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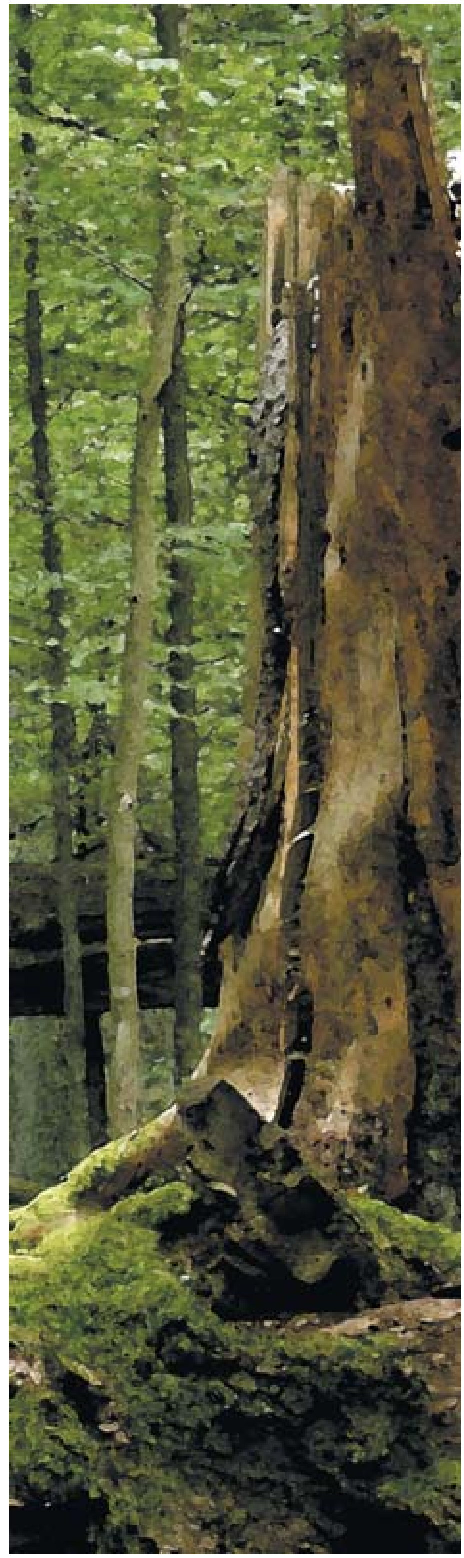
THE AFTERLIFE OF A TREE



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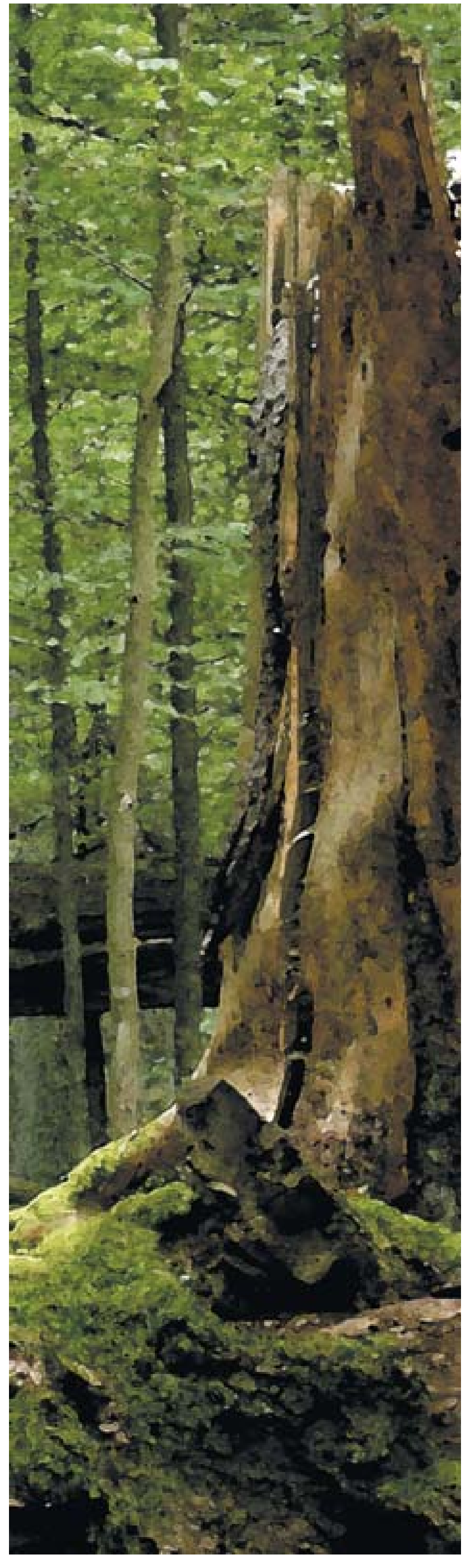

INTRODUCTION

Below, like wrecks of cities, on the ground
Vast, fallen oak-trees spread their ruin round;
A trunk like shattered walls and columns seems;
Here are branched stumps and there half-rotted beams,
Hedged in with grass. (...)

For when to pass the outskirts you are able
And the dense tangled copses, you will come
Upon a mighty rampart, in the gloom,
Of stumps, logs, roots, defended by a mire,
A maze of streams, a net of weeds and briar,
And anthills, nests o wasps and hornets keen;
And slimy coils of serpents there are seen.

("Pan Tadeusz" Adam Mickiewicz, translated by W. Kirkconnell
The Polish Institute of Arts and Sciences in America, New York, 1962)

A forest ecosystem is comprised not only of an assemblage of living trees or 'a stand' which provides the most significant part of the forest biomass, but it also includes all other plants and organisms living within this environment. This space includes the soil, with areas overshadowed by the trees' canopy, as well as open, treeless patches such as glades and gaps overgrown by shade intolerant vegetation and inhabited by specific fauna often different from that occupying the shaded areas of the stand. A forest such as the one described is a dynamic system, in which the growth and development of trees and their death and decay determine the temporal and spatial patterns of a variety of continuously ongoing processes. This network of interdependent species and their associations means that a change in any single element in the system can result in changes to other components, while the entire stand remains in a dynamic quasi-equilibrium for long periods of time.

Polish forests exhibit great variability in terms of species composition, structure and human impacts, from single-species plantations and multiple use managed forests, through to forests almost excluded from direct human activity and retaining many characteristics typical of natural systems. The present book is devoted to dead wood, mainly in forests subjected to minimal management. Despite the focus of the book on semi-natural forests, dead wood is also necessary in managed forests and amounts generally found there ought to be increased. Dead wood and old, hollow trees are essential to a functioning forest ecosystem and necessary for the conservation of a myriad of species including some that are endangered.

In recent years the value of dead wood for a variety of forest organisms and its function in the ecosystem have been identified. However, these discussions usually address the value of dead wood to only a few organisms and rarely is the significance of dead wood to the entire system explored. Perhaps more importantly, very little information on the value of dead wood has been communicated to the general public. The goal of this book is to provide the general reader with sufficient knowledge to understand the processes that create and remove dead wood as well as the value of dead wood to forests and their inhabitants. We have provided references for more specialised literature at the end of each chapter and hope that the inquiring reader will utilise this information.

Dead wood – what is it? Wood, in general, is the basic structural material that supports trees and shrubs. It is mainly composed of dead tissue (more than 90% of the total weight), but it also contains living cells. "Dead wood" is not a precise term, but is used to communicate the ideas about dead wood in a more understandable fashion. To be more accurate, one should speak about decaying wood

J. Walencik

Photo 1. Białowieża Primeval Forest

of dead woody plants or of their parts. When we talk about dead wood, we do not mean growing, living trees, but dead specimens (standing or fallen trees) or their parts (fragments of stems, branches, roots, stumps, etc.). We rarely mean the wood, living or dead, of a living tree or shrub. It would therefore be sufficient to refer to "wood" without additional descriptions, however, we have decided to use the adjective "dead" to avoid any misunderstanding.

Forests are the most complex and structurally rich as well as the most abundant terrestrial vegetation assemblage on earth in terms of organisms. Of all terrestrial organisms, half of the species are associated with forests and this number is expected to climb as knowledge about organisms found in tropical forests increases. Dead trees and shrubs and their parts are integral components of a forest (photo 1), which are necessary for proper ecosystem functioning and the maintenance of a large part of the forest biodiversity ■, leading to the complexity and perhaps long-term stability of forests.

Biodiversity:

is the variety of forms of life in a given area, usually considered at three levels of the ecological hierarchy: genetic or the variety of genes within given populations; the variety of species (species richness), and the assemblages of ecosystems and landscapes

In many northern temperate climates, the process of wood decay is completed within 5 to 100 years (depending on species, debris dimension, type of environment, position with respect to the ground, etc.; in Tasmanian temperate forests, however, it can take from 2 to 300 years). In unmanaged Central European forests, dead wood usually comprises up to 25% of the entire volume of wood ■ in the forest. If forests lacked an essential element like dead wood, we would be discussing tree stands rather than functioning ecosystems.

Entire volume of wood:

the volume of wood per unit area, usually expressed in cubic meters per hectare.

Although we have used our own studies and observations to discuss the role and importance of dead wood, we have also drawn on the vast amount of information on dead wood in world-wide literature. One of the most prominent examples of forests abounding in dead wood is the Białowieża Primeval Forest – the largest and best preserved remnant of unmanaged, semi-natural deciduous and mixed forest in Europe, that is relatively well studied. However, the subject of this book is not only the Białowieża Forest. It is dead wood, an element that should not be missing in any forest. In this book, we will explore the myriad forms of forest life associated with dead wood. We will discuss its importance to the array of forest inhabitants including the relatively unknown world of plants, animals and fungi that are associated with decaying logs, the root plates of uprooted trees, stumps and branches.

The present book is an adapted English version of the Polish edition of "The afterlife of a tree" by Gutowski J.M. (ed.), Bobiec A., Pawlaczyk P. and Zub K., updated with a more global perspective provided by the North American and Australian experience of dead wood management.

We will generally use the English names of species, followed after their first appearance by scientific names. In the instances, however, where English names do not exist, only the Latin nomenclature will be used.

At this point, we would like to thank all the people who contributed to this work: Stefan Jakimiuk for inspiration and the very idea of the subject, Małgorzata Bobiec for drawing most of the figures, Mirosław Waszkiewicz for drawing selected species and Piotr Galicki for drawing woodpeckers. We were authorised to use without charge the photographs made by Jan Baake, Cezary Bystrowski, Marek Czasnojć, Wojciech Janiszewski, Zbigniew Kołudzki, as well as, Janusz Korbel and Jan Walencik who also made remarks on the draft manuscript. We are indebted to Roman Królik, Daniel Kubisz, Andrzej Lasoń, Tomasz Majewski, Andrzej Melke and Marek Wanat for completing the checklist of beetles associated with spruces, to Anna Bujakiewicz for information on relict fungus species, Ireneusz Ruczyński for unpublished materials on bats, and Dorota Szukalska for unpublished material on plants. Krzysztof Sućko helped with indices and several drawings. Our special thanks are due to Dr Mark E. Harmon, Oregon State University, and Professor Sven G. Nilsson, Lund University, for their thorough reviews of the manuscript. We are equally thankful to Professor Janusz B. Faliński, Białowieża Geobotanical Station Warsaw University, for his insightful comments on the Polish version of the book, which are also very helpful in the present English edition. We are indebted to Dr Simon J. Grove, Forest Research and Development, Hobart, Tasmania, for his fundamental contribution to the book, including editorial layout and crucial comments on the content. The authors are solely responsible for any possible shortcomings. Many thanks are due to Johanna Willi and Eunice Blavascunas for their great effort to make our English readable.

1.1

HOW LONG DO TREES LIVE?

Sclerenchyma:

a tissue usually made of dead cells with strongly wooded walls; it is composed of fibres and of stone cells (or brachysclereids).

DBH:

diameter at Breast Height, with breast height being 1.37 m

Woody plants are vascular perennial plants with woody stems. They include trees (e.g. pine), shrubs (e.g. hazel Corylus avellana), dwarf shrubs (e.g. cowberry Vaccinium vitis-idaea) and lianas or creepers (e.g. ivy). Their woody parts contain tissues saturated by lignin or sclerenchyma ■. They often reach gigantic sizes (in height and diameter) and may live up to thousands of years. The widest trees in Polish forests are poplars *Populus* species with DBHs up to 4 m ■, oaks *Quercus* species (more than 3 m), elms *Ulmus* species (2.9 m) and ashes *Fraxinus excelsior* (2.2 m). The tallest trees in the Białowieża Primeval Forest and in the Beskids (the mountain chain in southern Poland), are Norway spruces *Picea abies*, where they can reach 55 m. The Beskid silver firs *Abies alba* are the tallest trees in the region (at 58 m), whereas the beeches *Fagus sylvatica* in Pomerania grow up to 50 m in height.

North American redwoods *Sequoia sempervirens* may reach heights of 112 m and DBHs of 6-9 m during their lives which may last 2200 years. The volume of a single redwood can total 1000 m^3. Giant sequoias *Sequoiadendron giganteum* in California can live 3200 years. The largest specimen, The General Sherman Tree in Sequoia National Park, is 100 m tall and 9 m wide (DBH) totalling 1500 m^3 in volume (in contrast, the average tree volume per hectare of forest stand in Poland ranges from 200 to 300 m^3). The Australian mountain ash *Eucalyptus regnans* is considered the tallest flowering plant in the world and grows to 100 m in height (whilst another giant in the southern hemisphere, *Eucalyptus obliqua* grows in Tasmania and reaches 90 m in height), and the African baobab *Adansonia digitata* can grow as wide as 15 m DBH. However, Montezuma baldcypress *Taxodium mucronatum* in Mexico grows even wider (up to 16 m DBH) during its lifespan of 2000-5000 years.

Although famous in Europe for their size, oaks may seem modest compared to the giants listed above, but they too may live long lives and reach considerable dimensions. Apparently the oldest pedunculate oak *Quercus robur* specimen lived in Montravail (France) for approximately 2000 years, and the widest one resides in Rumskulla (south-eastern Sweden) with a DBH of 4.6 m.

The oldest trees, however, do not exhibit impressive dimensions. Struggling with harsh climatic and site conditions in the White Mountains (eastern California), the age of the bristlecone pine *Pinus aristata* Methuselah is estimated at 7,000 years. Japanese cedars *Cryptomeria japonica* in Japan and China are also known to live for similarly long periods. The plants, however, that live the longest are not trees, but the clones of the rather small creosote bush *Larrea tridentata* in the Mojave Desert of California that may reach 12,000 years of age, and a relative of the cow- and bilberry *Gaylussacia brachycera* from Pennsylvania that are known to be as old as 13,000 years.

The oldest tree in Poland is the 1280 year old English yew *Taxus baccata* in Henryków Lubański. Both silver firs and Norway spruces in Babia Góra National Park (southern Poland) are known to live for long periods – 435 and 370 years, respectively. The oldest European larches *Larix decidua* – 360 years – occur in Świętokrzyski National Park (central Poland).

Among the oldest broad-leaved trees in Poland is a pedunculate oak near Piotrowice – about 760 years of age. The widest tree is a white poplar *Populus alba* in Leszno near Warsaw, with a DBH of 4.3 m, and the widest oaks at 3.3 m are in the valley of the Odra river near Zielona Góra and in south-eastern Poland near Jasło. Also, small-leaved limes *Tilia cordata* may live very long lives and reach immense sizes. The oldest is probably an individual from Cielętniki near Częstochowa (central Poland), aged 540 years. The largest and one of the oldest European white elms *Ulmus laevis* (460 years, DBH 2.9 m) resides in Komorów near Gubin. In the Radęcin forest (a part of Drawieński National Park, north-western Poland) there are 470-year-old sessile oaks *Quercus petraea* and 340-year-old beeches.

In the Białowieża Primeval Forest there is a plethora of old trees: oaks, pines, limes, ashes and other species. A detailed study in this forest showed that the widest Scots pine *Pinus sylvestris* has a DBH of 1.24 m and the tallest one reaches 44 m in height. The age of the oldest Białowieża Scots pine – 370 years – was considered the record for Poland for some time, but one recently discovered small, twisted Scots pine growing on the rocks in Pieniny National Park (southern Poland) is 550 years old. Although it is a remarkable age for this species, the oldest Scots pine, over 800 years, was found in Finland. The European ash *Fraxinus excelsior* from the Białowieża National Park is considered the tallest specimen in the world – 43 m, DBH 1.6 m.

1.2

WHAT IS WOOD?

Wood (xylem) is a complex tissue of vascular plants made of vessels and tubes that transport water and minerals, and of supporting components (woody fibres, fibre tubes) and parenchyma. Wood commonly occurs in stems and roots of woody plants. The vessel elements created in the stems form the layers of (1) sapwood, which transmits water from the roots to the crowns, and (2) heartwood, which does not transmit water and is created by woody parenchymal cells and vessels clogged by thyloses (fig. 1).

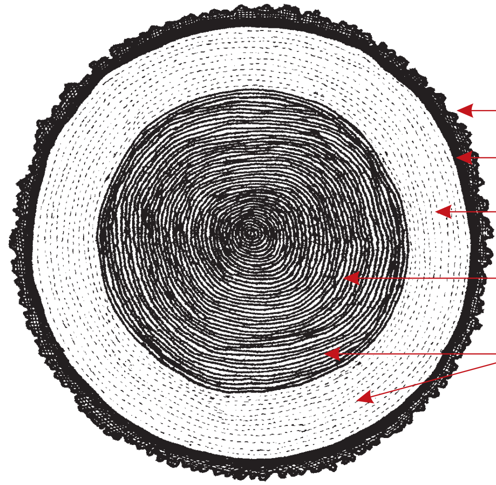

Figure 1. Cross section of a tree trunk
(M. Bobiec)

The weight of a unit volume of wood

is considerably lower than that of steel. Thus, if two blocks of the same weight are compared, one of wood and one of steel, they will reveal a similar resistance to bending or breaking.

From a utilitarian point of view, wood is the raw material generated from harvested trees and processed into various products. Its properties include high relative resistance (low density) ■, matching that of steel, and low thermal and acoustic conductivity. However, wood, despite being a renewable resource, has technical disadvantages not found in steel and other structural materials. Wood absorbs water, contracts, cracks and deteriorates rather quickly.

In many temperate climates, trees lay down concentric annual rings of alternately succeeding layers of early (spring) wood and late (summer) wood; the latter is characterised by a darker hue and 1.5 times greater density than that of the early wood.

Wood is a conglomerate of several multiple-particle organic compounds: cellulose (40-60%), hemicelluloses (23-35%), lignin (21-30%) and other substances such as resins, waxes, fats, tannins, alkaloids and minerals.

Wood may persist for hundreds of years if stored under dry conditions or if permanently submerged in water. Ancient (in Europe mainly pedunculate) oak wood that was preserved for hundreds of years lying under thick layers of peat or silt under anaerobic conditions is considered a very valuable material for exclusive furniture. Saturation with anti-decay preservatives increases wood durability.

Depending on the species, wood exhibits various physical and chemical characteristics. Lime wood is very soft and easy to process, and is a favourite sculpting material. The wood from balsa *Ochroma*, a tree species occurring in South and Central America, is exceptionally light (about 0.1 g/cm^3). Balsa was used as a material for the construction of T. Heyerdahl's raft Kon-Tiki.

The woods of hornbeam *Carpinus betulus* and oak are relatively hard and heavy. One of the heaviest and most hardwearing woods is lignum vitae *Guaiacum officinale* (about 1.1 g/cm^3 – heavier than water) which has been used for the bearings of ship propellers (its highest resistance to friction is achieved in 100% humidity) as well as for other purposes.

Ebony is a very valuable wood obtained from various tropical species. Its dark brown or black coloured heartwood is hard, heavy and hardly fissile. The most precious is black ebony, the wood from the genus *Diospyros* (mainly *D. ebanum*). It is used as a material to make furniture and musical instruments. The palisander wood obtained from trees from the genus *Dalbergia*, growing in the tropics of America, Asia and Oceania, has similar qualities. It is fragrant, with a dark irregular hue.

