branch. Cambium is particularly vulnerable in Spring and Summer when it is most active – producing new layers of wood and bast. When damaged, it generates wound-covering tissue – callus.

CALLUS

is an amorphic meristem generated from cambial or parenchymal cells at a wound. Callus cells are unspecialised and unorganised. They can become any tissue, depending on the needs and environmental conditions. For example, when bark is peeled of the trunk, callus is formed from cambium and medullary rays and it subsequently generates cambial cells to restore phloem and bark. In a wounded root, dark and moist soil environment favours formation of regenerative roots. Sometimes callus generates roots in a cracked fork – where dust, organic particles and rainwater stimulate soil-like conditions. **Through differentiation of callus, trees are able to cover wounds with new tissues. The damaged tissues, however, are not healed, as in animals - they are isolated (compartmentalised) and new tissues grow over them.**

WOOD (XYLEM)

consists primarily of non-living cells, the function of which is to transport water from roots to leaves (as long as they are young). In conifers (and some broad-leaved), these are called tracheids; in broad-leaved trees, the elements are called vessels. In temperate climate zone, wood is generated by vascular cambium in an annual cycle: in Spring, the cells tend to be thicker, as their main purpose is to efficiently pump water (early wood). Vessels and tracheids grown in Summer demonstrate smaller clearance, thicker walls and they serve primarily construction function (late wood). Wood contains also reinforcing fibers and parenchyma cells, some of the latter are concentrated in medullary rays that begin in phloem and reach deep into the wood.
In conifers and ring-porous broad-leaved trees (oak, ash, robinia), early and late wood vascular cells are concentrated in discernible layers - annual rings. In diffuse-porous trees (maple, lime, poplar) the vessels are more evenly distributed, and it can be difficult to distinguish annual rings. Generally, water is transported in few external rings, while older wood is shut off and serves only mechanical support. In oaks, where vessels are very thick (discernible with the naked eye), water movement happens practically in the last, youngest ring. In some species, the internal part of the wood (not functional in water transport) is impregnated with preserving substances.

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This part of a trunk is called **heartwood**. The external, physiologically active layer, is called **sapwood**.
The creation of heartwood is interpreted as a passive defence against fungal decay, even though there are fungi that specialise in consumption of the heartwood (such as beefsteak fungus *Fistulina hepatica* and chicken of the woods *Laetiporus sulphureus*). Heartwood of diverse species demonstrates diverse resistance to decay: it can be very durable in some oaks and rather vulnerable in ash. Willows are considered a genus that does not generate heartwood, as their wood easily succumbs to fungal decay. The term "false heartwood" originates in timber classification and relates to tree species that do not generate heartwood, such as beech. It is a discoloration, usually a response to trunk damage or death of a branch. False heartwood may be a symptom of a defence reaction, however, it is not heartwood *sensu stricto*.

PLANT CELL

unlike an animal cell, is surrounded by the cell wall. **Cellulose** fibers provide reinforcement, similarly to steel bars in concrete. Cellulose chains are braided together into fibrils, a bit like wires in a multi-strand rope. This makes them durable and flexible.
In growing cells, the primary cell wall is capable of expanding. Their cellulose fibrils are immersed in a matrix consisting of pectins and hemicellulose, with proteins added. When the cell completes its growth, the secondary cell wall is deposited on the internal side of the primary wall. It is richer in cellulose and its matrix contains additional components, notably lignin (in lignified cells). Such cell walls are becoming rigid, and the cell cannot grow anymore. Lignin is a very complex and durable compound. It provides the cell wall with compressive strength and decreased permeability. Bark cell walls are impregnated with suberin, making them

impermeable to air and water, as well as resistant to environmental factors.

Decomposition of lignin in land ecosystems is conducted mainly by white decay fungi, such as tinder fungus (*Fomes fomentarius*) or *Phellinus*. The white colour is provided by cellulose, which is left after lignin is removed. Brown decay fungi, such as chicken of the woods or birch polypore (*Fomitopsis betulina*), generate brown rot, consisting mainly of lignin (as cellulose has been decomposed). Cellulose is more easily decomposed than lignin by microorganisms, including bacteria and protozoans living in digestive tracts of ruminants and termites.

Wood dry mass consists of 35-50% cellulose, 25-30% lignin, and 20-30% hemicelluloses.

Softwood (wood of conifers) tends to contain more cellulose and lignin than hardwood (wood od broadleaved trees).

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3. HOW DO TREES GROW?

As already mentioned, trees grow only in specific generative tissues – meristems. Old cells are replaced by newly formed ones, to be ultimately eliminated or stored. Leaves (even those of evergreens), fine roots and twigs, flakes of bark are shed. Certain non-living tissues, such as wood and bark, can keep fulfilling some of their functions.
Fully functional wood (sapwood) consists of non-living vascular elements and living parenchyma. While a tree growths in girth, the distance between the most internal rings and the nourishing phloem increases. With time, older parenchyma cells dispersed among vascular tissue are starved and wither. In some trees (such as oaks, ash, robinia, pine), the interior of the trunk is impregnated with inhibitors of decay – phenolic compounds or resins – to form heartwood. The non-living wood keeps providing mechanical support, however, with time, it often succumbs to fungi. The nutrients it contains are released, taken up by roots, and built in into new tissues. Adventitious roots, growing inside cavities and directly penetrating the mulm, are best positioned to close the nutrient cycle (see Fig. 7).

Fig. 7. Cross-section of an old willow demonstrates: living sapwood, with a part colonised by a fungus (not growing anymore, as cambium was killed, a fruiting body seen on the bark), decayed interior of the trunk, and defence barriers. An adventitious root (arrow) takes up nutrients from the mulm. (PTCh)

Every year a new mantle of vascular tissues is created on a tree – on the trunk, roots, and branches. It is often physiologically self-sufficient and uses the older tissue only as a scaffolding (Fig. 8). This particularly happens when damage to the trunk triggers creation of a barrier zone on the internal side of a new ring. Hence, a tree is able to compartmentalise damage and to continue its growth. Integrity of old wood inside the trunk is not necessary to assure tree stability. The shape of a pipe serves this purpose well, provided the walls are thick enough. There are also standing trees, where basal decay left only buttresses. Such trees are reminiscent of the Eiffel Tower and their stability depends on state of roots and buttresses. Below you will find more on impact of fungi on tree stability and on tree's defence mechanisms.

The age of ancient trees is usually impossible to determine by ring count, as all early rings are long gone, thanks to fungi, bacteria, nematodes, insects, and other mulm inhabitants. Also many, if not all, of the primary branches and roots have been shed. The body that we see is much younger than tree's whole history. Similarly, young are individual quaking aspens in the 80-thousand-year-old grove-tree Pando in the Rocky Mountains. The capacity to recycle its own body and thus to fertilise its own habitat is one of the longevity mechanisms the trees have mastered. Additional nutrients are delivered with faeces of animals nesting in hollows and on branches.