Mahogany is harvested from various species found in the Americas and Africa (e.g. *Swietenia*, *Khaya*, *Entandrophragma* species). This cinnamon or red-brown wood has a moderate hardness and is relatively resistant to moisture and cracking; mahogany is used in furniture and veneer production. The red-brown, fragrant resinous teak wood of *Tectona grandis*, from the Indian Peninsula, Laos and Burma, is very durable and very resistant to insects and fungi.

Summary of Chapter 1.

Wood is a complex tissue of plants, including the vessels and tubes that conduct water and minerals and the supporting elements (woody fibres, fibre tubes) and parenchyma. It is a conglomerate of several multiple-particle organic compounds: cellulose (40-60%), hemicelluloses (23-35%), lignin (21-30%) and other substances.

Wood is produced in woody plants: trees, shrubs, dwarf shrubs and lianas. Although wood is generally composed of dead cells, this book uses the term "dead wood" for the wood of dead woody plants or their parts.

Trees may reach immense size (more than 100 m in height and up to 16 m in diameter), and may live for centuries (up to 7,000 years). In Poland, there are no trees of such size and age, but on a European scale, the trees in Poland are among the most magnificent, and the large expanses of forests are relatively well preserved.

One of the basic indicators of the naturalness of a forest is the presence of dead wood. Its quantity in natural forests may exceed 25% of the volume of living trees.

* Original published English translations are anticipated by slash /. Our own translation is put within brackets [ ].

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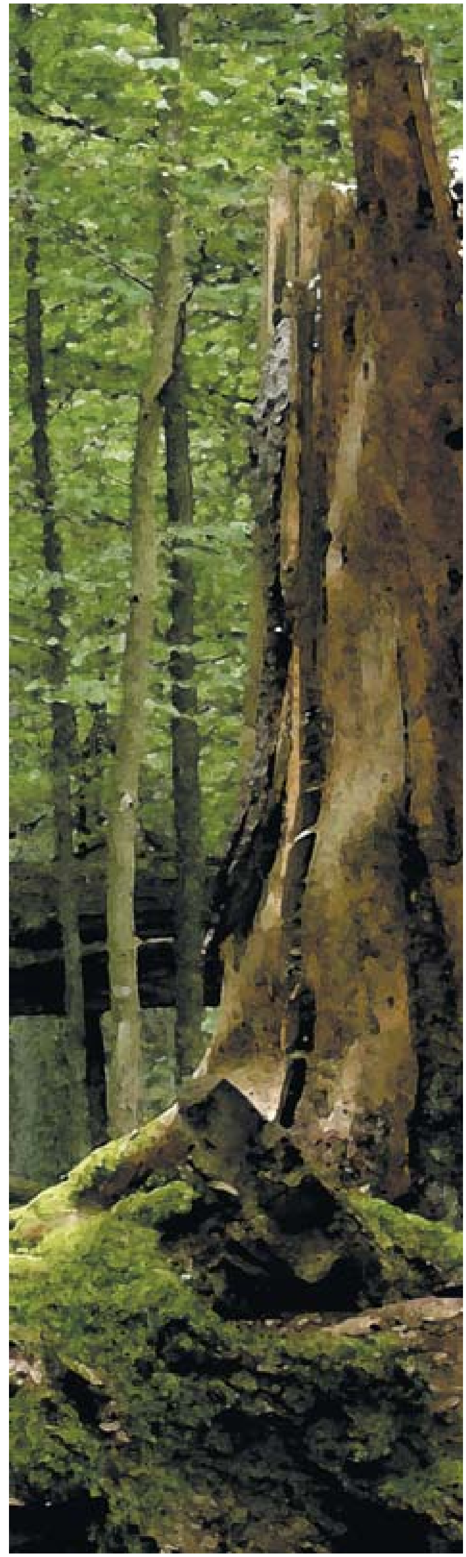
Chapter 2

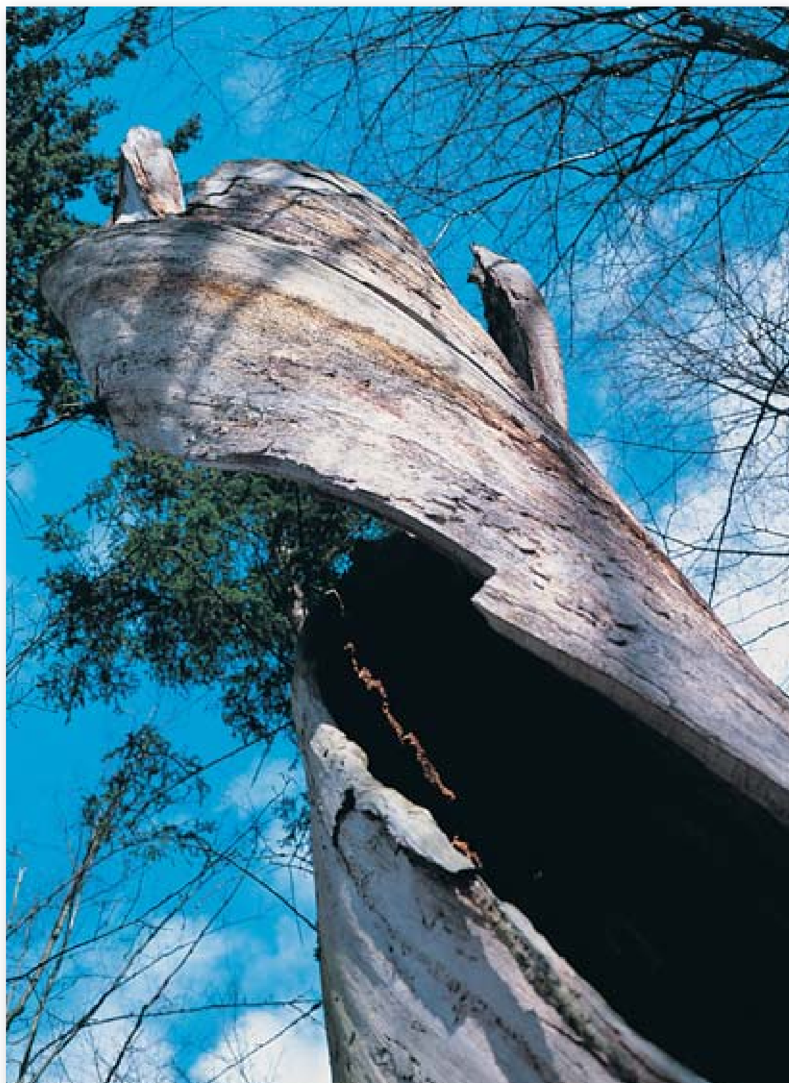


DYNAMICS OF DEAD WOOD

2.1

DEAD WOOD IN FORESTS

Dead wood occurs as dead fragments of living specimens (e.g. rotten parts of trunks, dead boughs and branches, dead roots) or whole standing or fallen trees. Studies from forests in North America show that dead wood (or Coarse Woody Debris, CWD) may cover up to 25% of the ground surface. As the wood of living trees is the primary construction material of forest stands, resisting disease infection and insect attack, the death of a tree or of its components opens the door to myriads of organisms ready for just such an opportunity in order to exploit the dead wood. And such opportunities in natural forests can be common depending on the numbers of trees available.



J. Walencik

Photo 2. Each year approximately 100 trees die in 1 km^2 of this natural forest; dead Scots pine in the Białowieża Primeval Forest.

The average increment of wood volume accumulated in the living trees of natural stands in the Białowieża Primeval Forest totals 3.3 m^3/ha per annum. As these ecosystems are considered to be in a sort of equilibrium, approximately the same amount of wood is thought to decay. This volume is approximately equal to that of one specimen of a sizeable spruce (DBH 45 cm, height 40 m) or hornbeam (DBH 55 cm, height 23 m). Extrapolated over a landscape, these numbers suggest that, on average, 100 such trees are expected to die on every 1 km^2 of forest annually (photo 2)! Mortality may claim trees of any age or size. However, it is primarily the abundant smaller trees in these forests that become dead wood.

If dead wood did not decay, or was not removed through some other process such as fire, the ground would eventually become covered by the accumulated CWD. Approximately 3.3 m^3/ha CWD is accumulated on the ground yearly. However, the material on the ground includes the current year's input plus the smaller and smaller remnants of the previous years' inputs that have been subjected to gradual decay. The oldest recognisable CWD may be 100 years old. This rate of decay results in a relatively constant average of 120 m^3 of dead wood lying on the ground per hectare of forest.

What does dead wood contribute to an ecosystem? It provides an enormous number of ecological niches and microsites. Imagine how a smooth cylinder of wood placed on the ground might diversify the site's microclimate. There is a 'contact zone' defined as the contact of wood or CWD with the soil, a 'shadow zone' caused by the shade from the piece of CWD characterised by higher humidity and relative thermal stability compared to areas further away from the

Snag – a standing dead tree, SDT:

intact snag – a standing dead tree with at least its major branches still attached

broken topped snag – a standing dead tree which has lost its top and attendant branches

hard snag – snag whose exterior surface remains hard and resistant

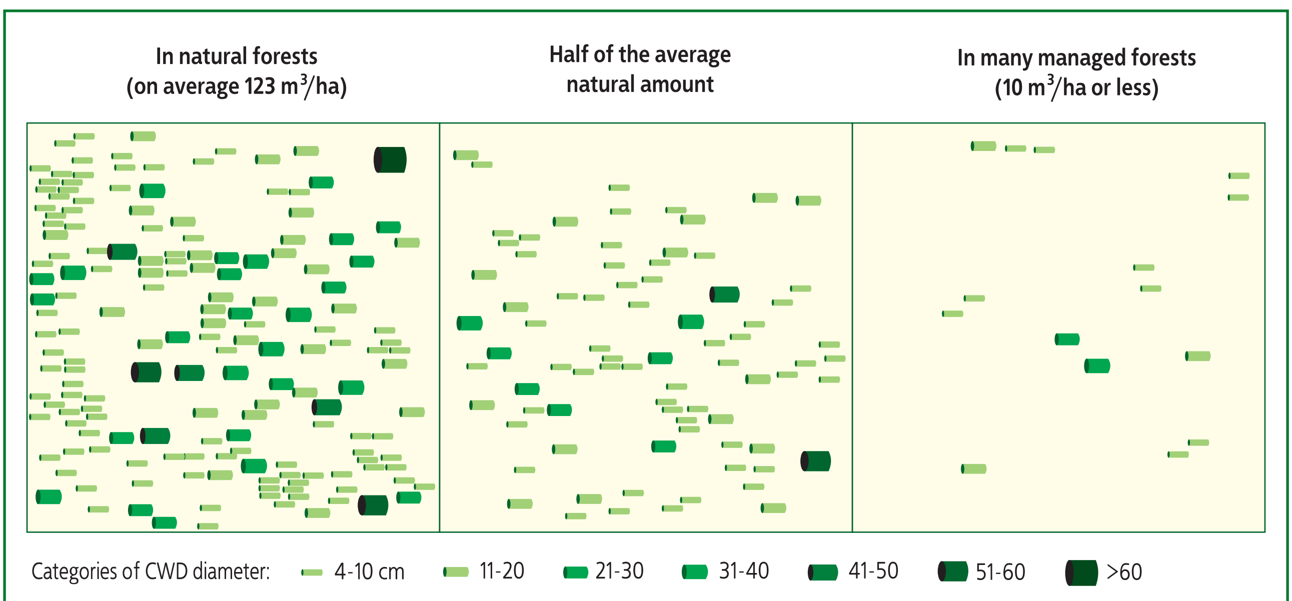
soft snag – snag whose exterior surface has become soft through decay

stump – a short remnant of a snag extending from the root crown that is unlikely to become shorter except through decay or animals ripping it apart in search of insects or other food items

log – any part of a tree lying horizontally on the ground, at least 10 cm in diameter and 1 m in length

Figure 2. Together with standing dead trees or snags ■ the average CWD volume in the BPF ranges from 130-140 m^3/ha. Under natural forest conditions, CWD contributes more than one fifth of the entire above-ground wood volume (on occasion, it may make up to half of the total biomass volume).

If fallen dead wood were evenly cut into 1 m sections, this figure shows how an average 100 m^2 of forest would appear (after BOBIEC 2002)



CWD, and an 'insolation zone' characterised by intensive evaporation and sharp temperature changes at the surface of the CWD. However, this description is a mere model, not a real piece of CWD. A real wood "cylinder" is an intricate microrelief of cracks, furrows, knots, insect-bored galleries, and other imperfections. Each of these features introduces its own variability and microclimate. The exposed surface of CWD, however, does not describe all the potential resource opportunities associated with dead wood. Its interior "flesh" is equally interesting and provides a diverse environment and food to myriads of organisms. Some organisms bore galleries and chambers in hard, fresh wood, whereas others (especially fungi) cause its disintegration (decay) so that rotten wood is made available to other groups of organisms that require either loose, powdery material or wet, sponge-like rot. If CWD consisted of absolutely smooth cylinders, it would on average provide 65 m^2 of additional surface for each 100 m^2 of forest. However, the additional surface provided by the complex surface and porous interior must be several orders of magnitude greater than a mere 65 m^2. It is hard to imagine the magnitude of habitat loss caused by the removal of dead wood from forests.

Dead wood dynamics

The quality, amount and distribution of CWD in a forest depends on the rate and mode of its input and output, and that is determined by the stand dynamics – that is the phase of stand development – as well as topography, soil characteristics, vegetation, and the rate of the processes that recycle CWD (e.g. decay, insect activity and fire).

Beginning with the seedling and sapling stages, young trees in stands undergo competition for nutrients and light. Faster growing trees outcompete less adapted individuals that gradually die. Such natural self-thinning corresponds to silvicultural thinning applied to commercial forests. ■ Self-pruning of the lower branches also occurs; these branches are shaded by the upper parts of crowns, causing the loss of photosynthetic capability and eventually the loss of the branches themselves. Gradual development of the stand in this time period is accompanied by a constant and relatively even input of CWD to the ecosystem. After reaching the age of the most intensive self-thinning when a relatively large number of trees are stressed and subject to mortality (at the age of 20-60 years, depending on the species and site characteristics), fallen boughs and branches contribute more and more to the overall CWD volume. With time, mature trees infected by disease or attacked by insects, dying of old age, or subjected to

Pre-commercial thinning:

a silvicultural operation performed in thickets in order to adjust species composition, spacing, stand density and tree quality. Commercial thinning – a silvicultural operation performed in premature stands, aimed at the removal of trees deemed less valuable from a commercial point of view, as well as shaping the desirable stand structure.

Photo 3. A fragment of a lime-hornbeam-oak stand in a stage of relative equilibrium – a rather small amount of dead wood originates from 'self-pruning' and the decay of single trees – Białowieża Primeval Forest

A. Bobiec

events such as fire or strong winds, become the source of the larger-sized CWD (photo 3, 4). Such a state of relative dynamic equilibrium can persist for fairly long periods (probably more than 200 years) if the stand maintenance processes remain intact. In general, such forests are characterised by a relatively small amount of dead wood (on average 40-80 m^3/ha) and by the fact that thecompositional quality of the CWD reflects the species composition of the stand. However, there is variation in the CWD related to stand composition, structure and other variables. Exceptions to this pattern are "reorganizing" pioneer stands, established by spontaneous invasions of shade-intolerant and fast-growing but short-lived species (in particular birches *Betula* species, aspen *Populus tremula* and goat willow *Salix caprea*) on abandoned fields, clearcuts and areas affected by intensive disturbances such as fires or hurricanes. As an example, in European hardwood forests, pioneer stands in the transition stage after reaching the age of 80 years enter a period of massive atrophy, when dying pioneer trees are replaced by shade-tolerant, 'climax' species (usually hornbeams and small-leaved limes characteristic of the dominant forest assemblage in the Białowieża Primeval Forest – mesic oak-lime-hornbeam). In such a case, at this stage of transition, the type of dead wood does not reflect the actual species composition of the living stand (photo 5).

K. Zub

Photo 4. Dead Scots pines, Białowieża Primeval Forest

Photo 5. The natural change in stand composition (natural 'remodelling') from the pioneer (birch-aspen) stage to the 'climax' (shade-tolerant) stage is a period of intensive creation of dead wood in the ecosystem, Białowieża Primeval Forest

A. Bobiec

Abiotic factors:

chemical factors and atmospheric and weather phenomena: precipitation, wind, frost, etc.

Biotic factors:

impact of living organisms: insects, fungi, bacteria, etc.

An inseparable component of the dynamics of forests are the various types of disturbances causing local mortality of the stand by abiotic or biotic factors ■. From the point of view of the forest ecosystem dynamics, these phenomena should not be considered as negative. Disturbances vacate space that can be occupied by a new generation of shrubs or trees. The process of tree mortality or loss followed by tree renewal in the new gaps creates a mosaic of forest patches in a variety of developmental stages that perpetuates forest cover. Disturbances can be natural (e.g. strong winds, bark beetle outbreak). However, natural disturbances can be enhanced or reduced by human impacts such as fire suppression or thinning, or disturbances can be directly caused by humans (e.g. clearcut, arson). Natural disturbances are irregular and hardly predictable either spatially or temporally. If a disturbance affects a stand, gaps are created and an immense local stock of CWD may be deposited (photo 6) consisting of the trees that died as a result of the disturbance. However, some disturbances (e.g. fire) may remove existing CWD as well as create new CWD.

Disturbances in natural forests may occur at various intensities, at a variety of spatial scales, and for some disturbances, at a variety of temporal scales; as an example, the effects of a windstorm may range from a single uprooted tree to perhaps hundreds of hectares of windblown trees.

Abiotic disturbances (e.g. fire, snowfall) may occur regardless of biotic factors, but they usually work together. A fungal disease (e.g. root fomes, *Heterobasidion annosum*), often infects groups of neighbouring spruces or other species. The disease results in the decay of the lower part of trunks and roots, thereby increasing the potential for infected trees to be snapped or uprooted by wind. Insects living under bark are often an additional complication in the disturbance

K. Zub

Photo 6. Natural disturbances provide locally abundant reserves of dead wood, Białowieża Primeval Forest

process. In stands dominated by spruce this is usually a spruce bark beetle *Ips typographus* (photo 55) that, at relatively regular time intervals of several years, undergoes an abrupt population expansion. During such periods, single trees and whole groups of trees (sometimes over vast areas), and often those with lower resistance (because of fungal infection or drought), are killed. These insects open infection 'gates' and increase a tree's susceptibility to breakage or uprooting through the introduction of decay fungi and diseases. When a tree falls, it often injures its neighbours, facilitating and sometimes transmitting infection. In this way, small disturbances can lead to a cascade of effects that influence the stand at larger scales.

As a result of disturbances interacting with site characteristics such as topographic situation and soil, natural forests are characterised by high spatial and temporal variability. This variability includes fragments of mature stands with a relatively small amount of CWD, senescent stands where the CWD volume (200-400 m^3/ha) can exceed that of living trees, as well as young stands with relatively small CWD volumes. Disturbances in the forests of Białowieża are often a factor causing local changes in tree species composition, such as the replacement of spruce by broad-leaved tree species. Thus, conformity between living species and CWD composition is reached only after complete decay of the pre-disturbance CWD.

Monitoring of CWD is important from scientific and practical viewpoints. Careful observation of CWD in forests in terms of species composition, volume, decomposition rate, spatial distribution and its reference to the living stand will provide invaluable information on past and present developmental trends of these forests, and will enable a better understanding of CWD and the processes underlying its formation across space and time.

2.2

DEAD WOOD IN PARKS AND GROVES

In parks and groves there is almost no dead wood, however in places, larger and less managed parks do contain much dead wood. In these areas, dead wood is managed in the high use zones of the parks where visitors have a much greater chance of being injured. In smaller parks, especially those associated with our cities and towns, dead wood is rigorously managed. In intensively managed parks and groves, dying trees and shrubs, withering boughs, fallen branches etc. are likely to be removed or burned because they are thought to reduce the visual quality or because they present safety hazards. Managers are often unable to keep up with the deposition of dead wood, therefore in practice even such parklands are far from being without dead material. Dying or dead trees and withered boughs, even if removed after a short time, may provide habitats for species with short life cycles able to reproduce before the dead wood is removed. Therefore such parks are not dead wood deserts. Various species of insects and other invertebrates associated with CWD can be found in such situations. Because stumps in parks and groves are rarely grubbed out, habitats for underground species requiring CWD are more prevalent. Dead stumps and roots are important habitats for numerous saproxylic species.

Parks and groves also harbour old hollow trees – a habitat often lacking in commercial forests (photo 7, 8). Such monumental or 'veteran' trees, if only barely alive, are usually retained in these ecosystems. Rotting wood microhabitats, or rotting fragments of wood in living standing trees, e.g. side necroses, cavities and hollows resulting from the loss of withered boughs, rotting trunk interiors, dead and dying tissues inside cavities, etc., are unique habitats for stenotopic invertebrate species. Unfortunately, sometimes concern about the structural stability of veteran trees is expressed through tree 'surgery', such as the removal of the rotten substrate from cavities, application of wood preservatives, or filling hollows with inorganic filler such as concrete. Obviously, such treatment kills many of the organisms inhabiting cavities, hollows or side necroses. Such actions can help extirpate species associated with such habitats from parks and groves and may help endanger some species. If extinction does occur, the loss to nature is irreparable, and the 'surgery' results are in any case scarcely beneficial to tree health and longevity.

Las Bielański, a designated nature reserve located in the Warsaw metropolitan area, is an example of a park where old hollow trees exist and are retained, harbouring interesting, rare and even endangered species of invertebrates. Such species are more numerous there, in a relatively small area, than in most homogenised and impoverished commercial forests. Similarly, many rare species of birds find favourable nesting and breeding habitats in Las Bielański.

Groves:

single trees and shrubs or their groups outside the forest and urban areas, fulfilling ecological and aesthetic as well as production functions through the supply of wood, fruits, etc; groves can exist in isolation, in rows, groups, belts or patches, and can occur at roadsides, in fields and meadow-pastures, at watersides, etc.

Saproxylic species:

those species that are "dependent during some part of their life cycle upon the dead or dying wood of moribund or dead trees (standing or fallen), or upon wood-inhabiting fungi, or upon the presence of other saproxylics" (Speight, 1989); we distinguish obligate saproxylics (those that need dead wood) and facultative saproxylics (those that "prefer" it).

Side necrosis:

outer layer of wood killed by local destruction of the cambium as a result of fire, intense insolation, strong frost, damage induced by animals or machines.

Stenotopic species:

species that can live only in strictly defined environmental conditions; fastidious with respect to humidity or other abiotic and biotic environmental features.

J.M. Gutowski

Photo 7. An old hollow willow is not a blot on a park's reputation but provides a habitat for the lichens on the bark and invertebrates in the rotten wood, Białowieża

In parks and groves, dead trees, shrubs and their parts, unless there is a safety issue, ought be left until completely decayed or until some other natural and expected process intervenes (e.g. fire). In particular, those trees with cavities or hollows should be retained and on no account should one alter or remove their rotting wood microhabitats.

A. Bobiec

Photo 8. Old and dying oaks are unique and essential habitats for a variety of saproxylic organisms, southern Sweden

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Summary of Chapter 2.

The usefulness of a dead tree as a microsite increases along its decay trajectory. Weakened by stress from competition or age, trees become susceptible to infection and infestation by numerous species of flora, fauna and fungi affiliated with dead wood.

Dead trees and shrubs, snags, fallen logs and branches provide a multitude of unique microhabitats in a forest. Such microhabitats add a great deal of diversity to a forest: a combination of shapes, wood species and degrees of decay, that enable the co-existence of many species with diverse preferences and life strategies, in a relatively small area.

Dead wood is a very dynamic system, with continuously changing characteristics. Changes result from altered positioning (e.g. tree fall) and progressive decay of dead tissues.

The maintenance of forest biodiversity is dependent upon a continuous and steady supply of CWD, balancing the rate of its mineralisation or loss through processes such as fire. For example, the forest floor in a temperate climate where decay is the dominant process for mineralising wood (e.g. in Białowieża Primeval Forest) ought to contain an average volume of 120 m^3/ha CWD i.e. a fifth of the entire above ground forest biomass. Reduction of the CWD quantity may risk the loss of many of the species associated with dead wood.

Input to the dead wood supply is governed by two basic processes: competition among trees and their branches and disturbances. The latter includes phenomena of discrete and relatively sudden occurrence caused by biotic (e.g. spruce bark beetles) and/or abiotic (e.g. windstorm) factors. Loss of the dead wood supply is governed by processes including decay and fire.

Parks and groves, though usually lacking CWD, often provide rich habitats for species associated with dying and dead parts of living old trees.

Tree 'surgery' – the cleaning and filling of cavities and the use of chemical preservatives – does not substantially prolong the life of old trees, but may cause irreparable losses in the assemblages ■ of rare insects and other species dependent upon old trees' necroses.

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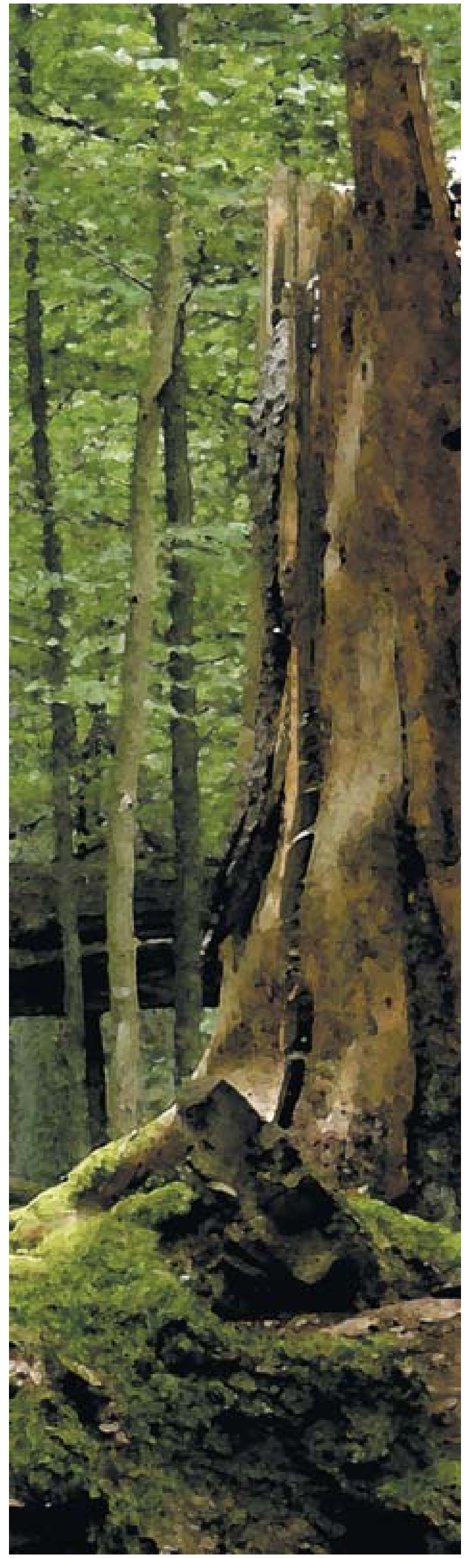
Assemblage of species:

a basic natural unit of co-occurrence of plant, animal and fungi species, related to its environment and subjected, together with this environment, to ecological succession.

Chapter 3



LIFE AFTER DEATH

3.1

STAGES IN AND CONSEQUENCES OF THE DEATH OF TREES

A variety of factors can cause tree death, either by themselves or in concert with others. These include: violent winds overturning whole trunks including roots (windblow photos 9 and 10) or snapping trees at various heights (windbreak); heavy snowfall breaking boughs and branches or whole trunks, long-lasting droughts lowering the level of groundwater or a general shortage of soil moisture, leading to tree instability; competition for light in thick compact stands; old age; fire; flood; periodical flooding; lightning strikes (photo 11); insects; fungi and

J.M. Gutowski

Photo 9. Windblow, Białowieża Primeval Forest

J.M. Gutowski

Photo 10. Windblow, Białowieża Primeval Forest mammals (e.g. beavers – photo 12, wild boars – photo 13). Every weak, declining and dead tree (in various degrees of decay) provides a habitat (a place used as a home, shelter, hunting space, etc.) for many species, especially invertebrates.

The death of a tree causes substantial environmental change in its neighbourhood. More water and light may reach the forest floor and soil temperatures may rise. The additional light and water and higher temperatures have the potential to change the habitat conditions for soil bacteria, fungi and animals; those organisms that decompose dead organic matter into simple mineral compounds. Cessation of mineral uptake by roots and the gradual decomposition of the wood contribute to a better supply of nutrients that, coupled with additional light, stimulate the growth of the surviving and newly established plants.

J.M. Gutowski

Photo 11. Lightning may be a cause of or a factor in tree death: a struck spruce

J.M. Gutowski

Photo 12. In stands close to standing water or streams, dead wood can be created by beavers; the river in the Białowieża area

J. Korbel

Photo 13. A spruce next to a mud pool used by wild boars, with visible traces of woodpeckers searching for ants *Camponotus* species living inside the trunk

Photo 14. Windblow in spruce stands triggers the succession of many organisms that develop on and under the bark and in the wood; Białowieża Primeval Forest

For those seedling and sapling trees whose growth was limited by competition for nutrients or limited light due to a dense canopy, openings created by tree death permit a sudden increase of growth.

Let us observe a tree that was uprooted by wind (photo 14). The thinnest branches are broken first, followed by thicker and thicker limbs and, eventually, the largest boughs. At this moment, the tree hitherto supported by these boughs like 'stilts' which had no contact with the soil, gradually collapses until it finally settles on the ground. At this time, the decay process is accelerated due to the increased moisture of the wood tissues and there is greater activity by soil organisms entering the softened wood. Insects, by mechanically crumbling the decaying wood, facilitate its penetration by bacteria and fungi, thus increasing the decomposition rate that returns organic matter to simpler chemical compounds. Wood decomposition occurs unevenly. The fastest decaying tissues in many trees are those lying immediately under the bark (sapwood). The hard wood of the trunk interior (heartwood) and the bark, which contain toxic alkaloids and tannins that played a protective function through the tree's life time, generally decompose at a slower rate. Sapwood decay is particularly evident in pine trees, whereas heartwood decay is common in other species.

In our temperate climate, frost plays an important role in the decay process, especially in more advanced stages of decay, when logs contain an increasing amount of water. The ice established in the inter-cellular space tears the wood tissue, softens it and changes its structure. Sharp fluctuations of temperature and severe frosts allow easier penetration of the wood by animals, fungi and plants.

A. Bobiec

Photo 15. A decaying oak in the Białowieża Primeval Forest – home to about one thousand different species

With time, the initially smooth surface of logs which have lost their bark undergoes substantial changes. The emerging cracks and hollows created by processes including freeze-thaw and desiccation, capture the spores of liverworts, mosses, ferns, and the seeds of flowering plants. At the beginning, only certain species attached to the log surface are able to cope with such difficult living conditions. As the soft rotten layer grows, logs are then colonised by other species of bryophytes that require more moisture than that available from the log surface. They are gradually accompanied and partially replaced by ferns and flowering plant species (photo 15). The compact bryophyte mats covering some logs maintain high humidity, which increases the decay rate and modifies the local microclimate. The more decayed the wood becomes, the more suitable a substrate it provides for the invading plants. Flowering plants usually cannot colonise, persist and grow until the rotten layer is several centimetres deep.

Each year the decaying log sinks deeper and deeper into the ground, changing shape and consistency from hard wood to an amorphic sponge, loose powder or amorphous wet mass (photos 16 and 17). After some time, the decayed log becomes a mere elongated hillock overgrown by slightly different vegetation to that in the surrounding area, but still recognised as the remnants of a log (fig. 3). This process is often truncated at some place in its trajectory in forests where fire is frequent and has an important role in the reduction of dead wood to soil components.

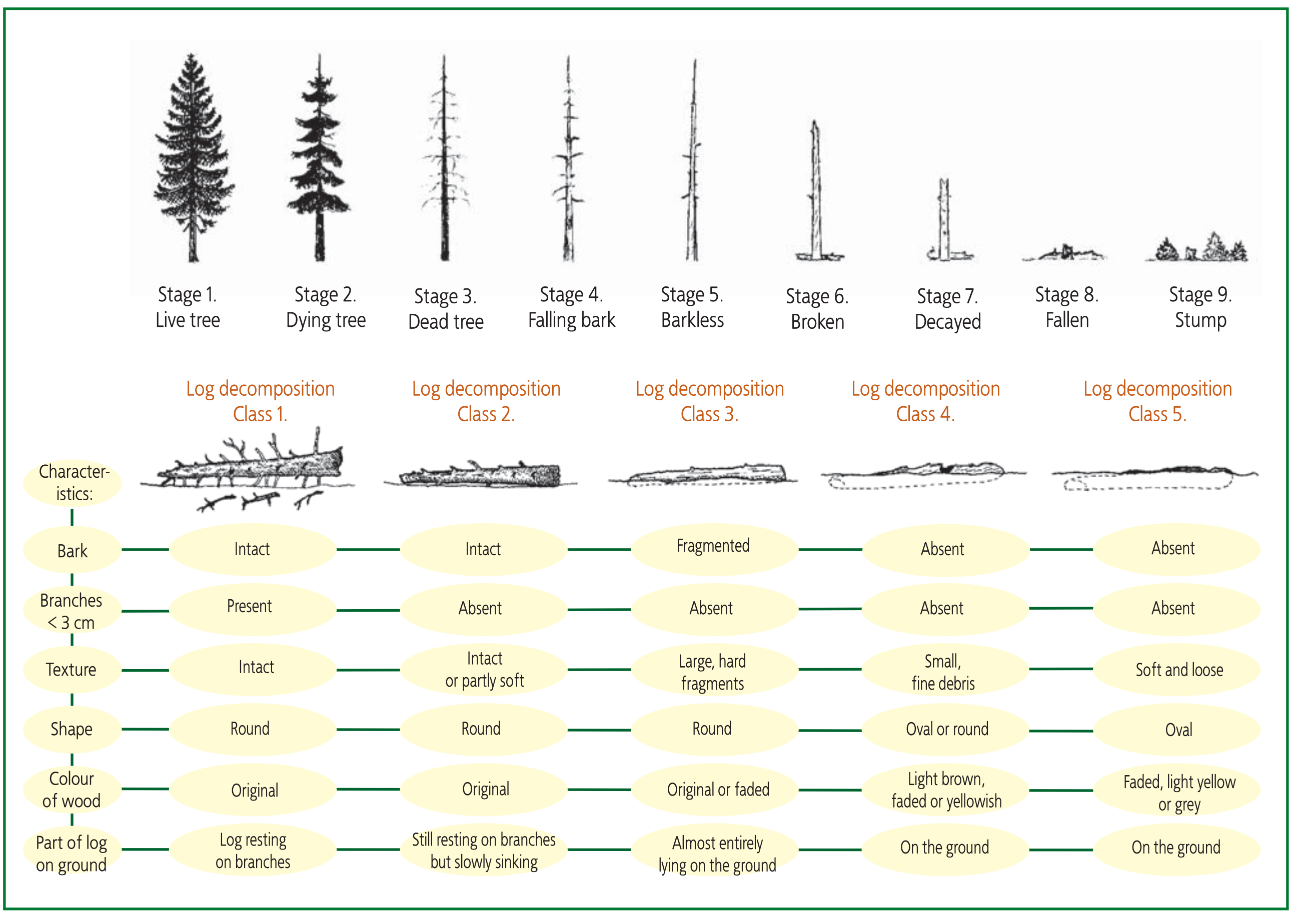
J. Walencik

Photo 16. A dead spruce 'growing into' the soil, torn apart by wild boars searching for insect larvae, Białowieża Primeval Forest

Photo 17. The last phase of a spruce log's decay; Białowieża Primeval Forest

J.M. Gutowski

Figure 3. The decomposition classes, illustrating the gradual decay of a standing spruce and a fallen log (M. Bobiec after MASER et al. 1979)



The decay of standing dead trees is different and considerably slower, however there is no universal pattern or model for the process. As in the case of CWD, the decay of a snag depends on the species, DBH, site, slope (exposure, aspect and steepness), insolation, etc. (fig. 4). At some time, snags generally become logs as they break apart or fall to the ground intact. Following that, the resulting logs undergo the process described above.

As mentioned above, in lowland Central Europe, total decomposition of wood usually takes from one to several decades. The situation is quite different in colder and more arid climates. Thus high in the mountains, this process may take hundreds of years. Douglas-fir *Pseudotsuga menziesii* logs in North America may persist for up to 250 years, and *Eucalyptus obliqua* logs in Tasmania may take even longer to decay. Wood submerged in water, an environment inaccessible to wood-boring invertebrates and poor in oxygen, decays very slowly.

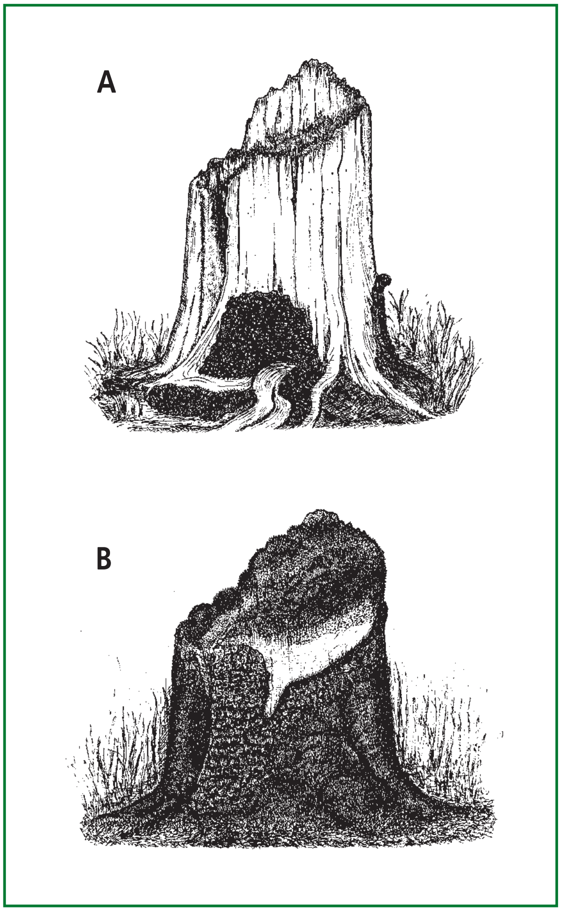


Figure 4. Decaying stumps: A – in a sunny spot, B – in the shade (M. Bobiec)

3.2

HOW DOES LIFE CONTINUE IN 'DEAD' TREES? COLONISATION OF DEAD TREES AND DEAD WOOD

Succession is a process, a linear trajectory of species replacing other species and assemblages through time. In the case of succession (colonisation) on and in dynamic environments such as wood, we are really talking about microsuccession.

Whether dying or felled by wind, animals or humans, the tree is quickly invaded by microorganisms, in particular by fungi (photo 18). This invasion is often facilitated by insects, such as the spruce bark beetle that conveys to the dead spruce the spores of *Ceratocystis polonica* – a fungus causing wood cyanosis ■. Enzymes, secreted by the fungi and present in the alimentary canals of the larvae of numerous insect species foraging in dying and dead trees, decompose cellulose and partially decompose hemicelluloses leading to the creation of sugars on which the larvae feed. In pine snag and stump wood, the sugar quantity increases, reaching a peak about five years after the tree's death, after which it decreases. In addition to the changes in sugar composition, significant microclimatic changes occur through time, such as changes in wood humidity and temperature. These changes also have a substantial influence on invading organisms. Changing the food content and microclimatic conditions of a given dead tree or its fragments offers hundreds of niches to a myriad of arthropods, fungi, lichens, slime moulds and other species. With such a variety of ecological associations exhibited by organisms connected with decaying wood, every stage of decay has its own species. The transition of the following species associations can take place on the same decaying piece of dead wood. On pine stumps, for example, five distinct successional stages can occur throughout the decay process. The particular times, organisms and characteristics mentioned below are typical of

Wood cyanosis:

a wood disease caused by fungi, manifesting itself in bluish irregular trails or spots of diverse size in sapwood.