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TREE ASSESSOR

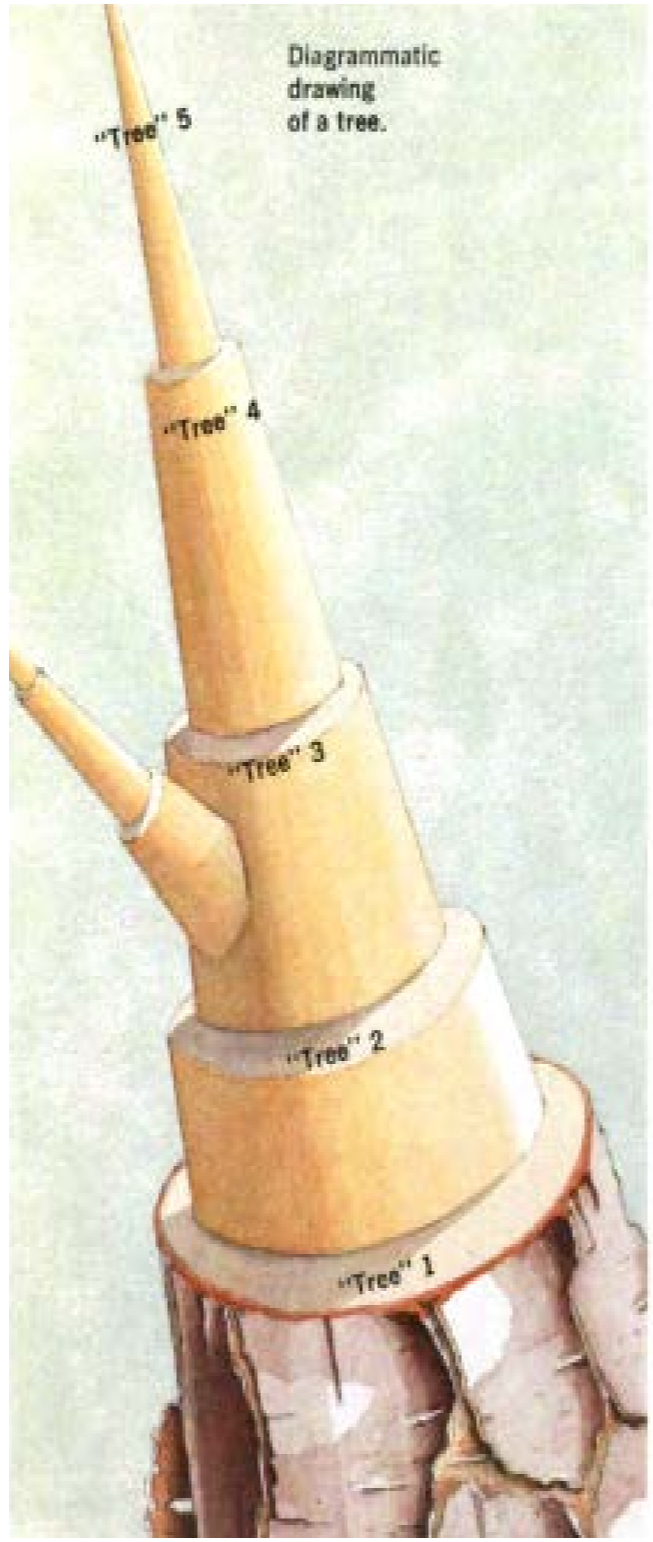

Fig. 8. Every year a new tree is created on the old one (Shigo i Marx 1977).

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4. HOW TREES DEAL WITH DAMAGE AND ENVIRONMENTAL STRESS?

The modularity seen in tree architecture is also expressed in its anatomy. Living and active tissues are isolated from those non-living, or damaged, in the process of compartmentalisation. Trees create barriers that assure functioning of the intact parts of the body, for example after a mechanical damage or colonisation by a pathogen. The damaged tissues are "compartmentalised out" and usually subjected to decay.

"Healing" of the wound is achieved through overgrowing it by callus. When regeneration occurs, it does not lead to literal reconstruction of the damaged body parts. Restored are the lost functions, e.g. a broken branch is replaced by a bundle of epicormic (adventitious) sprouts, a stub can be overgrown by bark, and a peeled off bark can be replaced by a new one.

4.1. ALEX SHIGO AND COMPARTMENTALISATION

That trees are defenceless when faced with fungal invasion had been a common belief among tree surgeons until over 30 years ago (since then, they have been replaced by arborists). This belief inspired tree care practices analogous to those of dentistry. Just as in the case of an aching tooth, the decayed tissues were to be removed from the trunk and internal walls were to be milled clean, dried, and treated with a biocide. As a collateral damage, hollow-inhabiting creatures were annihilated, including now-protected saproxylophagous (eating dead wood) insects, such as the hermit beetle. However, these practices were based on the understanding of tree physiology of the time.

A revolution in the understanding of relationships between fungi and their tree hosts has been taking place since the 80's. It was initiated by a US forester and arborist Dr. Alex Shigo. He believed that the best source of knowledge about trees are trees themselves and his motto was:" touch trees". As Shigo worked as the chief scientist at the US Forest Service from 1960-85 ,he dissected countless trunks and branches, conducted diverse experiments. Based on these observations he formulated his vision of how a tree functions (see Literature for references).

"People should know that trees are generating organisms, instead of re-generating organisms like human beings. Trees generate their own food from carbon dioxide, sunlight and water, while human beings must intake food from elsewhere. Therefore, tree food is a misnomer. While such supplements, like fertilizer, provide important elements, they do not provide an energy source. (...) While humans put new cells in old places countless times during a lifetime, trees continue to put new cells in new places. Similarly, a tree doesn't heal, because it doesn't replace injured cells with new ones."[1]

The central concept of Shigo's vision of tree is **CODIT- Compartmentalization of Decay in Trees**, which explains mechanisms of defence against decay caused by fungi. Shigo discovered that trees are not passive victims of fungi - quite contrary, they are able to put limits to the decay and to slow it down or stop altogether. From the perspective of today's knowledge, "D" stands rather for "damage" or "defect", as we now suppose that it is the tree's reaction is initiated by the damage itself, most often a decompression of vascular elements. In the CODIT model, the tree creates barriers, dubbed **"walls"** (Fig. 9, 10) by Shigo, that enclose decay in **compartments** and prevent it from expanding to sound tissues. Similarly, a ship is divided into compartments by watertight bulkheads (partitions), to prevent sinking if the hull is punctured.

1 shigoandtrees.com/about-alex-shigo/, 15.01.21

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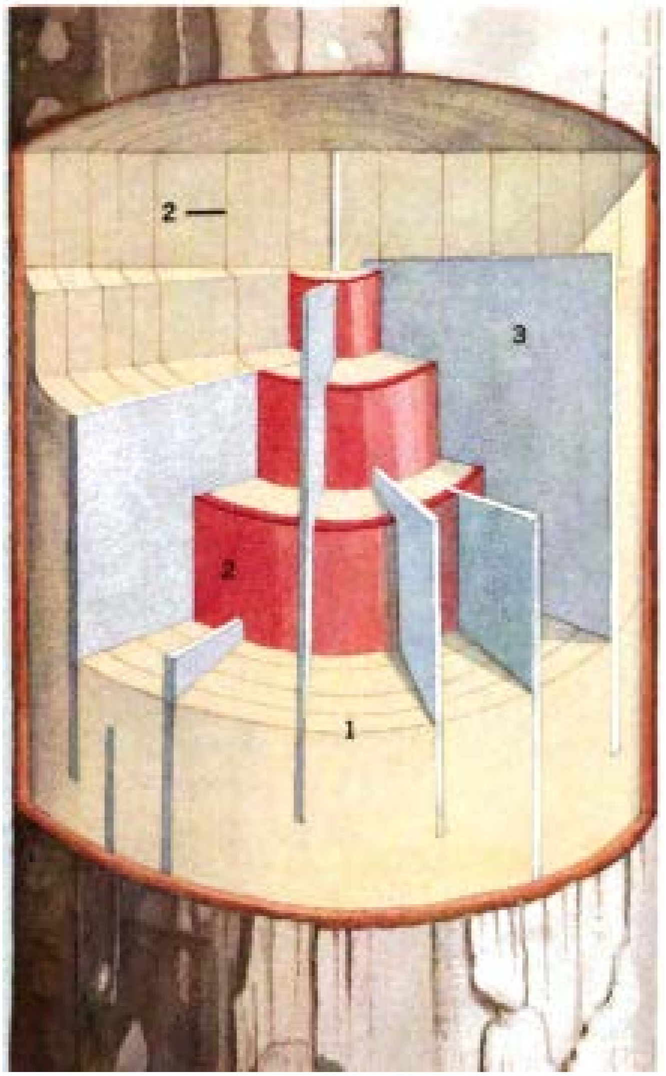

FIg. 9. Shigo's boundary layers - walls 1, 2 i 3 (Shigo & Marx 1977)

Shigo differentiated two categories of „walls". The first one is **boundary layers**, established through impregnation of cells with decay inhibitors. They are generated and transported in parenchyma, particularly in rays. Shigo marked them with numbers 1,2,3, reflecting their location and function (Fig. 9). The walls limit spread of the decay along the trunk (no.1), towards pith - radially (no. 2), and around the trunk – tangentially (no. 3).