J.M. Gutowski

Photo 18. Bracket fungi on trees provide an essential environment to many insect species, Białowieża Primeval Forest mesic northern European forests; for other forests, the time intervals, organisms and characteristics may vary considerably.

During Stage I, lasting less than one year immediately following the death of a tree, insects feed in and under the bark including the cambium, [e.g. *Acanthocinus aedilis*, the longhorn beetles (Cerambycidae) and the pine shoot beetle *Tomicus piniperda* (Scolytidae)] and a few bore deeper into the wood [such as the large timberworm *Elateroides dermestoides* (Lymexylidae) and the striped ambrosia beetle *Trypodendron lineatum* (Scolytidae)]. ■ At this stage, the bark remains tightly attached to the wood that is still hard and not yet exhibiting obvious traces of decay.

In Stage II, (from the second half of the first year to the fourth year), bark begins to loosen from the wood and the cambium ■ gradually dies if it is not consumed by insects and fungi. The number of insect species able to digest wood (due to their own enzymes or to symbiotic microorganisms living in their digestive canals) steadily increases. These include the longhorn beetles (e.g. *Arhopalus rusticus*) and jewel beetles (Buprestidae, e.g. *Chalcophora mariana* and *Buprestis rustica* – photo 19). Also, more and more insect species accompany the xylophages (wood eaters) ■, including predators and parasitoids ■. The loose bark provides a secure environment for insects and other organisms requiring shelter throughout the year.

Stage III, (5-6 years after the tree's death), is favoured by insects requiring or preferring partly rotten wood, such as the longhorn beetle *Corymbia rubra*. Under remnants of bark one can also observe ants (Formicidae), principally *Lasius niger*. The fairly soft wood becomes an ideal wintering habitat for ground beetles.

J.M. Gutowski

Photo 19. *Buprestis rustica* is associated with dead coniferous wood

Large timberworm and striped ambrosia beetle

Not all insects that bore into and live in wood also consume it. Several species eat fungi that they then spread and "grow" on the walls of their galleries. Such a strategy is used by the striped ambrosia beetle, a common European forest bark beetle that consumes the fungal mycelium of the genus *Ambrosia*. Other species of *Trypodendron*, as well as *Xyleborus* species, flatfoot ambrosia beetle *Platypus cylindricus*, platypodids and the large timberworm feed in a similar way.

Cambium:

a layer of living cells between bark and wood, from which plants add to their girth; it produces wood inwards and phloem outwards.

Xylophages:

Xylophages and other related terms are explained in chapter 4.1.2 devoted to invertebrates (pp. 62).

Parasitoid:

a parasite that always causes the death of its host; parasitoids are particularly numerous in the world of insects [e.g. dipterans representing families of ichneumons (Ichneumonidae), braconids (Braconidae) and chalcids (Chalcididae)], where they usually parasitise other invertebrates.

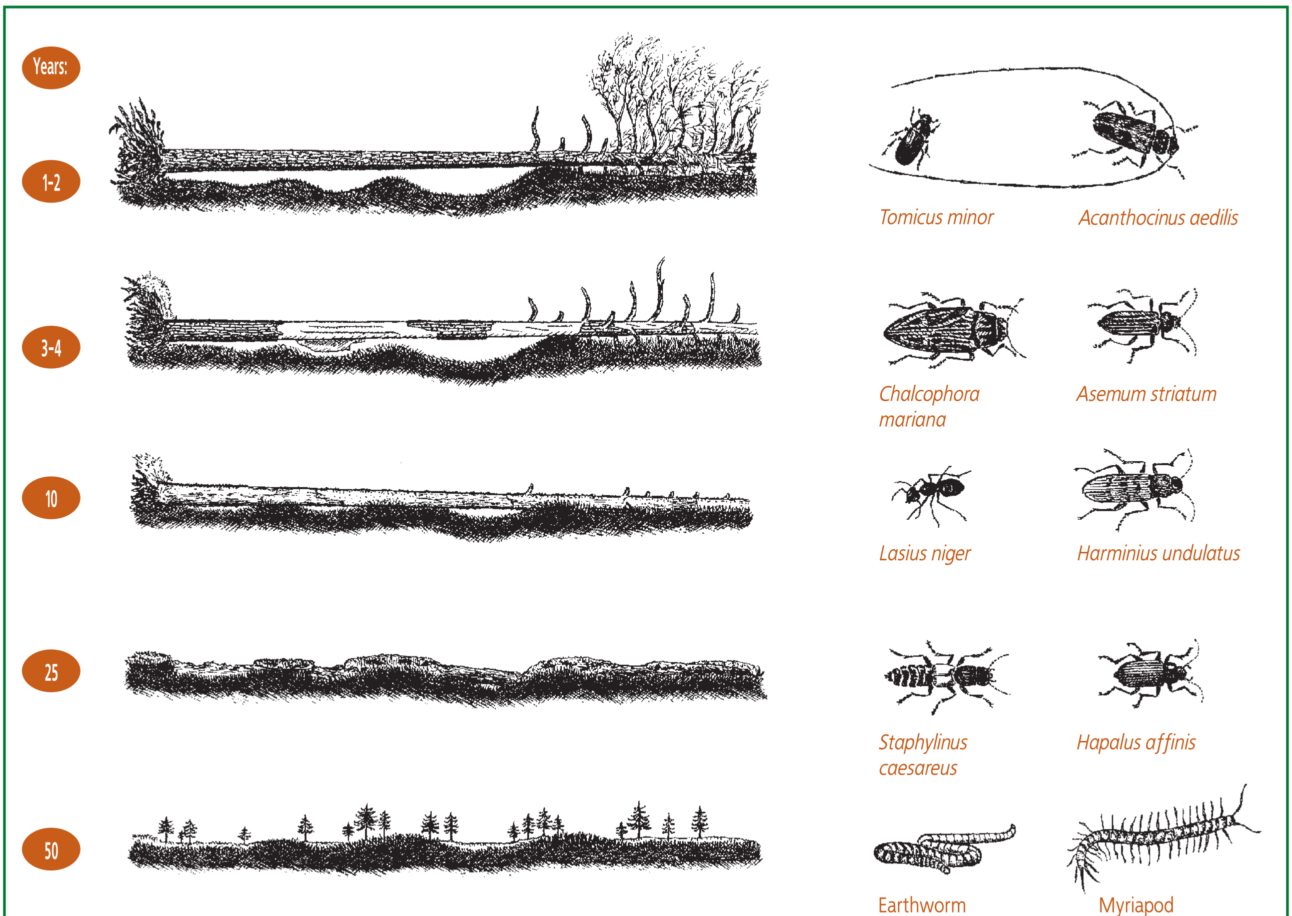
In Stage IV, (7-9 years), wood decay proceeds; in this stage the sapwood is already very rotten, but the heartwood and remaining sapwood maintains its general shape. There is an increase in wood humidity. Ants, elateroid and darkling beetles (Tenebrionidae), as well as the larvae of robber flies (Asilidae) and winter gnats (Tipulidae), are typical faunal representatives at this stage. Predatory insects are common.

In Stage V, (more than 9 years from death), only heartwood is left. Wood humidity is very high and the dead wood fauna is dominated by earthworms (Lumbricidae) and myriapods (Myriadapoda). Insects are represented by springtails (Collembola), earwigs (Dermaptera), ground beetles (Carabidae) and rove beetles (Staphylinidae), amongst others.

Large decaying oak trees and logs can be inhabited sequentially by invertebrates belonging to four successional stages:

I – dominated by Cerambycidae, e.g. *Plagionotus arcuatus* and Buprestidae e.g. *Agrilus biguttatus*;

Figure 5. Dead wood – an environment full of life; the gradual decay of wood coupled with the succession of colonists (M. Bobiec modified from PERSSON (ed.) 1990)



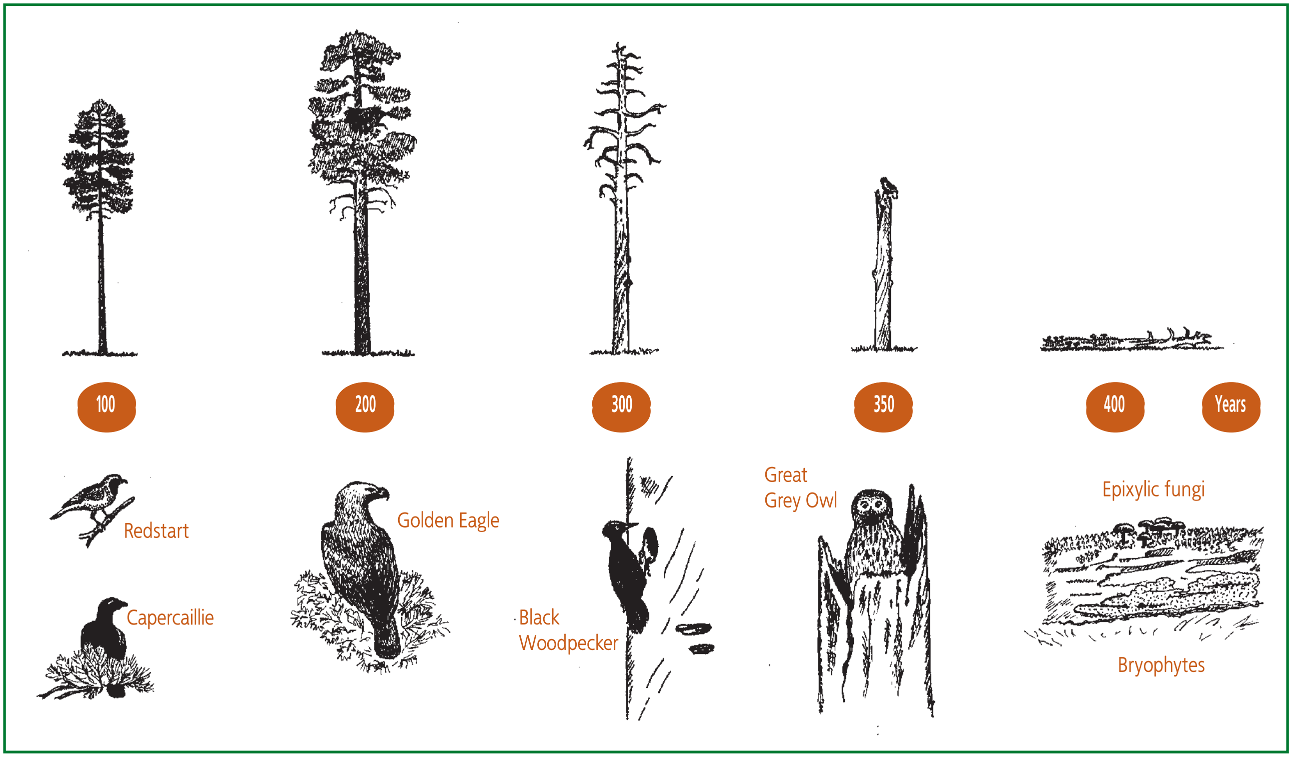


Figure 6. A tree – an environment full of life – the colonists
(M. Bobiec modified from PERSSON (ed.) 1990)

II – Lucanidae (stag beetles), such as *Ceruchrus chrysomelinus* and *Sinodendron cylindricum*, dipterans of the Sciaridae family, the Elateridae (click beetles) e.g. *Ampedus*, etc.;

III – mainly ants;

IV – wood decay and humification is mainly governed by earthworms and myriapods.

In general we can distinguish three distinct phases in the decay of wood:

- colonisation (invasion and colonisation of hard wood with closely attached bark and live but dying phloem and cambium): cambio-xylophages e.g. Scolytidae, Cerambycidae (e.g. *Acanthocinus aedilis*);
- decomposition (decay; crumbling and decomposition of the wood tissue by various organisms associated with dead wood): Cerambycidae and Buprestidae, ants and others;
- humification (further decay and mineralisation of wood associated with an increase in soil organisms): springtails, myriapods (Myriapoda), earthworms (Lumbricidae), enchytraeids (Enchytraeidae), mites (Acarina), bacteria, fungi).

In a mature forest that retains its functional integrity, and in which CWD is in equilibrium with the mature forest stand, one can observe numerous pieces of CWD in each of the different successional phases (fig. 5, 6). The colonisation of snags is different from that observed in fallen or lying logs, and that differs from the processes occurring in stumps or fragmented debris. Yet a different and very peculiar succession occurs in the rot powder inside the living trees' cavities (fig. 7).

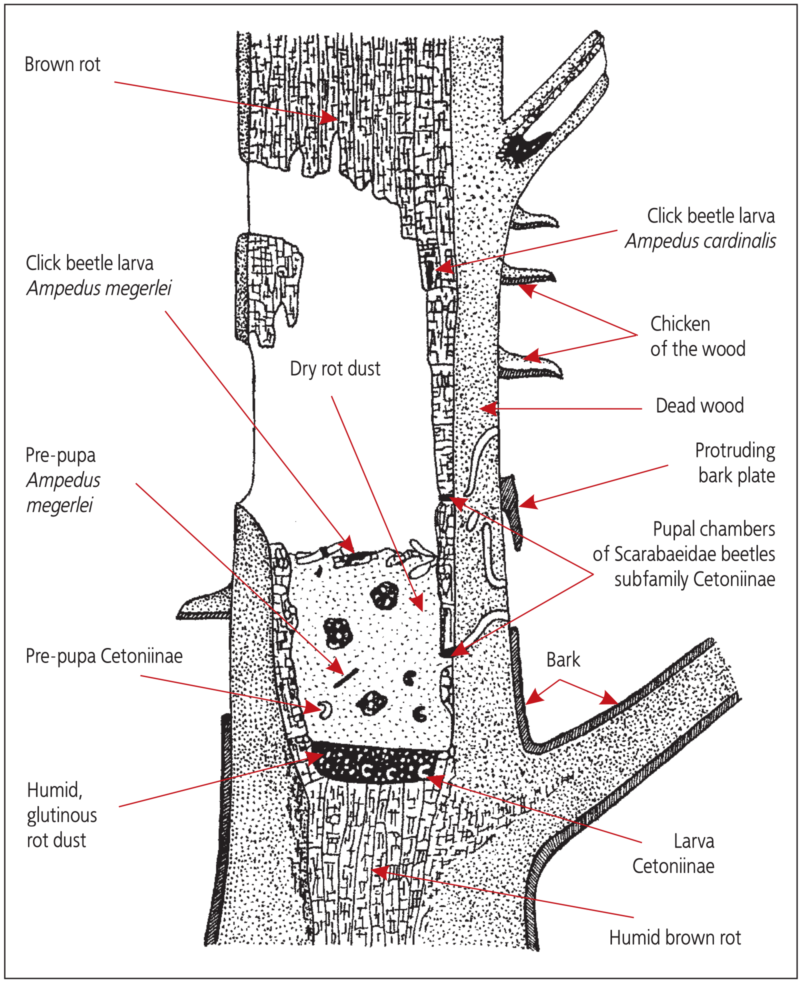


Figure 7. Vertical section through a hollow tree (M. Bobiec modified from SPEIGHT 1989)

The course of wood decay may be altered with increasing or decreasing tree diameter within a single tree species. The sequence and rate of colonisation vary between insolated and shaded sites. In insolated, dry sites, the decay process occurs at a slower rate than in sites without direct exposure to sunlight. The wood of some species decomposes quickly (e.g. lime, hornbeam) whereas other woods decompose more slowly (e.g. oak, pine). Although the variability in the course of succession is immense, there are certain similarities and functional rules characterizing the succeeding groups of organisms. Furthermore, as succession advances, the associations of organisms colonising dead wood become more similar.

Finally, it is important to stress that thick trunks and logs provide more stable microclimatic conditions and therefore are preferred by many organisms. Also, the most endangered invertebrate species are associated with larger-sized CWD.

The topical literature used in Chapter 3.

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Summary of Chapter 3.

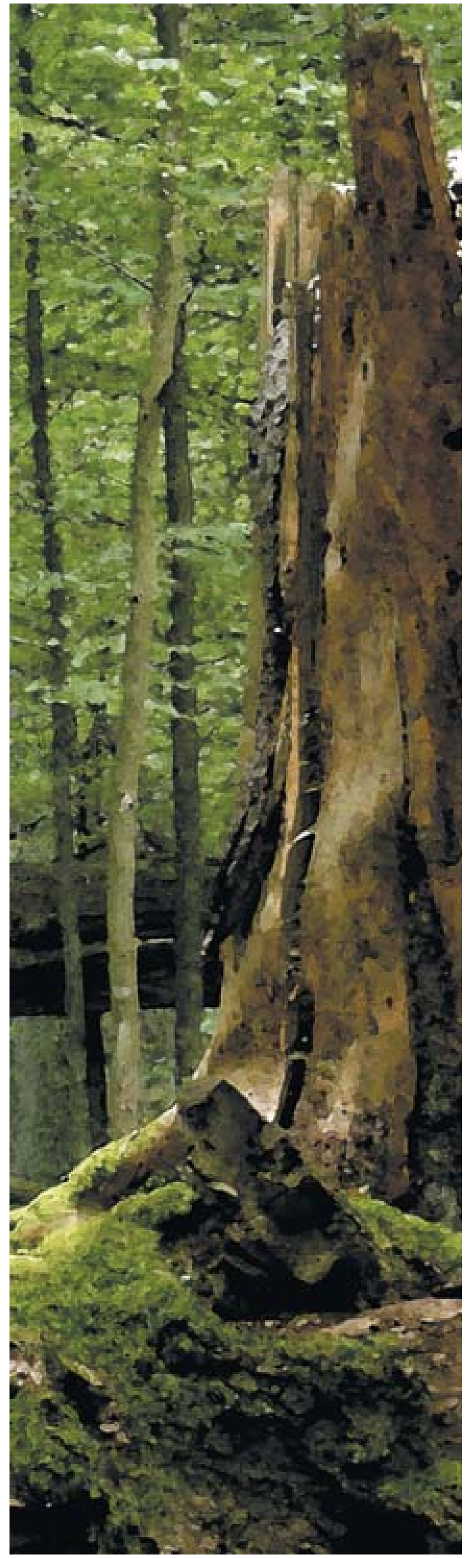
The death of trees and shrubs is one of the natural processes in forests. Tree and shrub mortality modifies the tree's immediate neighbourhood: light regime, humidity, nutrient availability, etc. Simultaneously, there is a gradual decomposition of the wood tissues of dead trees and shrubs and the release of elements to the soil.

Once a tree is dead, it is subsequently colonised by various groups of organisms. This process of succession is characterised by gradual compositional changes of dead wood communities and the changing quality of the substrate. The process is initiated by species that can live under strongly attached bark and bore galleries in hard wood. They are followed by organisms preferring more and more decayed and softened wood, and finally those that live in the rot powder, should decay proceed to that point.

Although there are certain common parallels, the course of succession may vary substantially depending on tree species, size, light regime, humidity and position (snags vs. fallen logs).

During the period from tree death to complete decay (over several decades if not a century in some forests) a single tree is colonised by dozens to hundreds of species of fungi, plants and animals.

Chapter 4



DYING AND DEAD WOOD IN LIVING FORESTS

4.1

DYING AND DEAD WOOD AS A WILDLIFE HABITAT

Besides the most obvious, though still poorly recognised, role of dead wood as a microhabitat for a myriad of species, from mammals and birds to fungi, bacteria and mites, dead wood plays a number of other very important functions. Several of these functions, such as the storage of minerals that are slowly but steadily released into the soil, and carbon sequestration, are inseparable from the decay and mineralisation processes that occur in every forest ecosystem. However, there are also functions connected with specific types of environments, which thereby affect their environment's character in terms of structure and dynamics while in other ecosystems these fuctions merely play a marginal role or do not occur at all. Examples of such functions include the capability of logs to stabilise soils on steep slopes and the regeneration of trees on decaying boles in swamps.

4.1.1. VERTEBRATES

In the same way as there are a variety of factors involved in tree death and a multitude of forms of CWD in forests, there are also many ways in which CWD is utilised by animals. The more diverse and numerous a vertebrate group is in a given region, the greater the ways its members utilise dead wood. CWD may also influence organisms that are not directly related to the forest ecosystem, e.g. fish. Dead trees sunk in watercourses may impound water and provide refuge and breeding space to several fish species, and the decaying wood fertilises and changes the water chemistry. However, for terrestrial organisms the role of dead wood is far more immediate. For instance in the Blue Mountains (USA), 179 vertebrate species were found to be dependent on dead trunks and logs. The importance of CWD to mammals, birds, reptiles and amphibians will be discussed and illustrated with information from observations and studies carried out in the Białowieża Primeval Forest.

Humid caves or sunny beaches – reptiles and amphibians

Reptiles are not numerous in the forest ecosystems of temperate climates, in terms of either species diversity or population densities. For these thermophilous animals, open, well insolated habitats are especially favoured. Broad-leaved forests with abundant herbaceous vegetation, logs, and particularly those found in sunny openings, offer favourable conditions for reptile thermoregulation.

Gaps created by tree death are preferred by other species, such as the slow-worm *Anguis fragilis*, the grass snake *Natrix natrix* and the viper *Vipera berus*. Lizards are frequently seen basking in the sun on barkless spruce logs and terrapins use logs lying in water as basking sites. Besides basking sites, logs, snags and stumps offer a multitude of refuges or hideouts enabling animals to escape from predators. As these forms of dead wood harbour a multitude of invertebrates, they also provide feeding sites for reptiles favouring such prey. Old decomposing logs can also be used as a habitat for hibernation.

Amphibians are more numerous than reptiles in the forests of Białowieża, and well rotted wood is used for their refuges and feeding habitats. Toads may hunt there for invertebrates, while other species, such as frogs and salamanders, hibernate in rotten logs and stumps. The presence of high humidity is an asset of CWD particularly important for amphibians, and high humidity also modifies the microclimate in the vicinity of the CWD. These moist conditions make an otherwise marginal habitat favourable for amphibians which are very susceptible to desiccation in dry environments.

In the mountains and foothills, decaying wood is an indispensable component of the spotted salamander's *Salamandra salamandra* habitat (photo 20). It is believed that all species of terrestrial salamanders depend on the presence of large-sized CWD.

J. Korbel

Photo 20. A spotted salamander – amphibian species often find refuge under fallen logs, protruding bark or in rotting wood in mountainous regions; southern Poland

Bird apartments

Birds are the best represented group of vertebrates of the fauna found in the Białowieża Primeval Forest. Among the 250 recorded species, 177 breed there, and 109 of them are referred to as 'forest birds'.

Most of these birds nest in cavities in dead trees. The cavity nesting birds can be classified as primary cavity nesters (those that excavate cavities by themselves, especially woodpeckers – photo 21) and secondary cavity nesters (birds that use cavities excavated by woodpeckers or the natural cavities caused by wood tissue decay).

J. Korbel

Photo 21. Foraging cavities excavated by black woodpeckers, who forage heavily on *Camponotus* species (carpenter ants) and often excavate their nest cavities inside internally rotten spruces; southern Poland

Woodpeckers are most closely associated with trees and dead wood. They possess numerous adaptations to exploit the tree surface and interior. The orientation of their toes, two pointing forward and two pointing backwards (in the case of the three-toed woodpecker *Picoides tridactylus* – only one points backwards), permits them to easily climb the stems of trees. Short, stiff tail feathers provide excellent support while the bird is moving and foraging. The anatomy of the beak, skull and tongue are the most remarkable of a woodpecker's adaptations. The beak is so strong that it can successfully excavate oak wood. The shock of impact is effectively absorbed by a special buffering tissue, which prevents its transmission to the skull and brain. The tongue is fixed to the prolonged hyoid bones, which are anchored at the very back of the skull, permitting the tongue to be extended deep into galleries beneath the bark and into the underlying wood to catch insects. The tip of the tongue is barbed and operates much like a harpoon, easily piercing and securing the soft bodies of insect larvae for extraction.

There are nine species of woodpeckers nesting in the Białowieża Primeval Forest. A tenth species, the Syrian woodpecker *Dendrocopos syriacus*, is found at the edges of the forest. Living in old orchards and groves, the Syrian woodpecker is not as strongly associated with the forest environment as the others. One species, the wryneck *Jynx torquilla*, does not excavate nesting cavities. It nests in existing cavities and hollows, but does excavate its prey, mainly ants and their chrysalises. All the remaining woodpecker species are typical primary cavity nesters: green *Picus viridis*, grey-headed *Picus canus*, black *Dryocopus martius*, great spotted *Dendrocopos major*, middle spotted *D. medius*, white-backed *D. leucotos*, lesser spotted *D. minor* and three-toed (photo 22).


Fot. 22. (J. Walencik)

Photo 22. The three-toed woodpecker

The cavities in dead trees probably provide a better microclimate than the natural hollows in living trees; even species capable of excavating the hard wood of living trees often choose dead trees when they are available. Such cavities in dead trees or the dead parts of living trees, used for nesting or roosting, are usually less exploitable by predators. Rotten trunks may not bear the predator's weight, and the bare wood provides little texture which the paws or claws can grip. For the great spotted, the most common woodpecker in the forest of Białowieża, 35% of its nest cavities are excavated in dead trees. More than 70% of the nest cavities of the middle spotted woodpecker are located in dead trunks or boughs. The lesser spotted and three-toed woodpeckers excavate their cavities almost exclusively in dead trees (photo 22). For three-toed woodpecker, periodical large-scale disturbances, such as wildfire, windblow, spruce bark beetle outbreaks or stand decadence caused by beaver activity, seem to be of critical importance (M. STRAZDS, pers. comm.) Another species strongly associated with dead, but almost exclusively broad-leaved trees, is the white-backed woodpecker. Half of its cavities are found in dead trunks and otherwise mostly in the dead boughs of living trees.

	Alder	Hornbeam	Oak	Other	Total
Tree status	%	%	%	%	%
Living	28	64	70	69	52
Entire dead tree	44	21	10	15	27
Snag	28	14	20	15	21

White-backed woodpecker: location of nests in the Białowieża Primeval Forest
(according to WESOŁOWSKI 1995; modified)

Black and grey-headed woodpeckers also excavate their nesting cavities in dead trees. Considering that almost all woodpeckers' nest cavities are newly excavated each year, the demand for dead trees by these birds is large and a dead tree shortage may seriously reduce the number of birds that could nest in a given area. Not surprisingly, in managed forests where dead wood has been largely or entirely removed, the density of those woodpeckers that are associated with dead wood is on average twofold lower than in the protected forests of Białowieża (fig. 8).

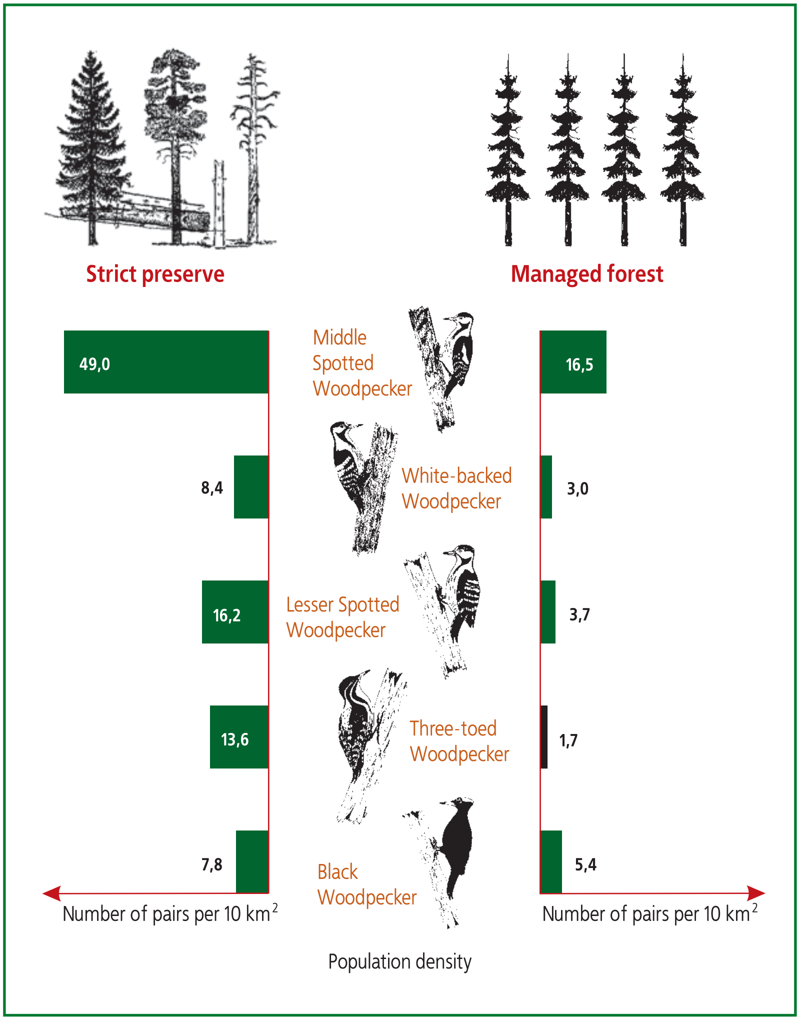


Figure 8. The density of woodpeckers utilising dying and dead trees; a comparison between natural and managed stands in the Białowieża Primeval Forest (after PUGACEWICZ 1997; modified)

Similar relations have been observed in Western Europe and North America. In Oregon, forests where logs cover more than 10% of the ground surface are clearly favoured by woodpeckers.

Dead trees are not only breeding habitats. Along with dying trees, they also provide an important food supply. However, the value of dead trees as a food supply changes through time depending on the food items of interest and the woodpecker species. While ants are the primary food for the wryneck and green woodpecker, the remaining woodpecker species feed on other insects and their larvae taken from under the bark. Studies from Germany showed that most woodpeckers forage more than 70% of the time on dead trees or dead parts of living trees. Dead trees or parts are particularly important for three-toed woodpeckers that forage on dead trees more than 80% of the time (fig. 9).

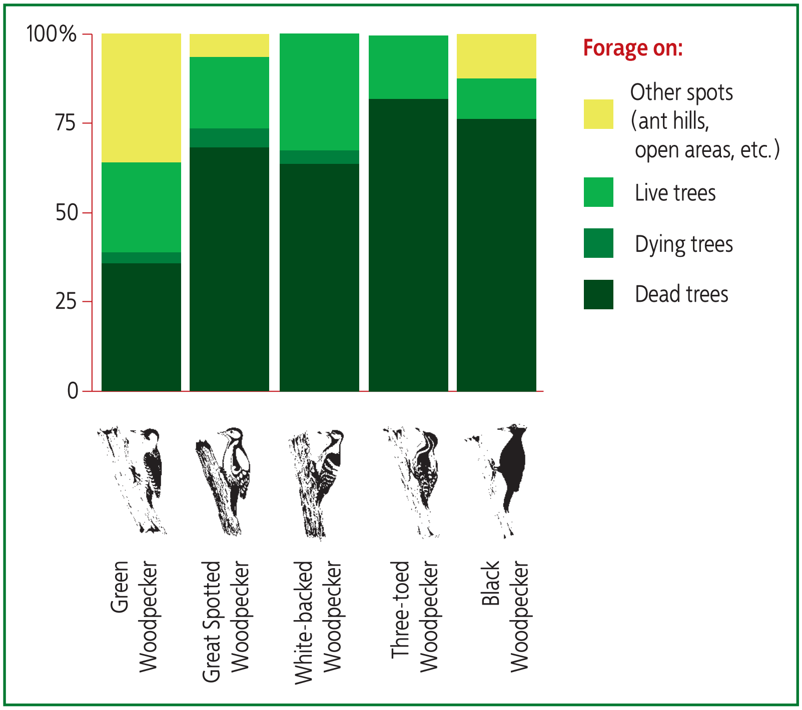
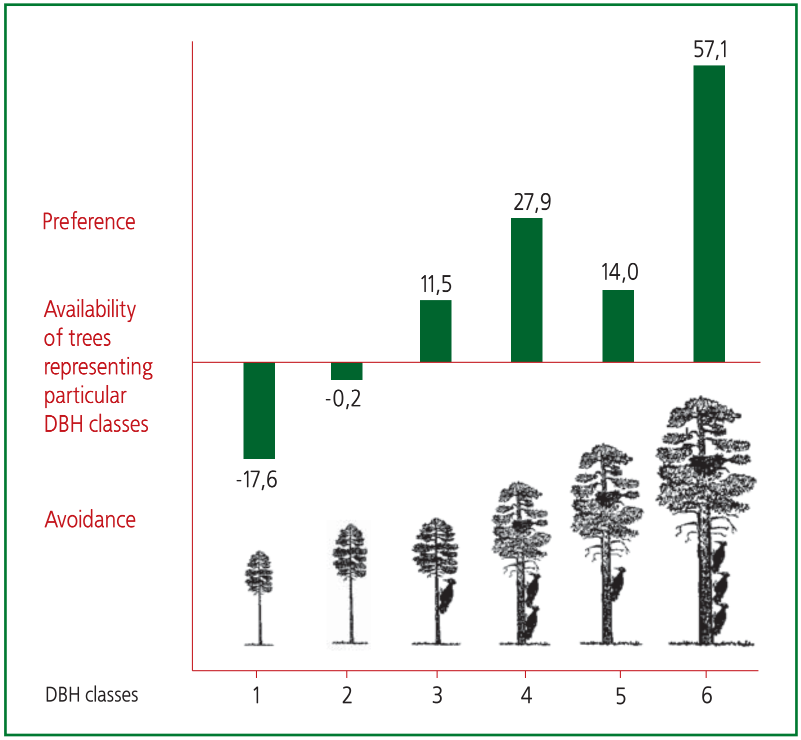


Figure 9. Woodpeckers' preferences related to different types of feeding substrates in the Berchtesgaden National Park, Germany (after PECHACEK 1993 and SCHERZINGER 1996; modified)

In the Białowieża Primeval Forest, three-toed, black and white-backed woodpeckers search more often for food on dead wood more often (60% of instances) than on living trees, and the remaining species (great spotted, middle spotted and lesser spotted woodpecker) search dead wood 20% of the time. The size of dead trees is also an important characteristic from the viewpoint of the woodpeckers' preferred diet. The larger trees are far more attractive foraging sites for woodpeckers than smaller young trees (fig. 10). In Białowieża, woodpeckers clearly prefer trees greater than 20 cm DBH. Thus, it is no surprise that woodpecker population density is correlated with the amount of CWD (fig. 11).

Figure 10. Woodpeckers' preferences related to tree diameter; the bars refer to selection or avoidance of a given DBH class relative to its proportion in the stand (modified from SWALLOW 1988, and SCHERZINGER 1996)



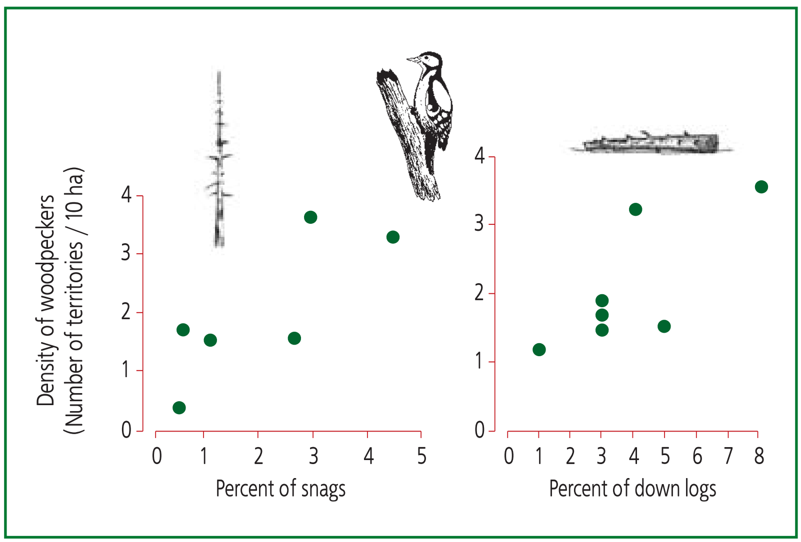


Figure 11. Dependence of the woodpecker population density on the quantity of dead trees in a stand (modified from KOMDEUR and VESTJENS 1983 and SCHERZINGER 1996)

Dead trees and dry boughs play another role in the life of a woodpecker: they provide ideal drumming sites. Drumming is caused by quick rhythmical hits of the beak on resonating, dry but hard parts of trees as well as other resonating structures. It is a very important mating behaviour, serves as a way for pairs to communicate and is used to delineate their territories.

Secondary cavity nesters, in most instances, utilise existing cavities, either natural or those previously excavated by a primary cavity nester. Only the willow tit *Parus cristatus* and nuthatch *Sitta europaea* are capable of excavating new cavities in soft wood or improving existing ones. The availability of tree hollows and cavities in the unmanaged and more natural forests of Białowieża is orders of magnitude greater then in intensively managed, production forests.

J. Walencik

Photo 23. Curious pygmy owl is looking out of its hollow in a three hundred-years-old Scotch pine

In addition to nuthatches, flycatchers, tits and sparrows *Passer montanus* commonly occupy cavities. Almost half of pied flycatchers' *Ficedula hypoleuca* and collared flycatchers' *Ficedula albicollis* nesting sites are situated in dead trees. Similarly, about 25% of starlings' and 10% of blue tits' *Parus caeruleus* and marsh tits'

Parus palustris nest sites are found in dead wood. Other species utilizing cavities are the spotted and red-breasted flycatchers *Muscicapa striata* and *Ficedula parva* respectively as well as the stock dove *Columba oenas*. An interesting peculiarity of the Białowieża Primeval Forest is that cavities are often used by species that are normally known to build open nests: the blackbird *Turdus merula*, the robin *Erithacus rubecula* and the dunnock *Prunella modularis*.

Another group of birds strongly associated with hollows and cavities are owls (Stringiformes). Three species dwelling within the forests of Białowieża typically inhabit tree hollows and cavities: the tawny owl *Strix aluco*, the pygmy owl *Glaucidium passerinum* (photo 23) and Tengmalm's owl *Aegolius funereus*. Tawny owls are fairly large birds that most frequently colonise large natural hollows or cavities, whereas the latter two species utilise cavities excavated by woodpeckers. Tengmalm's owl breeds less frequently in dead trees because it prefers hollows made by black woodpeckers in living pines, whereas pygmy owls favour cavities excavated by three-toed and great spotted woodpeckers, many of which are located in dead wood. Other owls, such as the great grey owl *Strix nebulosa*, breed almost exclusively in open nests placed on the top of broken dead trees (snags). Hawk owls *Surnia ulula* and Ural owls *Strix uralensis* use similar sites for nests and have similar nesting strategies.

Both woodpeckers and secondary cavity nesters prefer to nest in cavities in trees of a relatively large diameter. The average DBHs (cm) of some of the nesting trees for these species recorded in the Białowieża Primeval Forest are: the white-backed woodpecker 59, the middle spotted woodpecker 91, the three-toed woodpecker 39, the great tit 54 and the pied flycatcher 48.

As is the case in forests, dead and hollow trees play a very important role in various groves. Single dying trees are used by certain species of woodpeckers, e.g. green and black woodpeckers, for the excavation of cavities. Abandoned cavities are utilised by rollers *Coracias garrulus*, a rare and endangered species in Poland, and by other birds, e.g. the little owl *Athene noctua* (photo 24). The Syrian woodpecker uses dying trees in parks and orchards for nesting. After abandonment, their cavities are often used by certain species of secondary cavity nesters, including relatively rare ones such as the wryneck and the redstart *Phoenicurus phoenicurus*. Old, hollow roadside willows, which are gradually disappearing components of our landscape, are the favourite tree of little owls and hoopoes *Upupa epops*. The populations of many of the birds mentioned above are declining, and this trend is caused by the loss of habitats suitable for breeding and foraging, very often through the lack of old and dying trees.