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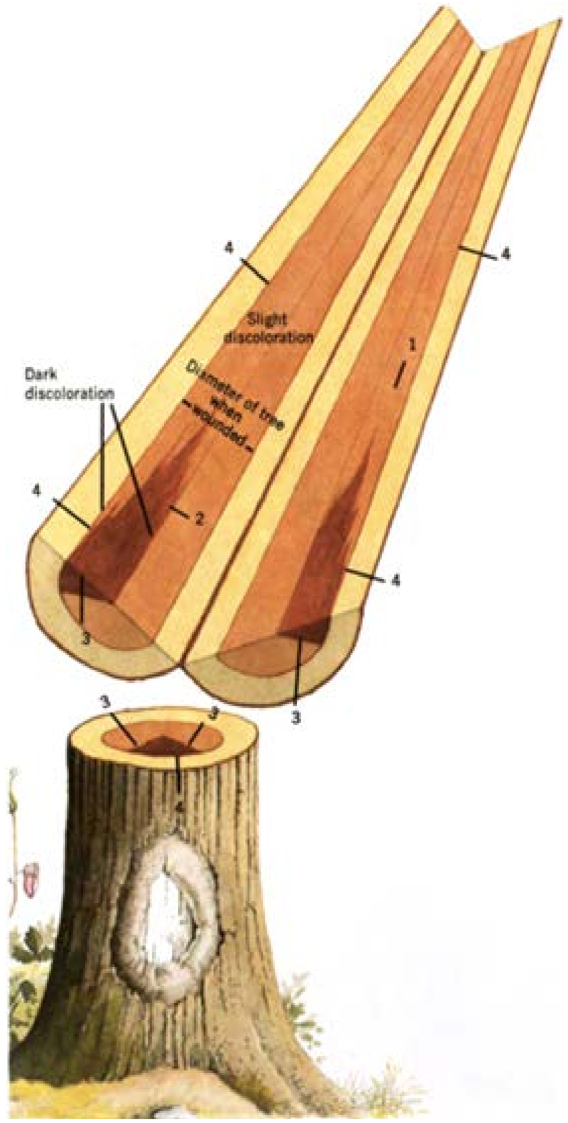

Fig. 10. Barrier zone or wall 4 (Shigo & Marx 1977)

The second category is the **barrier zone** (no. 4, Fig. 10). It differs from walls 1-3 as it is not only rich in decay inhibitors, it is also anatomically modified to be tight. The barrier zone is formed in the next growing season after the damage and it separates the newly generated wood from the older tissues. This is the most effective fungal barrier – all the wood enclosed by the barrier zone may be rotten and the wood outside remains sound. Then the range of the hollowing follows the growth ring where the zone was formed (Fig. 11).

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For fungi, the preferred environment is moist – not too dry and not too wet. Excess of water limits availability of oxygen, while lack of water makes their growth impossible. That is why lumber is traditionally stored either dried, or immersed in water (or sprinkled with water). Sapwood is relatively resistant to decay, not only because it has active parenchyma (see above) and is well-nourished by the not-too-distant phloem. Fungi are deterred by the high water content (90%, Shigo 1986). The wetwood phenomenon (wood with increased water content) can be also interpreted as a fungal control mechanism (Shigo 1986).

The teachings of Shigo contradicted the then-contemporary practices of tree surgery, particularly the widespread cleaning of hollows. During such operations, the Shigo walls were removed and the gate was made wide open to fungal colonisation of unprotected tissues. Application of fungicides would do little to prevent it. No surprise that his proposals were met with an ardent opposition of the tree surgery industry. Today, science confirms most of his observations and intuitions and some of them are further developed and modified. Today, we know that wood fungal infections cannot be "cured" – a tree can and has to manage them itself. What we can do for a tree, is to improve its living conditions, in other words – its welfare. To me, Shigo was a kind of Copernicus of arboriculture: based on a solid body of knowledge he collected, he questioned and changed the dominating paradigm.

Fig. 11. A concentrically (following a ring) trunk of an old small-leaved lime. (PTCh)

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4.2. HOW DO TREES ADAPT TO CHANGING ENVIRONMENT?

Animals adapt to changing environment mainly through their mobility. If it is too warm – we seek shade, if it is too cold – we bask in sun, if we are hungry – we start out to search food. Trees do not travel but they grow – and this is their way of adaptation. If a tree is shaded by a neighbour – it grows towards sunlight, if roots need water – they grow searching for moist areas in the soil. Redundant parts of their bodies stay behind and die off, such as shaded lower branches and unnecessary roots.

Trees are often forced to deflect from their preferred vertical growth direction, to struggle for light. Branches grow, by definition, horizontally. Thus, trees must possess mechanisms to control growth direction and the key one is apical control (see below). While an upright trunk can be perfectly round, an awry growing one is oval. The longer diameter indicates the tilt direction. The tree puts extra volume of specialised tissue in the strained spot – this is reaction wood, and it comes in two variants. Tension wood is deposited on the stretched side (in broad-leaved trees) and compression wood grows on the compressed side (basically, conifers – see below). Adaptation to increased strain is clearly visible at the base of slanted trees or trees experiencing frequent wind from one direction. The main buttress and connected root on the stretched side is clearly stronger (Fig. 12) and is crucial for tree's stability. The

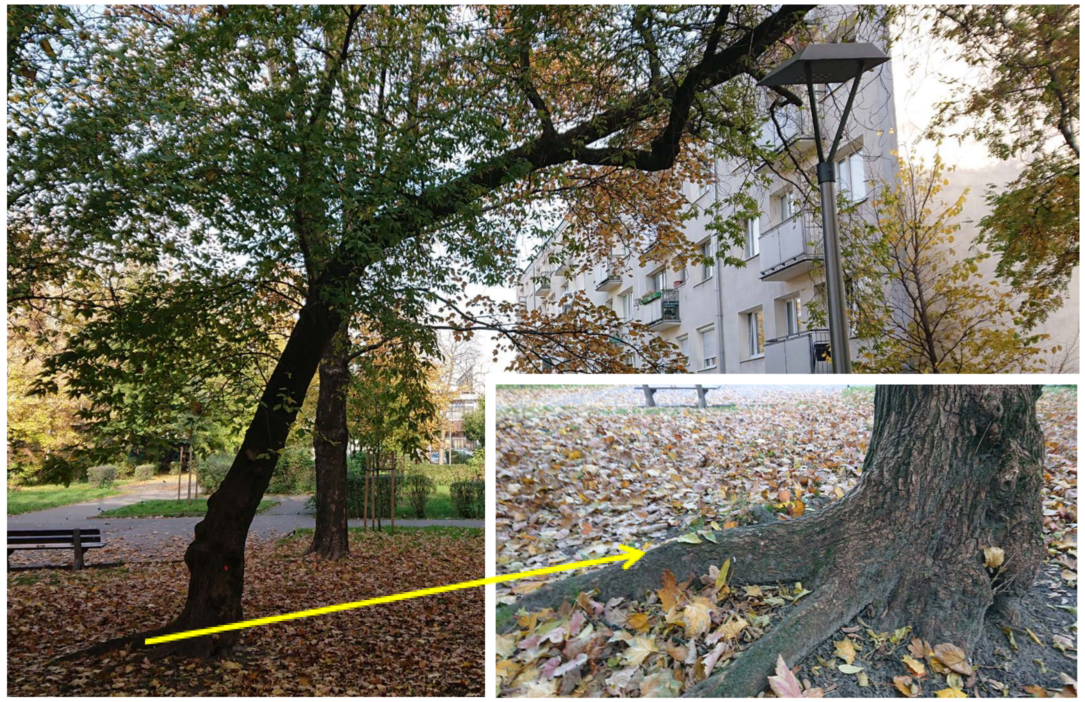

Fig. 12. A boxelder that grew aslant in search of light demonstrates powerful roots and buttresses on the strained side (Warsaw). (PTCh)

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compressed buttress and root, the one that supports the trees, also contributes significantly. So, it is important to tell leaning trees with inclined growth from those that are beginning to topple, as may happen because of rupture of roots by a strong wind, damage to roots by excavations, or liquefaction of water-saturated soil.

Similarly, a tree fortifies parts that are weakened by decay or fracture – trees evidently possess ability to detect and measure bodily strain. For example, internal basal decay may result in a bottle-shaped trunk base, as the tree accumulates more (and tougher) wood where the decay is more extensive. “Ears” sometimes form on forks with bark inclusion (see the photograph). If they fail to adequately strengthen the junction, it may fail (see also below a paragraph on axillary wood).

Adaptation via growth is certainly slower than that via movement. A tree can adapt, to certain degree, to gradual changes, such as sinking of raising of groundwater table – through reconstruction of the root system. However, this is only possible if the change is relatively slow. Adaptation to an abrupt change, such as that following construction of an underground parking lot, is beyond capacity of most trees, particularly mature ones. Trees, in their evolutionary history, encountered such challenges too rarely to develop adaptive mechanisms.