J. Baake

Photo 24. A little owl in a fruit tree hollow

Polish birds that nest in hollows, root plates and snags

Bird species		Excavation of holes	Nesting in holes	Nesting on uprooted trees and tree stumps
Goldeneye	*Bucephala clangula*		+	
Goosander	*Mergus merganser*		+	
Stock Dove	*Columba oenas*		+	
Pygmy Owl	*Glaucidium passerinum*		+	
Scops Owl	*Otus scops*		+	
Little Owl	*Athene noctua*		+	
Tengmalm's Owl	*Aegolius funereus*		+	
Tawny Owl	*Strix aluco*		+	
Ural Owl	*Strix uralensis*		+	
Great Grey Owl	*Strix nebulosa*			+
Swift	*Apus apus*		+	
Roller	*Coracias garrulus*		+	
Hoopoe	*Upupa epops*		+	
Wryneck	*Jynx torquilla*		+	
Grey-headed Woodpecker	*Picus canus*	+	+	
Green Woodpecker	*Picus viridis*	+	+	
Black Woodpecker	*Dryocopus martius*	+	+	
Great Spotted Woodpecker	*Dendrocpos major*	+	+	
Middle Spotted Woodpecker	*Dendrocopos medius*	+	+	
White-backed Woodpecker	*Dendrocopos leucotos*	+	+	
Syrian Woodpecker	*Dendrcopos syriacus*	+	+	
Lesser Spotted Woodpecker	*Dendrocopos minor*	+	+	
Three-toed Woodpecker	*Picoides tridactylus*	+	+	
Wren	*Troglodytes troglodytes*			+
Dunnock	*Prunella modularis*		+	+
Robin	*Erithacus rubecula*		+	+
Redstart	*Phoenicurus phoenicurus*		+	
Blackbird	*Turdus merula*		+	+
Song Trush	*Turdus philomelos*			+
Redwing	*Turdus iliacus*			+
Spotted Flycatcher	*Muscicapa striata*		+	+
Red-breasted Flycatcher	*Ficedula parva*		+	+
Pied Flycatcher	*Ficedula hypoleuca*		+	
Collared Flycatcher	*Ficedula albicollis*		+	
Marsh Tit	*Parus palustris*		+	
Willow Tit	*Parus montanus*	+	+	
Crested Tit	*Parus cristatus*		+	
Blue Tit	*Parus caeruleus*		+	
Great Tit	*Parus major*		+	
Coal Tit	*Parus ater*		+	
Nuthatch	*Sitta europaea*	+	+	
Treecreeper	*Certhia familiaris*		+	
Jackdaw	*Corvus monedula*		+	
Starling	*Strurnus vulgaris*		+	
Tree Sparrow	*Passer montanus*		+	

Birds associated with old, dying and dead trees constitute a significant part of forest fauna, and not only in Poland. In the boreal zone of Fennoscandia, for instance, 45 species build their nests in or on such trees, while in central and southern Sweden, 15 species inhabit cavities and hollows, and in North America 86 use such sites for nesting.

Another important form of dead wood is the root plates of uprooted trees. They are important breeding places for numerous species of birds, e.g. thrushes, robins, dunnocks, spotted and red-breasted flycatchers and wrens *Troglodytes troglodytes*. In wet communities of Białowieża about 80% of the nests of these species are constructed in the root plates of fallen trees. Eagle owls *Bubo bubo* often perch on the top of large root plates (photo 25).

J. Walencik

Photo 25. An eagle owl on a spruce's root plate

Hideouts and hunting territories: mammals

Among the mammals inhabiting the forests of Białowieża, insectivores, bats, rodents and certain carnivores are particularly connected with dead wood. Although CWD is of marginal significance for ungulates, it can effectively prevent access for foraging seedlings and undergrowth, and grasses and forbs growing under the forest canopy. Mammals, including the European bison *Bison bonasus*, sometimes eat honey fungus and other fungi growing on fallen logs, and wild boars *Sus scrofa* search for insects and rodents under decaying wood.

Rotten logs provide an excellent habitat for three species of shrews *Sorex* of the Białowieża Primeval Forest. Logs not only provide refuges or hideouts, but are also sources of food e.g. by harbouring small invertebrates. Fallen logs play an equally important role in the life of rodents. Bank voles *Clethrionymys glareolus* and pine voles *Microtus subterraneus* construct their burrows underneath logs, and if well rotted, rodent burrows may continue into the tree trunks. Rodents often store food including tree seeds in dead logs. Squirrels *Sciurus vulgaris* make a similar use of dead trunks and stumps. However, cavities excavated by woodpeckers as well as natural cavities are commonly used as hiding and breeding dens. Dormice (or glirids, Myoxidae: the fat dormouse *Glis glis*, the forest dormouse *Dryomys nitedula* and the common dormouse *Muscardinus avellarius*) and northern the northern birch mouse *Sicista betulina* (photo 26), use rotten hollow trunks both for stores and hideouts and for winter hibernation.

J. Walencik

Photo 26. A northern birch mouse

Bats are also often closely associated with dead trees. Of the 13 bat species that occur in the Białowieża Primeval Forest, 11 use cavities and hollows for summer roosts or hideouts, and two sporadically hibernate in trees.

Bat use of hideouts or roost sites in the Białowieża Primeval Forest
(according to RUCZYŃSKI, unpbl.)

Species		Summer hideouts	Winter hideouts
Common Noctule	*Nyctalus noctula*	Hollows	
Lesser Noctule	*Nyctalus leisleri*	Hollows	
Daubenton's Bat	*Myotis daubentonii*	Hollows	Cellars
Natterer's Bat	*Myotis nattereri*	Hollows	Cellars
Brandt's Bat	*Myotis brandti*	Hollows	
Whiskered Bat	*Myotis mystacinus*	Missing data	
Nathusius' Pipistrelle	*Pipistrellus nathusii*	Hollows/buildings	
Common Pipistrelle	*Pipistrellus pipistrellus*	Hollows/buildings	
Parti-colored Bat	*Vespertilio murinus*	Hollows/buildings	
Northern Bat	*Eptesicus nilsonii*	Hollows/buildings	
Serotine Bat	*Eptesicus serotinus*	Buildings	
Barbastelle	*Barbastella barbastellus*	Hollows/buildings	Hollows/cellars
Common Long-eared Bat	*Plecotus auritus*	Hollows/buildings	Hollows/cellars

Sometimes even closely related species exhibit distincly different preferences for cavities and hollows. Common noctules *Nyctalus noctula* almost exclusively use cavities excavated by woodpeckers, while lesser noctules *Nyctalus leisleri* generally use natural cavities most of which are located in dying trees. The characteristics of the habitat adjacent to the suitable cavities or hollows are often important. Bats often select tall trees either at the edge of an opening in the forest or extending well above the average canopy. Such locations permit easy entrance and exit from cavities and hollows. Presumably the microclimate of such cavities and hollows also varies in suitability. Ideal conditions are often met by old and dying trees.

Tree cavities and hollows are often used by carnivores as resting and breeding places, in particular by pine martens *Martes martes*. Pine martens, however, often leave their tree cavities and hollows and take refuge in logs when temperatures drop below -20°C. They especially favour logs that are covered with a thick coat of snow, which insulate them from the cold better than cavities and hollows in standing trees. In unmanaged forests, racoon dogs prefer hideouts in hollow logs to underground dens. They may even hibernate there.

For pine martens and weasels, logs are also an ideal hunting environment. These animals clearly favour such situations while searching for food, probably because logs are also an important habitat for many of the rodents on which they prey (fig. 12). Lynxes *Lynx lynx* often use logs to facilitate movement (photo 27). Dead

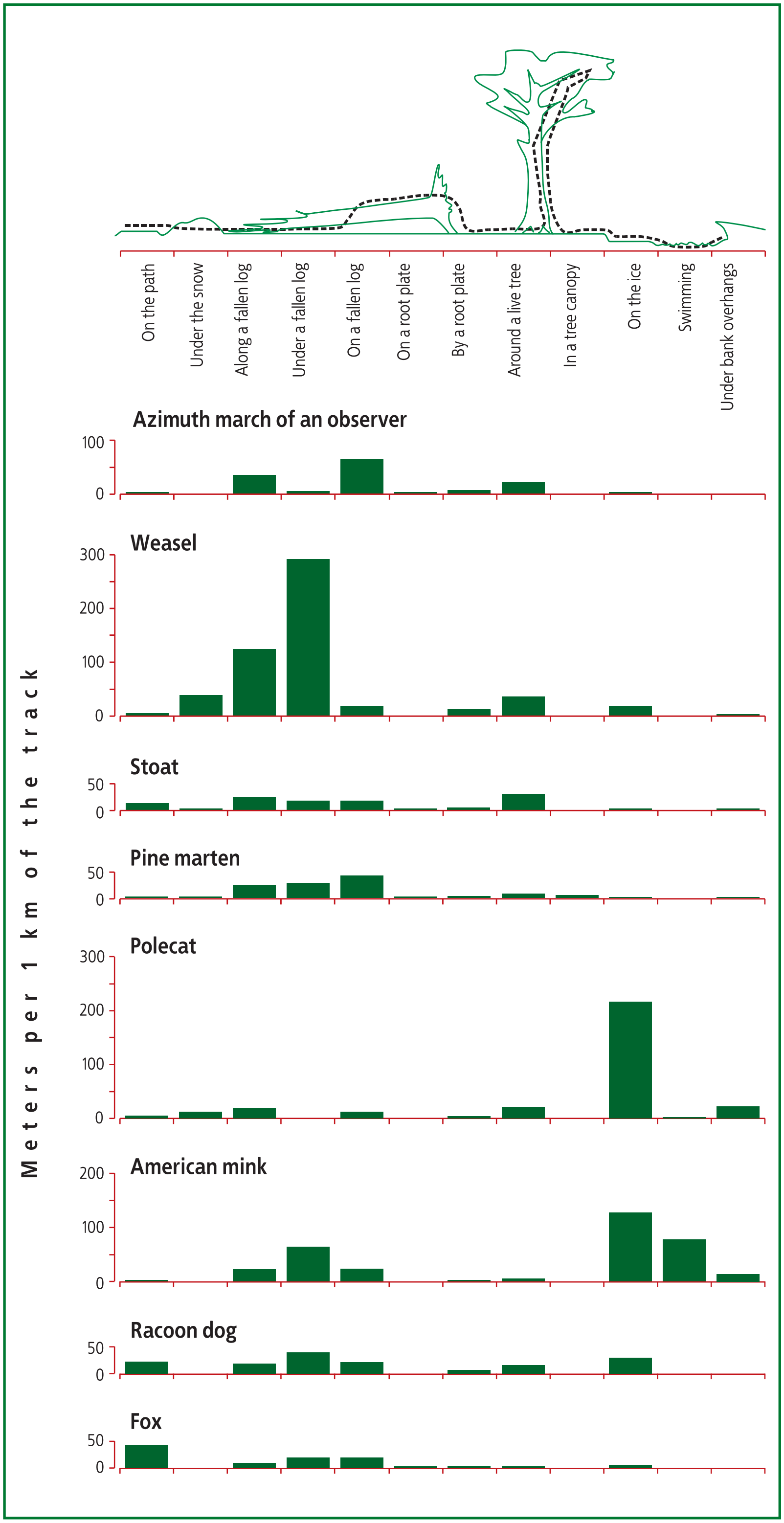


Figure 12. Movement pathways and terrain penetration by selected predatory species in Białowieża National Park. Data collected by an observer walking on azimuth, show the relative availability of various elements in the forest (modified from JĘDRZEJEWSKA and JĘDRZEJEWSKI 1998)

Photo 27. A young lynx on a spruce log has a better lookout than on ground covered with vegetation; Białowieża Primeval Forest

wood is also used by mammals for other purposes. Small mammals use suspended logs to cross forest streams, wild boars make their lairs from thin branches (photo 28), and beavers build their dams using logs, boughs and branches (photo 29).

As in the case of birds, a deficit in old hollow trees may cause a decrease in the numbers of certain mammal species. Bats, dormice and small carnivores such as pine martens, are particularly sensitive to amounts of old hollow trees. These animals will also use artificial nest boxes, but such "hollows" do not provide as suitable nesting conditions as do natural hollows. Also, the number of nest boxes is generally insufficient to meet the high demand for alternate nesting sites that are necessary to reduce the incidence of parasites and minimise the chance of predators finding the nest site.

J.M. Gutowski

Photo 28. A wild boar's lair is bedded with dry branches in the Białowieża Primeval Forest

J.M. Gutowski

Photo 29. Beavers' dams are mainly made of dead wood

According to studies conducted in the USA, the maintenance of a viable pine marten *Martes americana* population requires the preservation of at least 18 m^3/ha of CWD in the forest. Moreover, within this habitat requirement there needs to be large pieces of CWD for it to be suitable for most of the species needing dead wood. The diameter of the debris (snags, stumps and lying logs) preferred by these animals needs to be at least 80 cm and the length of logs more than 10 m.

Summary of Chapter 4.1.1.

Representatives of all taxonomic groups of vertebrates use dead trees or their products as refuges, roosts or hideouts.

Dead trees are most important for birds. Besides using dead trees as nest sites, roosts or refuges, many species also forage on dead trees.

Woodpeckers, tits, flycatchers and owls exhibit the strongest association with dead and hollow trees. White-backed and three-toed woodpeckers excavate cavities and hollows, and forage almost exclusively in dead and dying trees.

The continued residence or presence of many rare and protected bird species, such as white-backed and three-toed woodpeckers, red-breasted and collared flycatchers, pygmy and Tengmalm's owls, rollers and stock doves depends on the presence of dead trees.

Root plates of uprooted trees are important nesting habitats of numerous bird species.

Mammals use dead trees as refuges and foraging/hunting areas.

Dead and hollow trees are very important for bats, insectivores, rodents and small predators.

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4.1.2. INVERTEBRATES

The invertebrates, that is, mainly insects

A. Bobiec

There are more than 35,000 species of animals in Poland, most of which are invertebrates, including more than 26,000 insects. The invertebrates are the many and varied groups of animals without a backbone. The group includes numerous systematic groups including the roundworms ■, annelids ■ (photo 30), arthropods ■ and molluscs. Mites, which are arachnids *Arachnidae*, are a diverse group, many of which are associated with CWD, in particular with cavities, hollows and the environment just under the bark. Mites include wood eating *Rhysotritia duplicata* and *Steganacarus carinatus*, pseudoscorpions (Pseudoscorpionida) resembling miniature scorpions, and spiders (e.g. predatory species living under bark, including *Araneus umbraticus* and *Segestria florentina*). An even more diverse group associated with CWD is the insects.

Photo 30. This decayed spruce snag is a habitat for numerous fungi and invertebrates

Roundworms:

many nematodes belonging to this group are associated with dead wood and with other organisms in dead wood.

Annelids:

some earthworms live under the bark or in the well decomposed wood of stumps, snags and logs.

Arthropods:

e.g. crustaceans, arachnids, myriapods and insects.

J.M. Gutowski

Photo 31. *Monochamus galloprovincialis* – the larva of this longhorn beetle lives under bark and in the wood of pines

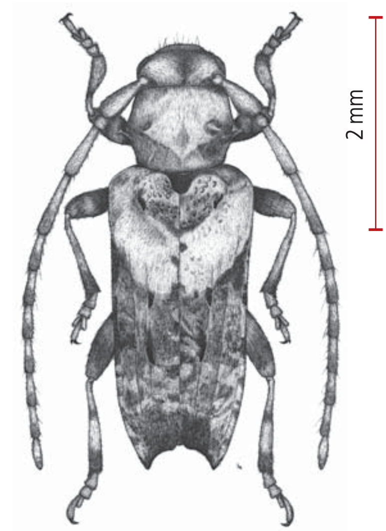

Figure 13. *Pogonocherus hispidus* – a beetle associated with the thin branches of many species of trees and shrubs (M. Waszkiewicz)

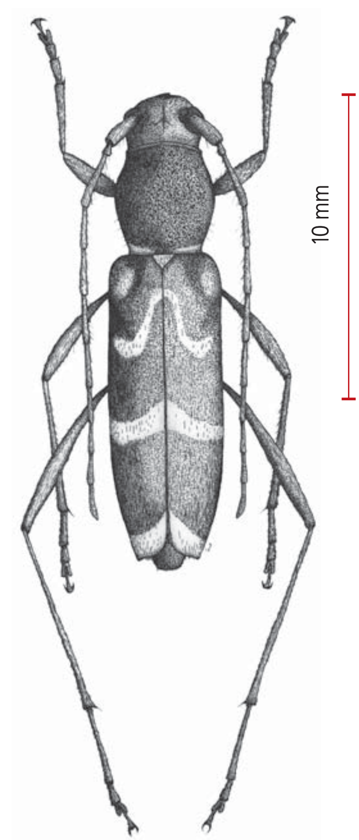

Figure 14. A very rare beetle *Chlorophorus gracilipes*, that develops in branches and boughs of broad-leaved trees and shrubs (after GUTOWSKI 1992)

Insects are the group of organisms exhibiting the greatest species richness in the world. They comprise about 50% of all living species on earth. The insects include certain groups that, despite their relatively small size, have a very significant influence on ecosystems and the human economy.

Forests are typically the richest of all ecosystems when insects are included, and one of the most endangered groups of forest organisms is the saproxylic insects. These are insects that, at some period of their lives, depend on dying trees and dead wood (at various decay stages) or on fungi or other insects inhabiting such substrates. One of the orders best represented by saproxylic species are beetles (photo 31; fig. 13, 14) – in Central Europe there are about 1500 species of beetles. There are 70 families of saproxylic beetles in Poland. Most saproxylic beetles belong to the families Cerambycidae (photo 31, 32, 33; fig. 15, 16, 17), Scolytidae, Buprestidae (photo 19, fig. 18), Anobiidae (death-watch or furniture beetles), Oedemeridae, Staphylinidae, Elateridae, Lucanidae, Scarabaeidae (scarabs), Carabidae (photo 36), Anthribidae, Curculionidae (weevils), Cucujidae (cucujids), Lymexylidae (timber beetles), Nitidulidae (sap beetles), Alleculidae, Eucnemidae (fig. 19) and Tenebrionidae.