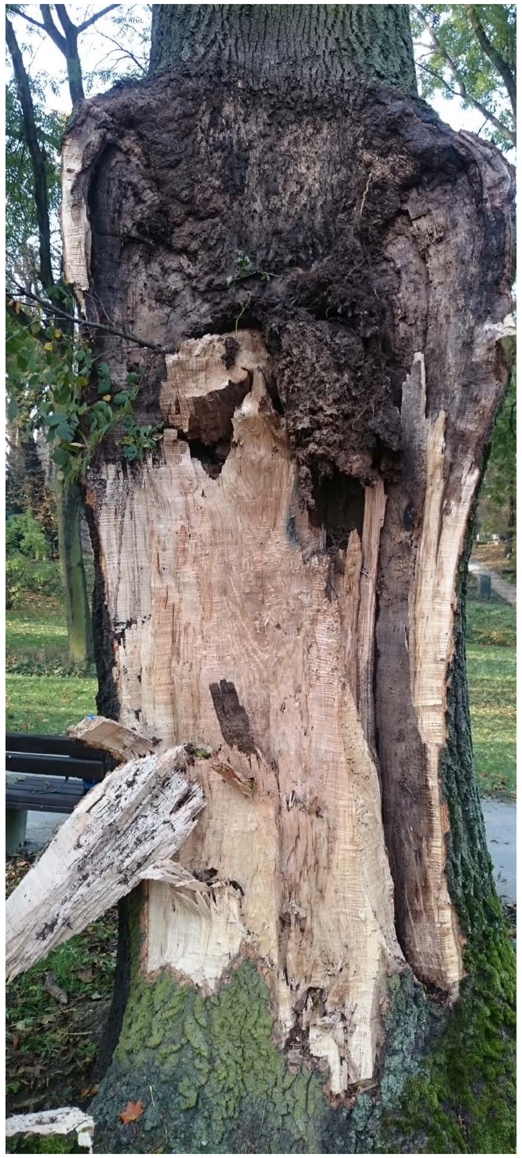

Fig. 13. The tree tried to fix a fractured fork by adding extra wood on both sides of included bark – but it failed. (PTCh)

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5. BASIC TREE ARCHITECTURE AND BIOMECHANICS

As it was mentioned before, from the moment of germination, a tree’s body expresses specific pattern of growth, which is then self-copied, with some modifications, over its entire life. Every species demonstrates a specific pattern of branching. The size of a tree is a result of an interplay of genes and environmental conditions.

A tree is a self-optimising structure that strives to achieve mechanical and physiological equilibrium. Through hormonal regulation and, as yet little known, mechanism of assimilate partitioning, it controls growth of particular organs to achieve balance and harmony. Trees create a root system that is adequate to the needs of the existing crown and properly supplies leaves with water. In turn, the crown is big enough to be able to nourish itself and the rest of the organism – including the roots and co-operating soil organisms. The size and shape of the trunk corresponds to the need to effectively compete for light and to provide a stable support to the crown. As any other part of tree’s body, it fortifies itself in strained areas. Wood in the trunk and branches is heterogeneous as to its structure, density, and strength. It demonstrates the greatest strength where the greatest strain occurs, that is at the bases of trunk and branches. Additionally, these areas are strengthened by intensive growth, which shows as buttresses and thickness of branch bases. Tree also strengthen with extra wood growth areas weakened by fungal decay or mechanical damage, hence a bottle-shaped base of a rotten trunk or “ears” by a fractured fork (Fig. 13).
Wood is anisotropic, meaning that its properties differ in various directions. **Biomechanics** is a field of practical science that researches strength and stability of trees (Buza 2021).

In **apical dominance**, also referred to as apical control, activity of branch meristems is controlled by the apex of the tree. A hormone secreted by the apical meristem of the main leader – auxin - makes branches grow horizontally and prevents them from competing for light with the main stem. Auxins also inhibits dormant buds. When the apex is damaged, the apical control disappears and lateral branches begin to grow vertically, while dormant buds become activated (Fig. 14). Dissipation of the hormonal control can result from damage to the apical bud by wind, animals, diseases, or its decline due to environmental stress. Often it is water stress - induced by drought, lowering of groundwater table, flooding, or damage to roots through excavations or soil compaction. Impairment of apical domination also characterises ancient trees.

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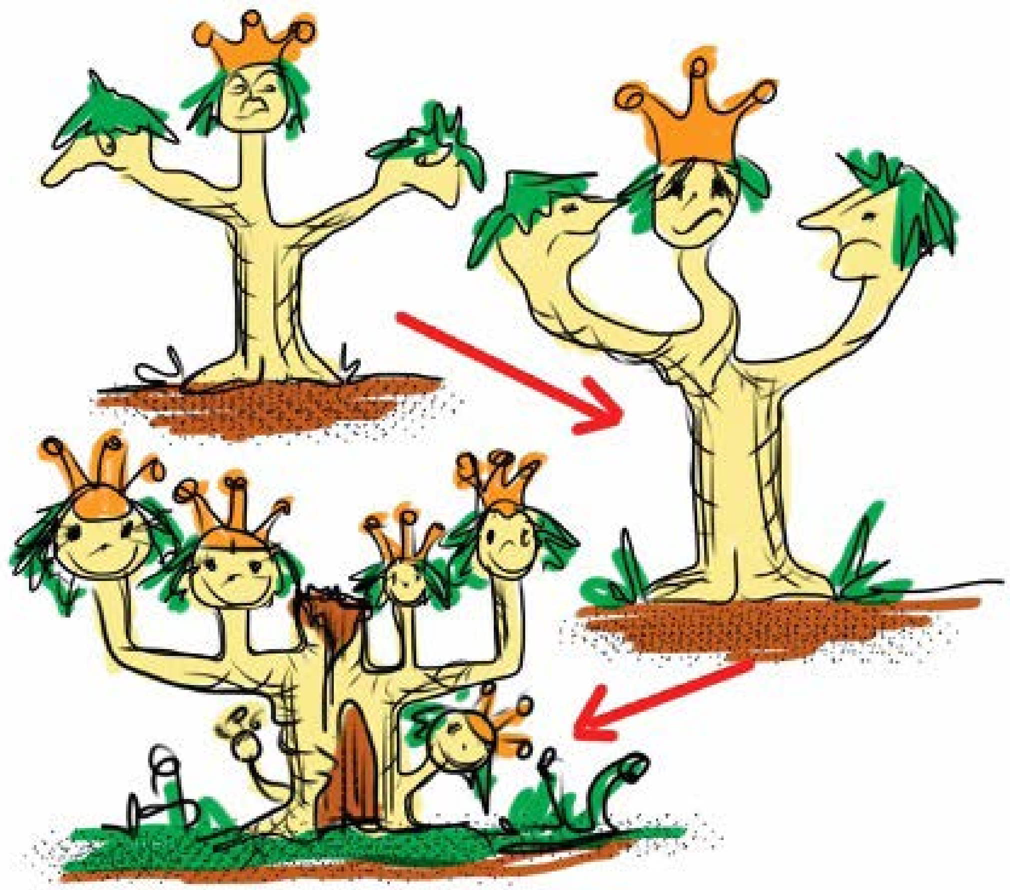

Fig. 14. The loss of apical dominance was humorously illustrated by Claus Mattheck, one of tree assessment's classical authors (training materials of the VETree programme, www.vetree.eu). The apex rules over branches like a king over vassals. However, as soon as his rule is weakened, the lesser lords raise their heads and take over control of the tree.

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Fig. 15. Here is an example of the loss of apical dominance: particular branches assume vertical growth and begin to compete for light as if they were separate trees. (PTCh)

5.1. ANATOMICAL MODIFICATIONS OF WOOD

Reaction wood is formed in areas that are subject to constant or repetitive strain. Its task is to sustain the strain and to enable the tree to follow its genetically determined pattern, while responding to environmental conditions (particularly light). Compression wood occurs in conifers, rarely in broad-leaves, and tension wood - only in broad-leaved trees.

Compression wood is formed on the squeezed side of a trunk or a branch. Cell walls are richer in lignin and poorer in cellulose than those in regular wood. Macrofibrils (bundles of cellulose chains) are arranged at ca. 45 angle relative to cell axis (the greater the strain, the wider the angle). The compression wood is able to expand, and thus can control the growth direction of a trunk or a branch.

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Tension wood is formed on the stretched side of a trunk or a branch. Cell walls are richer in cellulose than those in regular wood and macrofibrils are oriented almost along the longer axis of the cell. As the tension wood is able to contract, it can correct the growth direction depending on needs.

Axillary wood is formed within a fork (Fig. 16). Complex interlocking patterns of grain gives a junction extraordinary strength. Try to split a fork with an axe hitting from above. If cork inclusion stands in the way of developing proper axillary wood, then tree attempts to strengthen the fork with extra wood growth on the outside ("ears", see above). If this effort fails, the junction becomes weak.

Axillary wood, similarily to other modifications of wood structure, develops upon strain generated by moving independently elements of a fork. An external symptom of its presence is a bark ridge (Fig. 17). However, if the movement is restricted, e.g. by branch graft above (natural bracing in the crown), the fork will not be fortified and the probability of bark inclusion increases (Fig. 18). It is thus not recommended to remove a natural bracing, as the fork below may be weakened and risk of failure increases.

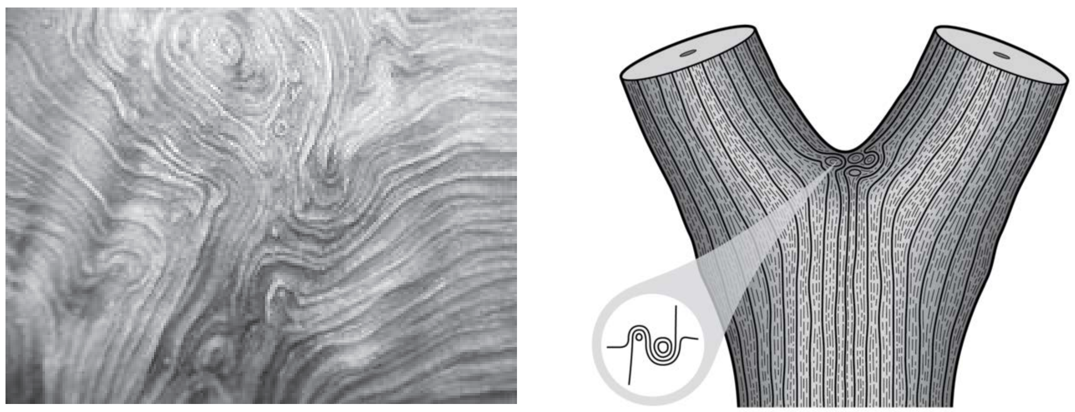

Fig.. 16. Axillary wood . The illustrations were borrowed from a Wikipedia article by Dr. Duncan Slater (en.wikipedia.org/wiki/Tree_fork).

Fig. 17. Bark ridge in the fork indicates that axillary tissue is properly formed, and the strength of the junction is appropriate. (PTCh)

Fig. 18. A fork with limited movement of leaders, due to natural bracing. Bark inclusion has formed and in the lower part of the fork extra wood tissue is laid to reinforce it. The picture on the right presents the other side of the fork. (PTCh)

Box 3.

BIOMECHANICS AND TREE ASSESSMENT

The modifications discussed above are only the most basic ones, as wood is a heterogenous and anisotropic material. Mechanical models used e.g. to calculate outcomes of pulling tests are approximations. It is not that easy to predict if, and in what spot, a tree would fail if it does not demonstrate evident symptoms. Tree inspection or basic tree assessment is concerned with visual identification of symptoms that indicate the increased probability of tree failure. Advanced tree assessment uses more detailed and sophisticated methods, including using diagnostic instruments.

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5.2. WHAT DO SHOOTS TELL US ABOUT A TREE

Trees develop two basic types of shoots and telling them apart is useful in estimating a tree's life stage and vitality. It is usually possible to identify the limits of an annual growth of a shoot, as they are marked by scars left by terminal bud scales. Additional scars can separate Summer shoots (Lammas growth) and, in some species (especially oaks) these little differ from annual scars. This can complicate telling the length and age of annual sprouting. Anyway, assessment of tree vitality is based on visually identifiable shoot pattern, as observed with a naked eye, if needed, helped by binoculars.

Long shoots, as the name suggests, are at least several cm long. They possess fully formed side buds, from which new sprouts develop in the following year.

Short shoots (spurs) are between few mm and several cm long. Apart from the apical bud, they develop only dormant buds which flush only in emergency (e.g. when the crown is damaged). Normally, short shoots do not branch out the following year.

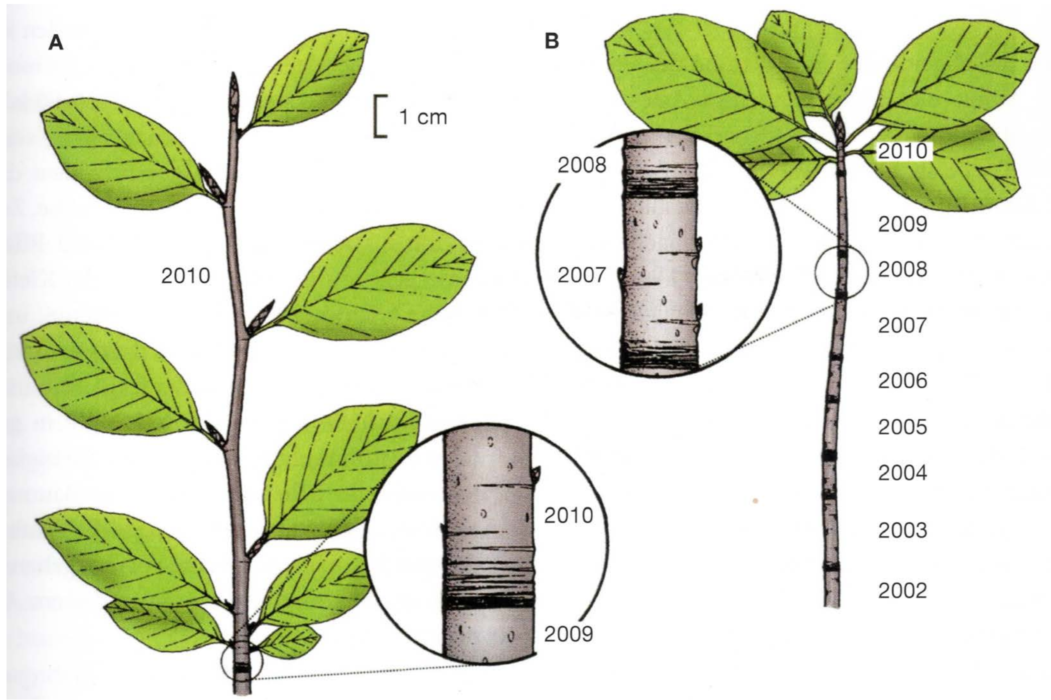

Fig. 19. On the left, a twig with one long shoot, on the right, a twig with a series of short shoots (annual scars indicated), in European beech. (Roloff 2018)

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Long shoots and short shoots have different functions. Long shoots serve crown expansion, so they are common in young and maturing individuals, as well as those regenerating ones, in any life stage – as a component of adventitious twigs. Short shoots serve to maintain the conquered space and to support basic tree functions. Hence, they are typical of mature and ancient trees. Short shoots may also bear flowers or leaves, although this is a different story. One tree can carry both long and short shoots, in differing proportions in different body parts.

VITALITY

Vitality is a commonly understood term, however, if one tries to use it to for assessing a tree, the matter gets a bit complicated. According to Wikipedia, it is „the capacity to live, grow, or develop". Shigo (1986, p. 120) defines it as "the ability of an organism to grow under the conditions in which it finds itself" and he distinguishes it from vigour, defined as "the genetic capacity to resist strain".

FLL [1] (2011), a German association in charge of guidelines and standards for the green industry, defines vitality as a life force of an organism, influenced by age, genetics and environmental factors. Further, vitality expresses itself in health of a tree, and specifically:

- Growth, crown structure and state of leaves,
- Ability to adapt to environmental conditions,
- Immunity to pests and diseases,
- Ability to regenerate

According to FLL, vitality is estimated, in forestry and arboriculture, based on crown structure and/or state of leaves (density, size of leaves, colour).

The author would add here that vitality is influenced by a life stage of a tree – which is correlated, although not identical, with age.

1. Forschungsgesellschaft Landschaftsentwicklung Landschaftsbau e. V., www.fll.de

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5.3. ROLOFF VITALITY CLASSES

Andreas Roloff, a professor at the Dresden Technical University, created a vitality scale meant to be used in forest health surveys. He based it on shoot growth pattern, as he found criteria related to state of leaves unreliable because of influence of current conditions (drought, pests). Long/short shoots assessment allows for insight into at least several years of growth, recorded in the twig pattern (Fig. 20, 21). With years, Roloff adapted his scale for assessment of urban trees of diverse life stage (Roloff 2018). Long shoots dominate in "exploration phase". In "degeneration" phase only side twigs become shorter, while the axial growth is still long. All shoots are short in "stagnation" phase, and "resignation" means that some shoots are dying.

I would love to endorse the original terminology by Roloff, however, I find the word "degeneration" inadequate, as it has a negative connotation to it. Each vitality class is naturally associated with a specific phase of tree's lifecycle. It is, therefore, not appropriate to use terms that sound judgemental. The "degeneration" phase has little to do with the common understanding of this word. This class is typical of trees that keep vigorously growing or regenerating after Andreas Roloff (2018) introduced recently the term mode (der Modus). He proposed, respectively: long-shoot mode (0), brush mode (1), short-shoot mode (2), and retraction mode (3).

Roloff recommends considering the upper one third of the crown when assessing vitality. However, in the case of ancient trees and those that are in the process of crown reconstruction (damage of roots, drought...), the upper third can represent class 3 and the lower third – class 1. In such cases, it is advisable to assess vitality separately for distinct part of the tree.