W. Janiszewski

Photo 32. A very rare beetle *Akimerus schaefferi* – its larvae live in the dead roots of large oaks

J.M. Gutowski

Photo 33. *Rhagium bifasciatum* – widespread in mountains and foothills – lives in stumps and snags

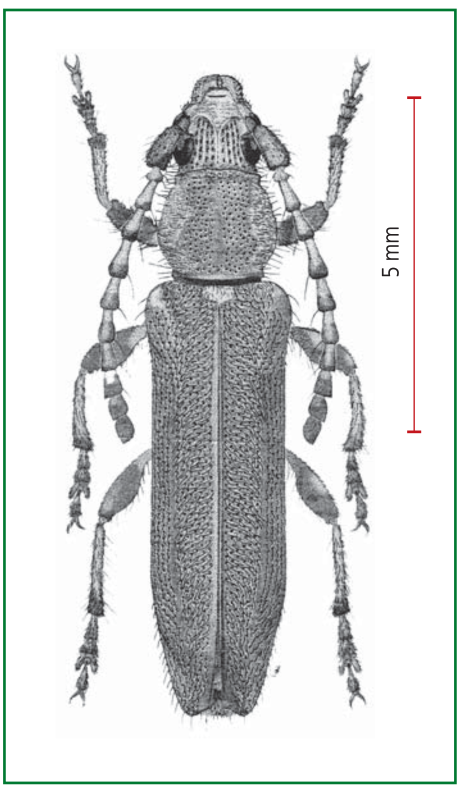

Figure 15. *Deilus fugax* – a longhorn beetle associated with the dying branches of bean-trees (after GUTOWSKI et al. 1994)

J. Walencik

Photo 35. A typically bent larva of the scarab family (Scarabaeidae) in a pupal cell located in a microhabitat of rotting wood

J. Walencik

Photo 34. The feeding habitat of the death-watch (or furniture) beetles (Anobiidae)

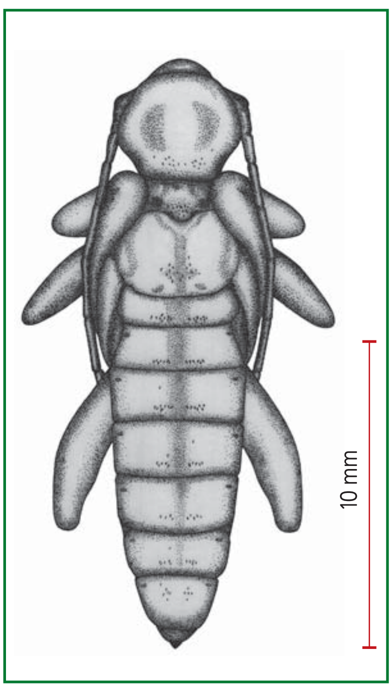

Figure 16. The pupa of *Callidium coriaceum* – dorsal side; a species associated with coniferous trees, in particular with spruce (after GUTOWSKI 1983)

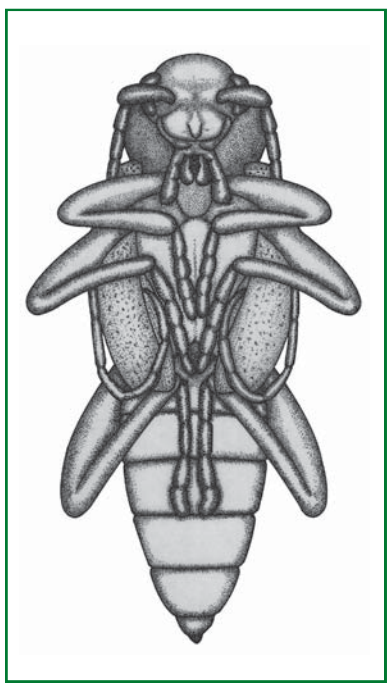

Figure 17. The pupa of *Callidium coriaceum* – ventral side (after GUTOWSKI 1983)

J. Walencik

Photo 36. A ground beetle that commonly winters in decaying stumps, snags and fallen logs

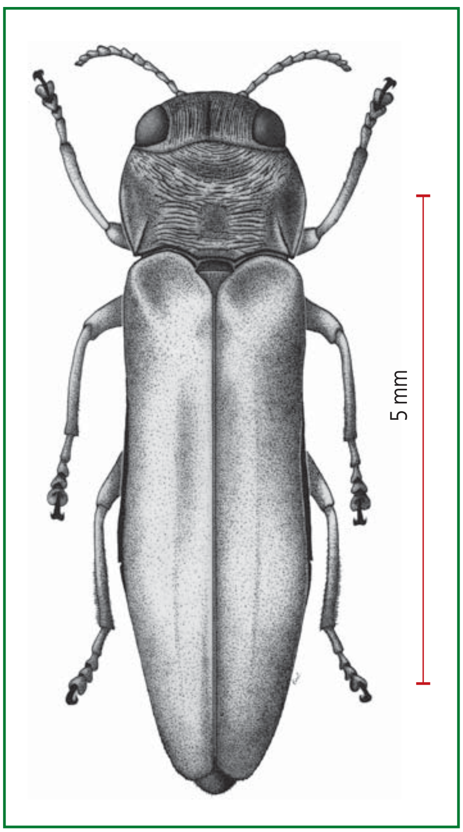

Figure 18. Buprestid beetle – *Agrilus pseudocyaneus* – a disappearing species associated with aspen (after GUTOWSKI 1993)

Figure 19. *Rhacopus attenuatus*, a member of the *Eucnemidae* family, is a very rare relic species associated with the wet wood of old aspens (after BURAKOWSKI 1989)

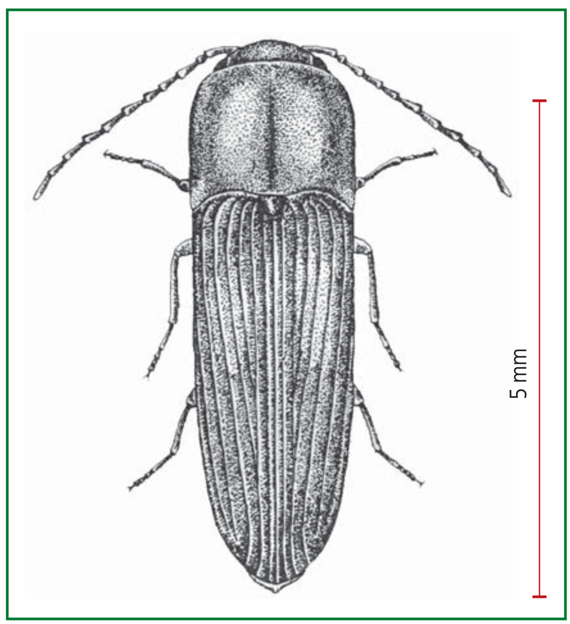

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Photo 37. A camponotus ant on the spruce trunk that is hosting its tunnels

Figure 20. Robber-fly *Laphria ephippium* (Asilidae) – its larvae live in dry, standing dead beeches, foraging on other invertebrates (after SPEIGHT 1989)

Many saproxylic insects belong to other taxonomic groups including true bugs (Heteroptera, e.g. Aradidae, e.g. flat-bugs), hymenopterans (e.g. Siricidae – siricid wasps), certain ants (photo 37), butterflies (Lepidoptera, e.g. goat moth), Cossidae, Sesiidae (clearwinged moths), dipterans (Asilidae, e.g. robber-flies, fig. 20), Syrphidae (hoverflies, photo 38, fig. 21), Tipulidae (craneflies), Mycetophilidae (fungus gnats), Cecidomiidae (cecidomyid midges), Stratiomyidae (soldier-flies) and others (photo 39). As an example, 72 saproxylic species of hoverflies are found in Poland (photo 38, fig. 21). Several of these, such as *Brachymyia floccosa*, *Caliprobola speciosa*, *Chalcosyrphus eunotus*, *Criorhina pachymera*, *Mallota cimbiciformis*, *Pocota personata* and *Sphecomyia vittata*, are endangered.

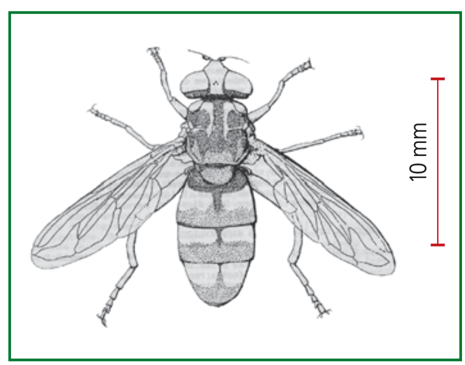


Figure 21. Dipteran *Milesia crabroniformis* (syrphid) – its larvae live in the decaying, wet wood at the base of deciduous trees' trunks (SPEIGHT 1989)

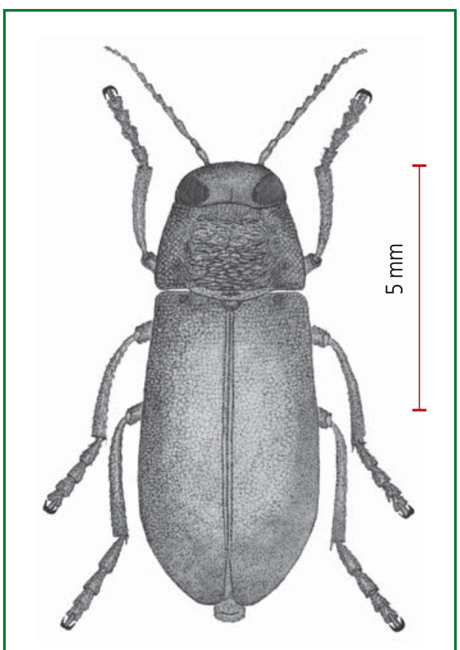
Z. Kołudzki

Photo 38. A beautiful dipteran *Temnostoma vespiforme* – a representative of the Syrphidae family, whose larvae live in the wet, rotting wood of birches and alders

J.M. Gutowski

Photo 39. The larva of the predatory dipteran of the genus *Erinna*, which lives under the bark of dead trees

Figure 22. Buprestid *Phaenops knoteki*, known in Poland from only a few sites in the south-east and from Świętokrzyski National Park (after GUTOWSKI and KRÓLIK 1996)



The greatest richness of saproxylic species is found in natural, unmanaged, forest ecosystems, e.g. in the Białowieża Primeval Forest.

Saproxylic invertebrates, including insects, either depend unconditionally on dead wood for their habitat or foraging substrate (obligate saproxylics), or 'prefer' dead wood but can exist in other situations (facultative saproxylics). These invertebrates can be further classified by the stages of decomposition or location of the dead wood that they use:

1. Cambiophages – species that live under and in the bark of trees and shrubs (photo 40, fig. 22).
2. Saproxylophages – species that consume either wood (xylophages – photo 41) or decayed wood or rot (cariophages – photo 42).
3. Mycetophages – species that consume the mycelia of fungi that decompose wood, as well as the fruiting bodies of fungi growing on dying and dead trees.
4. Predators – these invertebrates are indirectly related to dead, decaying wood; their larvae and often also adult forms (imagoes) feed on other invertebrates, including insects inhabiting CWD (photo 43, fig. 20).

J.M. Gutowski

Photo 40. The feeding habitat of larval buprestid beetles lies under the bark of pines

J.M. Gutowski

Photo 41. The impressive South European *Morinus funereus* depends on large fragments of dead wood from deciduous tree species

J. Walencik

Photo 42. Well rotted wood provides a habitat for the European rhinoceros beetle

Photo 43. A predatory wire worm or the larva of *Melanotus villosus* (Elateridae) – a click beetle that lives under bark

5. Parasitoids – their larvae parasitise saproxylic invertebrates (photo 44).
6. Coprophages – species that feed on the excrement of other organisms inhabiting dead, decaying wood.
7. Necrophages – species that feed on dead animals or parts of their bodies in dead wood or in cavities and hollows of old living trees.
8. Species that live in the sap leaking on to the bark.
9. Species that use wood as a construction material for nest building (wasps *Vespa*).
10. Species that nest in dead trees (termites, ants, wasps and bees – Aculeata).
11. Species that use dead wood as a refuge from predators and extreme weather conditions.
12. Species that use dead wood as winter hibernation sites.

Photo 44. The adult parasitoid *Xorides alpestris*, a representative of the Ichneumonidae family, that attacks longhorn beetle larvae living in the wood of deciduous trees and shrubs

Saproxylic invertebrates inhabit various dead wood microenvironments, such as dead standing trunks, stumps, roots, boughs, fallen and elevated logs, fallen branches, necroses on living trees, leaking sap, cavities and hollows, earth adhered to the exposed roots of uprooted trees (this is a crucial microenvironment for the development of *Anostirus castaneus*, Elateridae), and the fungi growing on dead wood. These microenvironments can be found at various stages of wood decay: initial, rotting, disintegration (break down of woody tissues) and putrefaction (breakdown of cellular structure).

Saproxylic invertebrates are very important elements of biodiversity. They participate in numerous ongoing processes in the ecosystem that are indispensable and irreplaceable, and lead to ecological equilibrium (homeostasis) ■.

These species participate, among other things, in:

- Decomposition and mineralisation of organic matter (with the help of microorganisms, mainly fungi),
- Limiting the numbers of phytophages ■ (through predation, parasitism, competition for food),
- Facilitation of the establishment of nesting and hiding sites suitable for numerous species of birds and mammals, several other vertebrates and a great variety of invertebrates (e.g. through collaboration in killing weakened trees after which the dead, decaying wood facilitates the excavation of cavities and hollows).

Saproxylic insects, one of the most numerous groups of invertebrates, are themselves important food for woodpeckers and other birds, as well as other animals. The insects themselves are utilised as a habitat for many microscopic organisms including nematodes, protozoa, fungi and bacteria. The excrements of insects are used by coprophagous species and their dead bodies become the food of necrophagous species.

Homeostasis:

an ecosystem's ability to maintain the relative dynamic equilibrium of composition and processes, through feedback relationships that keep the variation driven by a changing environment within narrow ranges.

Phytophages:

herbivorous animals adapted to collecting and absorbing living parts of plants, e.g. leaves, seeds, fruits, the wood of living trees, etc.

J.M. Gutowski

Photo 45. *Strangalia attenuata* – while its larvae live in decaying wood, imagoes pollinate flowers

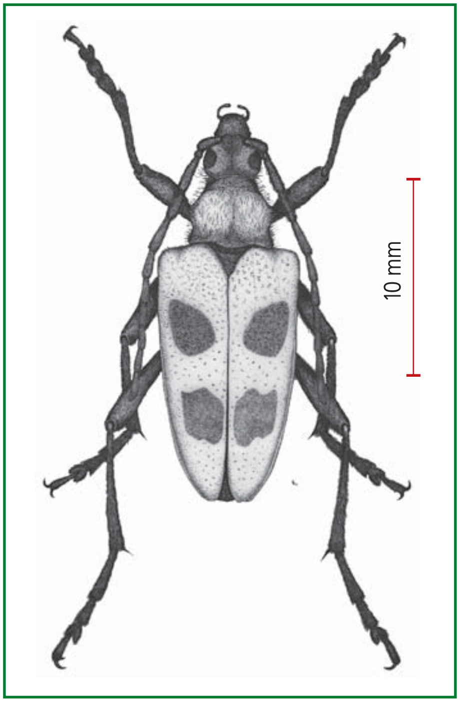


Figure 23. The longhorn beetle *Pachyta quadrimaculata* – its larva develops in decaying pine but the imago feeds on pollen (M. Waszkiewicz)

The adult stages (imagoes) of numerous saproxylic species, whose larvae prefer or are dependent upon dead wood, feed on the pollen and/or nectar of flowers contributing to their pollination (examples are Cerambycidae – photos 45, 46, 47; fig. 23, 24; Buprestidae; Scarabaeidae; Cleridae (chequered beetles); Mordellidae; Syrphidae – photo 38, fig. 21; and others).

Photo 46. *Alosterna ingrica* – a relic longhorn beetle today only found in the Białowieża Primeval Forest

J.M. Gutowski

Photo 47. *Evodinus borealis* – its larvae live in the wet wood of spruce but its imagoes feed on pollen and pollinate anemones

J. Walencik

J.M. Gutowski

Photo 48. *Leiopus punctulatus* is a very rare longhorn beetle associated with aspen

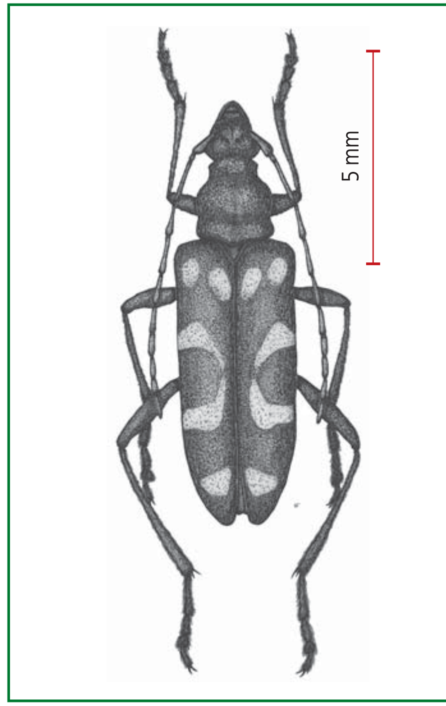
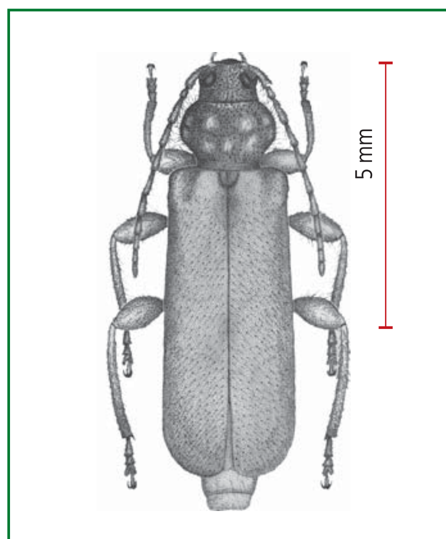


Figure 24. *Evodinus borealis* – in Poland this boreal longhorn beetle only occurs in the Białowieża, Borecka and Augustowska forests in the north-east of the country (after GUTOWSKI and KARAŚ 1992)

Figure 25. *Phymatodes pusillus* – a rare representative of longhorn beetles associated with oaks (after GUTOWSKI and HILSZCZAŃSKI 1997)



Saproxylic insects play a particularly important role in wood crumbling and decomposition. The fungi carried into the wood by insects accelerate this process. Therefore saproxylic insects accelerate the decay process, preventing dead trees and their parts from excessively accumulating in forests where decay rates are rapid. In most temperate latitudes, depending on the tree species and microclimatic site conditions, complete wood decomposition takes from one to several decades. In Europe, Cerambycidae play the most prominent role in wood decomposition (photos 48, 49, 50; fig. 23, 24, 25). In the tropics they are sometimes replaced by termites. Other taxonomic groups, mainly Buprestidae (photo 19; fig. 18, 22), Lymexylidae, Lucanidae, Anobiidae (photo 34), Scolytidae, as well as hymenopterans of the Siricidae family and dipterans of the Tipulidae family, also contribute greatly to the wood decomposition process.

J. Walencik

Photo 50. *Monochamus urussovii* – this Taiga species also occurs on spruces in the Białowieża Primeval Forest

J. Walencik

Photo 49. The longhorn beetle *Prionus coriarius* – its larvae forage underground on dead tree roots

Certain saproxylic species require special and rare habitats, such sap running on living trees, and these species are often rare or endangered. Leaking sap is an uncommon event and occurs mainly on elms, oaks and birches, and on horse chestnuts in groves and parks. This ephemeral environment is necessary for the development of certain species of dipterans (Syrphidae, Ceratopogonidae) and beetles. Among the beetles is *Nosodendron fasciculare* – the only representative of the Nosodendridae family in Poland. It is a rather small (4-4.5 mm), oval, black beetle with characteristic bunches of red-brownish hair on the elytra. The rare species of Syrphidae (photo 38, fig. 21) living in this environment are: *Brachyopa dorsata*, *B. panzeri*, *B. scutellaris*, *Ferdinandea nigrifrons* and *F. ruficornis*. The major threat to these insects is the decreasing number of diseased trees that exude sap, mainly caused by the removal of such weak trees to meet forest management objectives (in the case of elms, it is also caused by Dutch elm disease decimating these trees in European forests).

The species richness of spaproxylic insects is positively correlated with the quantity and quality (diversity) of CWD in forests, and with the diversity of natural fluctuations in the successional stages (phases) of forest development.

Photo 51. Larval galleries of the great capricorn beetle in oak wood


J.M. Gutowski

The Białowieża Primeval Forest is a rare unmanaged forest in eastern Europe where the highest numbers of saproxylic species in the temperate regions continue to persist. However, most of the forest is in the process of being converted to younger aged plantations. As extraction of old trees and dead wood continues across space and through time, losses in biodiversity increase. After over one hundred years of meeting 'a high hygienic standard' policy (frequent sanitation or removal of sick trees and dead wood) many of the European forests have become 'sterilised,' the number of individuals of most saproxylic species has declined, and many species have been lost. For example, it is estimated that the number of saproxylic species of beetles in Austria has decreased by 10% since the advent of intensive forest management.

Old living trees with dying boughs and branches, cavities, hollows and side necroses provide an extremely rich environment for saproxylic insects. Many of these species occur only on the very old trees that provide numerous, specific microsites. Among such stenotopic species ■ dependent on old trees are *Eurythyrea quercus* (Buprestidae), *Tragosoma depsarium*, *Stictoleptura variicornis*, the great capricorn beetle *Cerambyx cerdo* (photo 51), *Trichoferus pallidus* (Cerambycidae, fig. 26), and many others. Certain insects find suitable developmental conditions only on trees older than 200 years; these include *Boros schneideri* (Boridae) on pines, *Protaetia aeruginosa*, hermit beetles *Osmoderma eremita* (Scarabaeidae) and *Lacon querceus* (Elateridae) on oaks. The cavities and hollows of old trees are often occupied by forest bees. Semi-wild colonies of bees in hollow oaks and pines were cultured in the forests of Białowieża before the end of the 19th century.