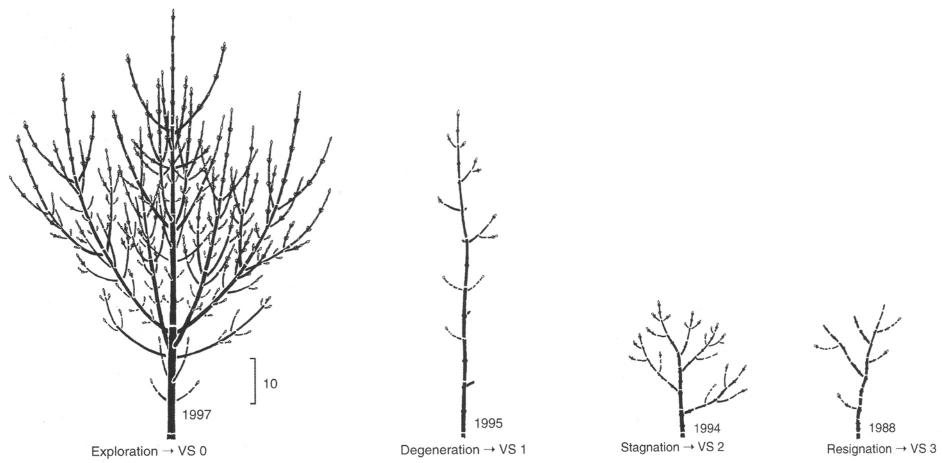

Fig. 20. An illustration by Roloff (2015) depicts branching patterns of common ash in diverse growth stages/phases.

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Table 1. Vitality classes based on Rollof (2015, 2018), as defined in the „Standard for tree assessment and diagnostics" (FER 2021). Numerical designations conform to the 1-5 scale, while Roloff's original scale covers 0-4.

NUMERICAL DESIGNATION	ROLOFF CLASSES	DESCRIPTION
1	0	A tree in the phase of a strong longitudinal shoot growth. Both terminal and lateral shoots grow dynamically and uniformly, generating mainly long shoots. Foliage is dense and uniform.
2	1	Lightly decelerated growth results in lateral buds generating short shoots, which makes branches look spear-like. Between them free spaces arise, also when foliage is on.
3	2	Shoot growth clearly decreases and only short shoots are generated. Tree height growth stagnates, gaps in foliage are evident.
4	3	Tree that is declining or with dying parts of crown.
5	(4)	Dead tree.

Fig. 21. Another illustration by Roloff (2015) demonstrates vitality classes in common lime (Tilia x europaea).

5.4. HOW TREE ARCHITECTURE EVOLVES OVER ITS LIFESPAN

The concept of Roloff classes will be useful when introducing tree life phases. There are numerous classifications of those. For the sake of simpicity, we distinguish three basic stages: young phase, mature phase, and ancient phase – the latter for few individuals only (Dujesiefken et al. 2016).

YOUNG TREE

A young tree demonstrates a strong apical dominance and height growth prevailing over lateral expansion. It usually lasts till ca. 20 years after planting. A properly growing young tree demonstrates initially the Roloff class 0, meaning that all shoots are long shoots. Later in this phase, class 1 begins to develop. In this life phase, formative pruning must be conducted and completed. An early weakening of vitality may indicate problems with plant health or site quality.

MATURING TREE

This is transition between youth and maturity - the tree slows down height growth while still expanding its crown.

MATURE TREE

In a mature tree, height and volume of the crown is stable and apical dominance is weakened.

The tree has reached or is approaching the maximum crown size for the species and site. A typical mature tree produces only short shoots, hence demonstrates Roloff class 2. Only regenerating shoots and reiterations have a class 1 pattern.

Box 4.

REITERATION

An adventitious (secondary) shoot, growing on a trunk of branch from an adventitious or dormant bud. A reiteration possesses main stem and side branches. With time, it is said to be able to develop an autonomous root system, connected via a dedicated and separate strand of vascular tissue. It is then like a young tree growing on an old one. An ordinary primary branch is programmed to emerge and it follows the tree's basic growth pattern. A reiteration is born by chance, as an effect of a damage or an effort by the tree to better use light. Some authors equate reiterations with adventitious branches, some others narrow it down to whose being a miniature of a mature tree (Hallé 2002).

Fig. 22. A Balkan pine (Pinus peuce), whose crown was restored by reiteration after a windbreak (Lądek Zdrój, PL). (PTCh)

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ANCIENT TREE

An ancient tree is the one "that has passed beyond maturity and is old, or aged, in comparison with other trees of the same species" (Lonsdale 2013, see there for more definitions). Trunk girth can also be exceptional. In case of long living species this may be the longest life phase. Crown can experience dieback of peripheral parts and establishment of a lower secondary crown (crown retrenchment, Fig. 23). Ancient trees usually demonstrate high biological and cultural value. In this phase, hollows in the trunk offer extensive microhabitats. The upper part of crown is usually in the class 3 – branches, including the leader, gradually die off. The secondary (lower) crown often consists of adventitious branches and can demonstrate Roloff class 2 or even 1.

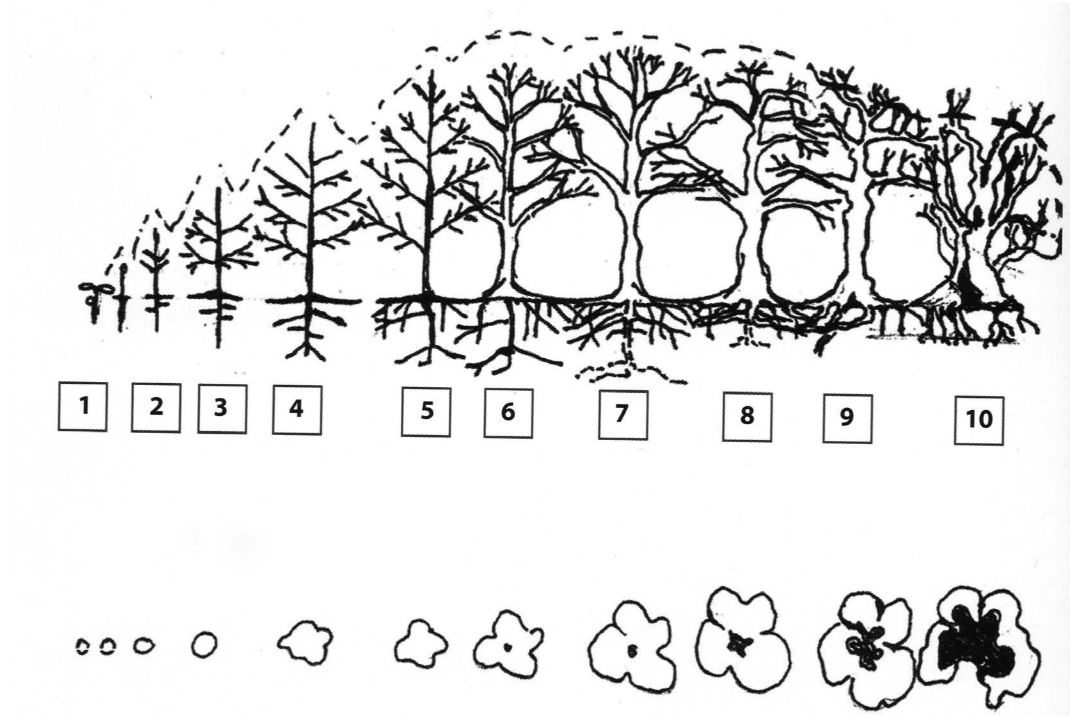

Fig. 23. Neville Fay, inspired by Lonsdale and Raimbault, illustrated the pattern of crown development in young phase, stability in maturity and retrenchment in ancient phase. This is accompanied by parallel transformations in root system and progressive hollowing of constantly growing trunk (Dujesiefken et al. 2016).

The life cycle of a tree does not necessarily end in the ancient phase. Trees possess mechanisms allowing them to „resurrect" and start a new life. Ancient limes and willows often begin anew thanks to shoots from the trunk base, while poplars are able to grow dense groves of root sprouts. New stems also develop their own new root systems.

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Box 5.

MIESZKO 1ST OAK – A PHOENIX TREE

A good example of that process is an oak (Quercus robur) in Natolin, a suburban part of Warsaw. The tree grows at a medieval highway once connecting towns on Vistula River and was named after Mieszko 1st, the first documented ruler of Poland. Construction of a huge housing project nearby cut off its water supply and the tree withered in the nineties – only one living branch was left on its huge carcass. Since that time, Mieszko used this single branch to restore its crown. Non-living parts were impregnated and are now undergoing slow decay. A fire of June 2019 damaged the dead part, however, did not impact vitality of the living crown. Mieszko is a Phoenix who rose from ashes.

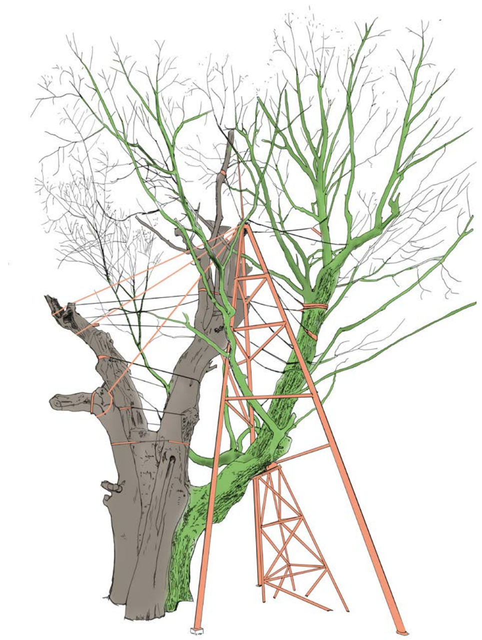

Fig. 24. Mieszko Ist oak in Natolin: the picture of September 2020 shows that last year's fire did not harm this vital patriarch (drawing by Jakub Józefczuk). (PTCh)

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6. FUNGAL DECAY VS. TREE STABILITY

Every decomposition by fungi weakens the wood mechanically, even in the initial stage, when it is not yet detectable with naked eye. Such wood, however, has already lost part of its structural components. In white rot, fungi decompose all components evenly. As lignin is a minority constituent, it disappears earlier than cellulose. That is why such wood loses rigidity, although it maintains for some time some of its tensile strength. In brown rot, cellulose and hemicelluloses are decomposed, so the wood becomes brittle and ultimately turns into a brown powder consisting primarily of lignin.

On the other hand, trees – over their long history - have learned to cohabitate with fungi that colonise them (and vice versa). They have mechanisms allowing them to control fungal expansion. Nevertheless, decomposition of non-living wood is a crucial link in nutrient cycling.

How does it happen that some trees cohabitate with fungi for hundreds and thousands of years and others succumb to them, sometimes within months?

The outcome of this confrontation depends on dynamics of relationship between the tree and the fungus. A healthy and strong tree, particularly in case of long-living species, one that possesses strong defence mechanisms, will keep the fungus at bay through compartmentalisation of the colonised territory. This comes easier if the fungus is benign. No problems are caused by saprotrophs like *Trametes sp.* or *Schizophyllum commune* – they deal with dead wood and do not enter the living ones. A more versatile fungus can, however, cross the line dividing saprotrophy from parasitism, if opportunity arises. This may happen if defence mechanisms are compromised, usually because

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of environmental stress. A tree that suffers from drought, salt or soil congestion, struggles for survival and has scant resources left for compartmentalisation. The fungus, no matter how aggressive, can break down the defences and invade areas crucial for tree functions and/or stability.

On the other hand, aggressive parasites, such as tinder (hoof) fungus *(Fomes fomentarius)*, are capable of defeating even a healthy tree – not to mention a weakened individual. In this case, the strength of defence mechanisms also matters. In a pedunculate oak *(Quercus robur)*, one can observe small tinder fungus "hoofs" slowly develop over decades, while horse chestnut, lime or poplar can succumb in few years since a fruiting body first appears. Wheras, Fomes, before weakening tree's condition, deprives it of stability. A honey fungus *(Armillaria sp.)*, to the contrary, first kills the tree, then decomposes it. The fungus then proceeds in saprotrophic mode and over following years consumes the dead wood.

As mentioned above, a hollowed tree may be able to stand firmly, because a tube is mechanically the optimal beam profile (see lighting poles or wind turbine towers). The strength of a tube is proportional to the third power of diameter, so the thicker the tree, the lower the wall thickness necessary for adequate support. One annual ring, 0,5 cm thick, on a tree which is 1 m in diameter, carries the same load as a full cross section of a tree that is 31 cm thick (Wessolly, Erb 2016, see also Fig. 25). There are ancient trees that stably stand on walls several centimetres thick (Siewniak et al. 2020).

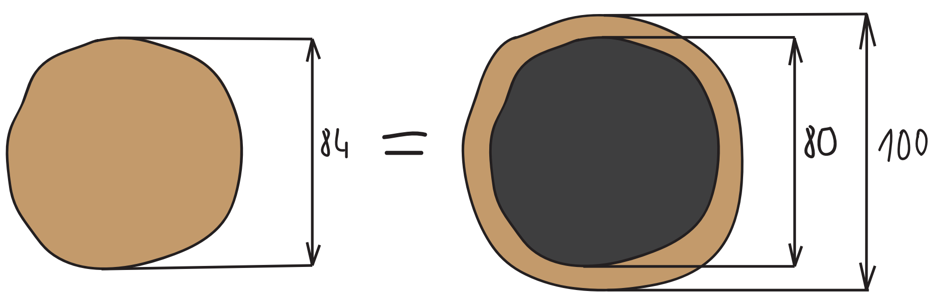

Fig. 25. A hollowed trunk with diameter 100 cm i sound wall thickness of 10 cm demonstrates the same bending strength as and intact trunk 84 cm diameter. Drawing by Paulina Sanecka after Wesolly, Erb (2016).

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Box 6.

WHERE DOES A TREE THINK?

How does a tree figure out how to grow? How does it process environmental stimuli into decisions on photosynthate partitioning? How does it know what should be invested in roots and what should be allocated to shoots? Where are decisions made on relationships with other connected organisms, such as neighbouring trees and mycorrhizal fungi?

Trees have no brains, which has been taken for millennia as a proof of their inferiority to animals. However, attentive observation, supplemented with reading current research papers on tree physiology and ecology, contradicts this belief. There must a place, somewhere in tree's body, where processes analogous to our cerebral activity are being conducted.

Where could it be then? It has been demonstrated that bioelectric impulses play a vital role in intra-organismal communication in plants. Bioelectric processes similar to those that occur in our neural system have been discovered in proximity of root and shoot apexes. Could it be that decision making processes in plants are conducted in a cloud composed of these sites? Similarly to the way computational clouds work, composed of numerous computers connected by the Internet. The jury is still out and more exciting discoveries on "where trees think" are expected in near future.

Study of communication processes within plants and with their environment, using analogies with animal world, is a subject of plant neurobiology - at least, this is what adepts of this field of science call it (Stefano Mancuso counts himself into this number). Other scientists consider this term a misuse, as there cannot be spoken of neurobiology in the absence of a neural system. One of leading plant neurobiologist, Monika Gagliano, points out that application of experience in animal neurobiology and behaviourism in plant research allowed for unprecedented progress in understanding how plants function. Gagliano had been trained as a zoologist, by the way.

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III.

Trees as social beings

1. HOW TREES ARE INTERCONNECTED

In a natural forest, a tree functions interconnected with other organisms. It has been since long known to foresters that neighbouring trees form root grafts. Alive stumps, decades since their trunks have been felled, are a common phenomenon (Fig. 26).

Wohlleben takes it as a proof of trees' altruism. I view this matter differently: neighbours of the fallen tree, connected with it via root grafts and mycorrhiza, simply take over an orphaned root system and adapt it for their needs. Another argument for tree altruism, put forward by Wohlleben, may be stronger. It was discovered that old beeches supplement their progeny with sugars - otherwise they would not

Fig. 26. An old Douglas fir stump still doing well thanks to being nourished by its neighbours (Warsaw University of Life Sciences arboretum in Rogów).

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survive in deep shade cast by dense canopy of the parent trees.

Although, here a philosophical question arises: what is altruism? Is a parent, who cares for a child carrying his/her genes, not acting egoistically, by all means? This dilemma seems to transgress the framework of this concise story on the nature of trees.

An interesting case of mutual support between trees of different species was documented by Suzanne Simard (Simard, Toomey 2016). Paper birch and Douglas fir supplement each other with photosynthates, depending on their needs. In Autumn, when birch loses leaves, while Douglas fir keeps photosynthesising, the latter shares their production with the former. In Summer, contrariwise, birch shares its surplus with Douglas fir. Simard supposes that this mutually beneficial exchange can be inspired by their joint mycorrhizal partner, which is vitally interested in keeping both associates in good condition.

Thanks to Suzanne Simard and other researchers, we now realise the role of mycorrhizal networks in maintaining connections among trees. Simard called it WWW – wood-wide web – as an analogy to world-wide web (Internet). Indeed, this network enables communication among plants, e.g. warning against imminent threat. If a forest is ambushed by a bark beetle, trees on its other end will soon know about the danger and will start putting up defences, e.g. calling for help of beetle's enemies – its predators. This sort of information is also transmitted via air – through pheromones, volatile compounds that carry information. As mentioned above, the role of WWW is not only communication: it is also a transportation network, carrying photosynthates among the network members – mainly trees and fungi. While sharing sugars interspecifically is not uncommon, supporting own progeny seems to be most common. An interesting, yet poorly-explained, phenomenon is coordinated blossoming of trees of one species over large areas. However, numerous cases of cooperation among trees should not overshadow significance of competition in vegetal communities. Of course, rivalry is common. It is probably like in the human world: some individuals and groups cooperate, some other compete, or establish other types of relationships.

Animals also have their own inter-connections, however, these are usually not physical as in the case of plants – because of our mobility. We are interconnected via immaterial social bonds based on psychological mechanisms, which is a kind of "software" solution. Trees, as sedentary organisms, rely largely on "hardware".

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2. HOW DO TREES CULTIVATE THEIR SOIL?

What makes trees able to live on one site for hundreds and thousands years and not exhaust the soil to the point of starving? This trick was often missed by human civilisations, whose downfall was sometimes due to the loss of soil fertility. Trees know how to do it: they cultivate and fertilise their site.

Forest soil, which is natural environment of tree roots, is not a sterile medium, like a garden soil you buy in a supermarket. It is a complex ecosystem, whose structure requires decades and centuries to form, and some features need millennia to take shape. Forest soil is being constantly cultivated by its inhabitants and role of trees is crucial in this process. They sequester carbon and other nutrients in their bodies and then pass them on for processing to a relay of other organisms. Part of that pool circulates in bodies of innumerable creatures, part is released back into atmosphere, and part enriches the soil, becoming incorporated into humus.

Mycorrhizal fungi are not the only beneficiaries of cooperation with trees. Roots exude compounds that stimulate growth of soil bacteria, that are a key link in nutrient cycling and take part in weathering of soil minerals. The newly released nutrients are taken up by roots and enter the local cycle. An effective trick that trees use is covering soil with a blanket of litter. Preservation of moisture and isolation from light foster development of the soil ecosystem. Members of this community, from tiny bacteria through rain worms and small mammals, all contribute to optimal structure, aeration and mixing of the soil.

As mentioned above, trees "abandon" old, unneeded tissues, such as those in the centre of trunk, fallen leaves, or rejected twigs and roots. They are decomposed by saprotrophic organisms and the released nutrients are incorporated anew into tree body. Additional nutrients, mostly nitrogen and phosphorus, are brought in by birds, bats, and other small mammals that nest of rest in hollows and on branches but feed elsewhere (and defecate in or near the tree). For a tree, it pays to be hollow, rich of dead branches and inhabited by insects, because it attracts fertiliser deliveries. When examining a hollow with a probe, be cautious not to harm its inhabitants, as they are allies of the tree.

Soil genesis processes are long-distance runners. Formation of an optimal soil structure and development of a complete soil ecosystem takes centuries and some processes require even passing through an ice age. Anthropogenic

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Box 7.

A HANDFUL OF HEALTHY SOIL

contains, among others:

- ONE TRILLION (1 000 000 000 000) BACTERIA
- 10 THOUSAND PROTOZOANS
- 10 THOUSAND NEMATODES
- 25 KM FUNGAL HYPHAE

(Sala 2020)

soils are usually congested by pressure and vibrations of moving vehicles. This degradation reaches deep and is basically irreversible in the framework of human life. Mulching may provide some relief, as it fosters restoration of soil life and gradual improvement of soil structure. In ancient trees (particularly those growing in natural forests), it is also the ancient soil that is of high value, as it could take long time to develop, in symbiosis with the tree.

At this point, philosophical questions arise: where does one tree end and another begin? Where does a tree end and a fungus begin? Can we talk about clear-cut boundaries between individuals? Maybe there are no individuals and forest is one big superorganism, consisting of plants, fungi, slime moulds, bacteria, as well as insects, mites, nematodes, vertebrates... Whatever the answers, it is quite clear that trees are firmly rooted, both literally and figuratively, in communities where they live.

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3. URBAN TREES – A HARD LIFE

In a natural forest, trees improve together their environment – a specific microclimate and fertile soil. They support each other with information and photosynthates. They use support of other organisms, particularly mycorrhizal fungi.

This is certainly not the case with street trees, growing in narrow squares of congested soil. We deny them water, poison with salt and exhaust fumes, expose to extreme heat. In addition, we remove green branches – their only source of food – to assure clearance and often even without a good reason. We damage their roots by building above- and below ground infrastructure. No wonder their life is short and miserable. If we want to have any trees in cities, we have to make extra efforts to create optimal conditions in the environment that is basically hostile to them. First of all, improve soil quality and quantity. A minimum is to fence off, a possibly large area, even if it is one of those piteous squares cut out of a sidewalk. Let's try to mimic natural processes. Trees, like chickens, love litter – and tree's litter is called mulch. So, do not rake the fallen leaves, because they are the fertiliser that trees make for themselves. If it is not possible to let a tree do their own site improvement, supplement the soil with mulch.

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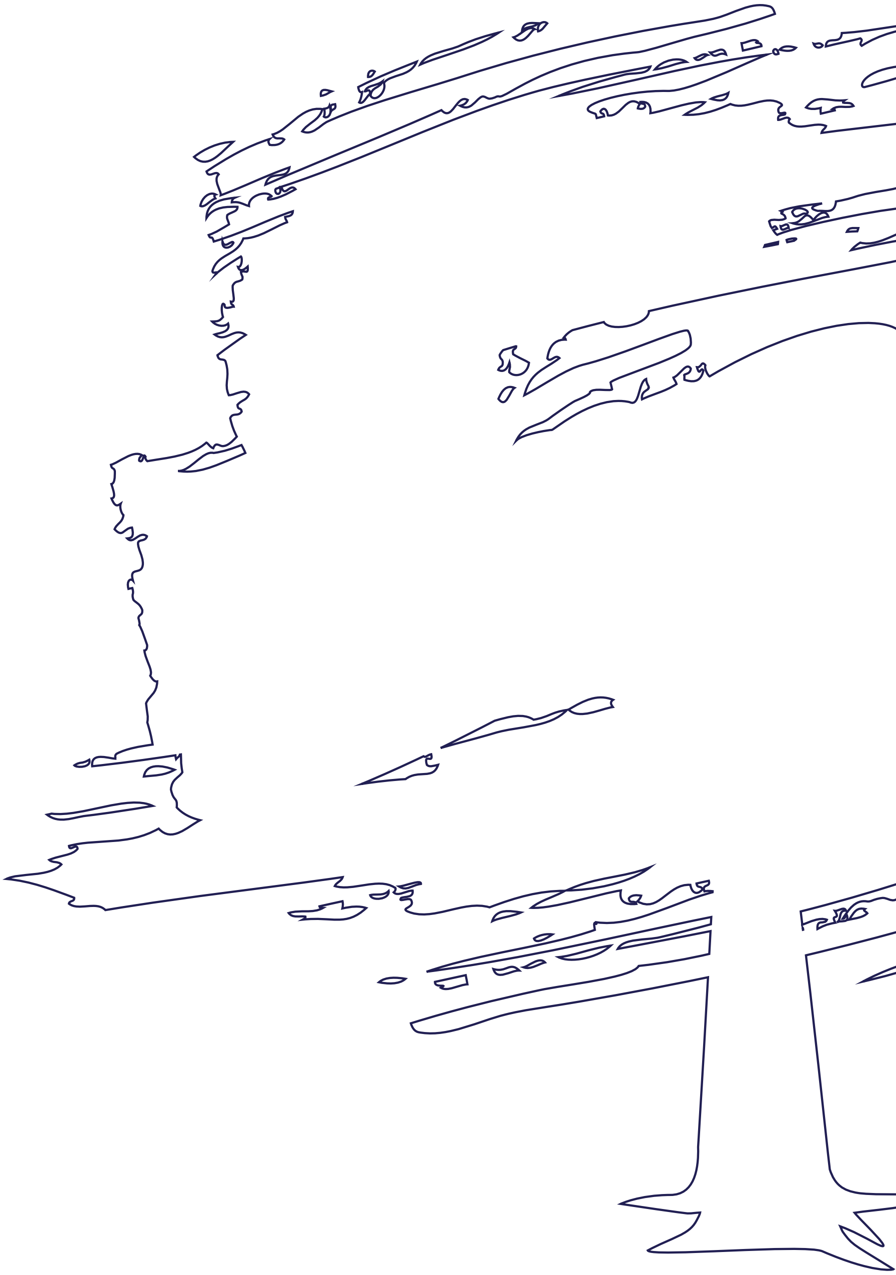

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Instytut Drzewa Sp. z o.o.

www.instytut-drzewa.pl

tel.: 789-032-424, e-mail: biuro@instytut-drzewa.pl

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