Stenotopic species:

species with very narrow environmental requirements.

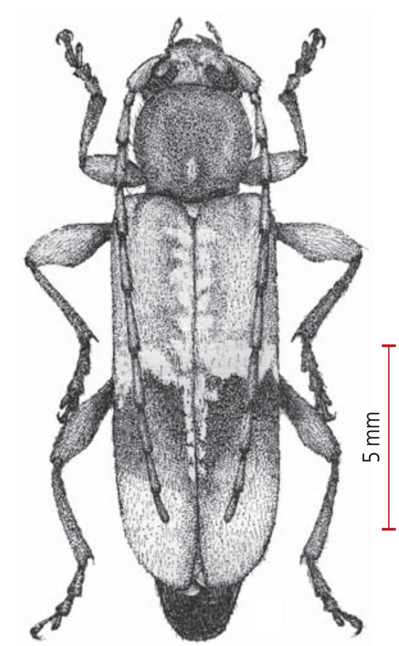


Figure 26. The longhorn beetle *Trichoferus pallidus* lives in dying oak boughs (after GUTOWSKI 1986)

Polyphages:

omnivorous organisms, feeding on a multitude of species of fungi, plants and animals, and demonstrating a broad dietary selection. Monophages are organisms feeding on only one fungus, plant or animal species or genus.

Types of wood root:

detailed data on the types of wood decay can be found in the chapter dedicated to fungi (4.1.4 – pages 107-128).

Obligatory (unconditional) xylophages:

species that can develop only in wood; facultative (occasional) xylophages are species that, if wood is not available, may develop in another kind of environment, such as soil.

The trophic relationships of saproxylic invertebrates, though not fully understood, suggest that most species depend on broad-leaved trees, in particular oaks. However, a rich saproxylic fauna is also found associated with pine and spruce, but relatively few saproxylic species are found on ash. Many saproxylic species are polyphagous and colonise the wood and rot of various tree species. However, there are also many monophages that depend on a single species or genus of tree. Therefore to maintain a full complement of these organisms, it is important that wood from all tree species living in a given region and environment are present.

Dead wood colonisation by insects does not depend only on tree or shrub species, size, insolation and humidity, but often on the sort of decay that is taking place in a given substrate (trunk, bough, stump, etc.). For instance, many species favour brown rot whereas others prefer white rot. There is also a large group of species that can develop in wood of various decay stages (for example, wet rot).

There are also saproxylic invertebrates that live in water, more precisely, in submerged wood (photo 52) and some even require submerged wood to persist. In Central European streams 15 obligatory and 22 facultative xylophages can be found. Other species may require submerged wood for crucial parts of their life cycles. For instance, the larvae of the beetle *Nacerdes melanura* (Oedemeridae) live in wet wood partially submerged in sea water, and obligatory xylophages such as caddice-flies *Lype phaeopa* (Trichoptera), the beetle *Potamophilus acuminatus* (Elminthidae), and the non-biting midge *Brillia modesta* (Chironomidae), live in European fresh waters.

Dead wood in forests or groves provides wintering habitats for many invertebrates, not only for forest species, but also for those living in the neighbouring meadows, steppes and arable fields. Myriapods, hemipterans, hymenopterans, dipterans and beetles find refuge from severe winter weather under the bark and in the humid wood of fallen logs, stumps, or the low parts of trunks. Dead wood is especially important as refugia for predatory Carabidae (photo 36) that either burrow into rotting wood, use crevices in the wood or occupy the space between the bark and wood.

It is worth discussing not only the existing relationships among the groups of organisms inhabiting CWD, but also the relationships between them and those species using habitats other than dead wood. Saproxylic insects serve as food for numerous species of amphibians, reptiles, birds and mammals, directly influencing the numbers, and in some cases the presence, of these animals. The relationship is simple: the more CWD in forests → the more saproxylic invertebrates → the more vertebrates, especially birds → the higher the aesthetic value of the forest landscape (noticed and appreciated by tourists and nature lovers).

J. Walencik

Photo 52. "The more CWD in forests → the higher the aesthetic value of the forest landscape;" Białowieża Primeval Forest

However, the maintenance of sufficient amounts of dead wood requires a constant supply of live trees in all of their growth stages. That is, the living component of the forest and its processes are just as important as the dead component in the perpetuation of a functional forest with all of its complement of plants and animals.

Threats to wood-related invertebrates

The habitats of saproxylic invertebrates are among the most endangered in Europe. The habitats of insects foraging on living plants, e.g. leaves, can be re-created within one to several years or even decades, however, the habitats of certain stenotopic saproxylic species may require centuries for replacement. This is especially true for species that require trees of large diameter, either living or dead, and the time required depends on the growth rates of the trees as well as the degree of decadence of living trees, or the degree of decay of dead trees. In Europe, about 40% of saproxylic species are threatened with extinction, and the populations of the majority of remaining species appear to be declining.

The forms of nature protection currently in operation in Poland do not eliminate the threats to the stenotopic saproxylic organisms. These species have little environmental tolerance and depend on very specific types of habitats, e.g. large-sized CWD, that currently are almost entirely lacking in most European forests.

Nature reserves that are intended to perpetuate the presence of old and dying trees or shrubs have been established in various locations in Poland and elsewhere. However, their total area is very small, they tend to be widely separated, and they do not represent the entire array of environments and communities that are native to Poland. The history of the reserve is very important to its conservation value. For instance, reserves established on the remnants of natural forests are more likely to capture the crucial elements of dead wood and perpetuate the natural decay processes than are other reserves. Saproxylic insects are good indicators of the continuity of these natural processes. The lack of these insects indicates that the forest in question may not possess the essential wood recycling processes. Such a lack also suggests that the forest was totally or intensively harvested or perhaps converted to another vegetation type at some time in the not too distant past (e.g. burned, cleared or transformed into arable land) and later restored (e.g. replanted with trees typical of the original forest).

The successful conservation of many saproxylic species with limited dispersal ability is dependent on the temporal and spatial continuity of their habitat and food base. For instance, if an adequate number of gravid monophagus insects do not find suitable sites for egg placement in trees or shrubs (acceptable species, suitable size, appropriate degree of decompostion of wood and cambium, favourable insolation, etc.) their subpopulation will be subject to extinction. *Bolitophagus reticulatus* (Tenebrionidae) does not migrate farther than 30 m from the place where it underwent metamorphosis. The hermit beetle, which develops in the cavities and hollows of old trees, spends all its life within a radius of 190 m from this breeding cavity or hollow. Considering that many saproxylic species occurring in Poland occupy only a single or a few distantly spaced refuges, (some of these species are unique and not found elsewhere in Europe or the world), the critical habitat and consequently the species could be easily lost and that loss would be irreplaceable. Perhaps only a few hundred hectares of forest, with all of its functional components (decay phases and DBH classes of dead trees) and processes present, would be needed to perpetuate most of the saproxylic invertebrates.

Many of the least mobile saproxylic insects and other invertebrates, e.g. mites, pseudoscorpions and beetles, require tree cavities and hollows, and often rot powder, in old oaks, limes, beeches and other veteran trees. In Poland, about 100 species of beetle live in cavities and hollows. The small number and wide dispersion of old, cavity-bearing trees in managed forests means that many of these species are becoming rare and threatened with extinction.

Beetles living in rotting wood microhabitats of living trees' cavities and hollows in Central Europe

HISTERIDAE
Abraeus granulum
Plegaderus caesus
Plegaderus dissectus
PTILIIDAE
Ptenidium gressneri
Ptenidium turgidum
LEIODIDAE
Nemadus colonoides
SCYDMAENIDAE
Euthiconus conicicollis
Microscydmus nanus
Scydmaenus hellwigii
Scydmaenus perrissi
STAPHYLINIDAE
Batrisodes adnexus
Batrisodes delaporti
Euplectus bescidicus
Euplectus brunneus
Hapalaraea pygmaea
Quedius infuscatus
Quedius microps
Quedius truncicola
Saullcyella schmidti
Thoraxophorus corticinus
Velleius dilatatus
TROGIDAE
Trox scaber
LUCANIDAE
Dorcus parallelipipedus
SCARABAEIDAE
Cetonia aurata
Gnorimus nobilis
Gnorimus variabilis
Osmoderma eremita
Protaetia aeruginosa
Protaetia lugubris
Protaetia metallica
Valgus hemipterus
SCIRTIDAE
Prionocyphon serricornis
EUCNEMIDAE
Eucnemis capucinus
ELATERIDAE
Ampedus cardinalis
Ampedus elegantulus
Ampedus hjorti
Ampedus megerlei
Ampedus nigroflavus
Ampedus rufipennis
Cardiophorus gramineus
Cardiophorus widenfalki
Crepidophorus mutilatus
Elater ferrugineus
Ischnodes sanguinicollis
Lacon lepidopterus
Lacon querceus
Procraerus tibialis
Reitteroelater dubius
LYCIDAE
Platycis minuta
CANTHARIDAE
Malthinus frontalis
Malthodes pumilus
DERMESTIDAE
Dermestes bicolor
Globicornis corticalis
Trinodes hirtus
ANOBIIDAE
Dorcatoma dresdensis
Dorcatoma flavicornis
Oligomerus ptilinoides
Xestobium rufovillosum
TROGOSSITIDAE
Grynocharis oblonga
Ostoma ferruginea
Tenebroides fuscus
MELYRIDAE
Charopus flavipes
MONOTOMIDAE
Rhizophagus cribratus
CRYPTOPHAGIDAE
Cryptophagus confusus
Cryptophagus fuscicornis
Cryptophagus labilis
Cryptophagus micaceus
Cryptophagus pallidus
Cryptophagus quercinus
LATRIDIIDAE
Latridius brevicollis
MYCETOPHAGIDAE
Mycetophagus populi
MELANDRYIDAE
Conopalpus testaceus
Hypulus bifasciatus
Hypulus quercinus
COLYDIIDAE
Cicones variegatus
Pycnomerus terebrans
Rhopalocerus rondanii
TENEBRIONIDAE
Allecula morio
Allecula rhenana
Mycetochara axillaris
Mycetochara flavipes
Neatus picipes
Pentaphyllus testaceus
Prionychus ater
Pseudocistela ceramboides
Tenebrio opacus
OEDEMERIDAE
Calopus serraticornis
Ischnomera caerulea
Ischnomera sanguinicollis
Nacerdes melanura
ADERIDAE
Euglenes oculatus
Euglenes pygmaeus
SCRAPTIIDAE
Scraptia fuscula
CERAMBYCIDAE
Alosterna tabacicolor
Anisarthron barbipes
Rhamnusium bicolor
CURCULIONIDAE
Cossonus linearis
Dryophthorus corticalis
Phloeophagus lignarius
Phloeophagus thomsoni
Phloeophagus turbatus
Stereocorynes truncorum

In relatively stable environments, such as in the remnant old forests in Poland, numerous generations of invertebrates have lived under relatively unchanged conditions for 100 or more years. The most endangered saproxylic species are those unable to disperse beyond short distances, requiring old, but live, hollow and well insolated trees situated at the forest edge, along roads or in open stands. The presence of these rare invertebrate species suggests that these forest ecosystems have persisted since prehistoric times or as long as 1,500 to 2,000 years.

Forest sanitation and sanitary status:

a forestry practice that minimises the presence of dying and dead trees in managed forests; sanitary status is measured by the percentage of dead trees in the forest: the smaller the number of dead trees the better the forest's sanitary status.

A major threat to the saproxylic organisms in Poland as well as in most European countries, is forest management objectives that focus on wood products and not old trees and dead wood. A basic principle of the current forestry practices is to sanitise the forest ■. The concept of 'forest sanitary status' is related to the health of trees in a given stand. The maintenance of an acceptable sanitary status requires the removal of most if not all of the weakened trees that have been inhabited by saproxylic insects and other organisms. The practice of sanitation leads to the reduction of dying and dead wood in the forest; followed by the possible reduction of some or all of the saproxylic species, or even the extirpation of some species. The change in the number of species that are key to a functioning forest may well be followed by a reduction in ecosystem homeostasis.

The Białowieża Primeval Forest: a paradise for saproxylic invertebrates

The Białowieża Primeval Forest (BPF), in Poland, hosts a great many saproxylic insects and this group is one of the most valuable and critical components of the BPF's biodiversity.

Owing to the unmanaged and well preserved natural character of the forest, the relatively vast area and the historical continuity lasting several thousand years, there are many species yet extant in the BPF that disappeared a long time ago in other parts of Europe. Species that used to be frequent, but have had no chance to persist in the European monocultures, have survived in the BPF. Therefore, the BPF should be considered a major reservoir of saproxylic fauna. These organisms will spread out of the BPF to re-occupy their original ranges should adjacent land be restored to reflect natural stand conditions, to harbour increased amounts of dead wood, and to permit natural forest processes to operate. This re-colonisation is likely to be successful as there are few physical barriers preventing the migration of saproxylic organisms, although the immense distances to be covered suggest that the time required will be in the order of millenia.

In the interim, the BPF is a place where ecosystem functions and the population structures of various species – the inhabitants of ancient primeval forests that used to cover lowland Europe – can still be studied. Because of these values, the BPF should be considered a benchmark, a reference model for other lowland forests in the temperate zone. It must be emphasised once more that, without dead wood, and copious amounts of dead wood with the full complement of the decay stages and expressions, and its continuous presence since prehistoric times, the BPF would not be such a model.

There are no 'pests' in a natural forest

While discussing the role of dead wood in the ecosystem, one cannot ignore the effects of spruce bark beetles. This species contributes to the 'production' of dead wood in forests by inducing mortality of spruce trees, thus it is an important component in the dynamics of forest stands with spruce trees. Studies from forests in Bavaria show that there are 173 species of beetles and 181 dipterans connected with spruce wood.

Spruce bark beetle populations tend to have cyclical outbreaks that can result in great economic loss in landscapes occupied by its host plant – Norway spruce

Photo 53. Dead wood covered by a carpet of mosses and fungi in the Białowieża mesic deciduous forest

J. Walencik

Photo 54. Dead wood in winter in the Białowieża Primeval Forest

J.M. Gutowski

(in Poland these spruces are mainly in the south and north-east). During outbreaks, beetle attacks may cause the death of weakened trees (e.g. weakened by drought, fire, windstorms, fungal infection and infestation by so-called 'primary pests,' insects that attack spruces in their old age), and even apparently healthy spruces. Together with other mortality agents, spruce bark beetles at outbreak levels can substantially increase the supply of dead spruce wood in a very short period of time.

The sanitary removal of spruce bark beetle-infested trees during the growing season causes serious damage to other forest components. On the other hand, not taking such action (e.g. in national parks) evokes protests among foresters from neighbouring areas because of the belief that dead trees in nature reserves and national parks have a negative influence on the sanitary status of the surrounding managed forests. Protected areas are often perceived as 'pest hatcheries' by those who do not understand the role of dead wood in functioning forests, and sanitation of the stand or removal of the dead trees often occurs well after the emergence and flight of the next generation of beetles and therefore has little effect on reducing the outbreak.

While there are undeniable negative economic effects (generally in terms of reduction of wood quality) of the spruce bark beetle outbreaks in commercial forests, there is a growing interest in the positive ecological role of this group of insects and its importance to other elements of the forest environment. We are beginning to understand the role that this and similar species play in properly functioning ecosystems from research conducted in protected areas. However, extending that knowledge to management in other forests, including management in Poland's national parks, is still considered 'controversial.'

Recent findings by forest ecologists and entomologists show that various natural disturbances, including outbreaks of spruce bark beetles and other cambiophages, are not necessarily catastrophes for ecosystems. Such events happen even in the most unaltered parts of the Siberian or Canadian taiga. These disturbances may cause the death of many trees (sometimes covering vast areas of forest), but the richness of these forests and their structural and species diversity is actually contingent on such phenomena. Thus, outbreaks of insects are unavoidable in protected areas. Their intensity and range are positively correlated with the degree of stand deviation from the natural forest model. Also climatic shifts may reduce the viability of the existing stand composition and structure, driving to their adaptive changes.

Current theories in forest ecology suggest that outbreaks of the spruce bark beetle and other species are expected parts of the natural processes in dynamic forest ecosystems where spruce is a prominent component of stands, and as such, outbreaks cannot be eliminated. On the other hand transformations of ecosystems caused by human management impacts may cause the outbreaks to be more intense, frequent and lengthy as they move the forest composition or structure beyond that which would be expected to persist at a particular site.

Spruce bark beetle in the Białowieża Primeval Forest

The spruce bark beetle (photo 55) is one of the most important cambiophages of Norway spruce in the BPF.

According to the results of palynological analyses (palynology results in descriptions of past vegetation compositions from the analysis of fossilized pollen preserved in old layers of sediments, peat bogs and lake bottoms), spruce has been a continuous resident of the BPF for at least the last 9000 years. Is it not likely that spruce bark beetles have attacked spruce in that time? Is it not likely that outbreaks have occurred frequently in the last 1500 years, during the period when spruce was a major component of the BPF? Assuming that the spruce bark beetle is not a non-native invasive, and there is no scientific premise for such speculations, outbreaks ought to have been relatively common events for centuries if not millennia. Accompanying various natural disturbances (fires, hurricanes, droughts), frequent outbreaks could have been quite intensive for a while, but inevitably, the outbreaks would have declined after a few years as conditions changed, the supply of weakened trees declined, or insect predators, parasites, and diseases reduced the spruce bark beetle population below outbreak levels.

K. Sućko

Photo 55. Spruce bark beetle *Ips typographus*: its tunnels provide a refuge to many rare saproxylic insects

BNP:

Białowieża National Park;
Usually BNP refers to the strict reserve of the National Park, the core area of the BPF, set aside in 1921. This is the oldest and largest non-intervention area in Europe representing lowland deciduous and mix forest. The BNP strict reserve covers 7474 hectares, which is merely 7% of the Polish side of the BPF.

Local outbreaks of *I. typographus* used to occur in the past after disturbances caused by windstorms, but the high diversity of environments and stands most probably prevented outbreaks from expanding beyond relatively local scales. In the 19th century, the forestry journal *Lesnoi Zhurnal* reported a remarkable spruce bark beetle outbreak in 1882-83, which followed a violent windstorm that "blew down many trees." The increase in more frequent and intensive outbreaks coincided with high densities of game populations, intensive cattle grazing, and a relatively cool climate at the turn of the 19th and 20th centuries, which favoured spruce over broad-leaved tree regeneration. The shift to spruce dominance was an anthropogenic effect, without which broad-leaved and mixed stands would have continued to dominate these rich deciduous forests.

According to available historical data and current observations there have been at least seven outbreaks of spruce bark beetles in the BPF since the late 1800s (1882-83, 1919-22, 1951-55, 1963-66, 1983-88, 1994-97, 2001-03). Numerous research studies on the spruce bark beetle and its role in the forest ecosystem carried out since the 1920s, have yielded some interesting and useful information. For instance, the factors of ecosystem resistance (e.g. predators, parasitoids, fungi) lead to a 95.7% decrease in the number of beetles in BNP whereas in Polish managed forests only an 82.5% decrease was observed. More recent studies showed that the mortality of spruce bark beetles in BNP results in about half as many adults emerging per unit of spruce bark surface compared to beetle emergence in the managed part of the BPF!

Massive outbreaks of bark beetles are triggered by factors leading to an increase in abundance of weakened spruce trees, the beetle's appropriate food stock. The spruce predisposition to bark beetle attack can be increased by a long period (several years) of drought (with a very shallow root system, spruce is very susceptible to a lack of water in the soil), coupled with fungal infections and old age. Stochastic events, such as windthrow or forest thinning or clearing, can also cause a sudden flush of fresh CWD or induce sufficient stress for bark beetles to attack trees.

The basic factors that limit the spruce bark beetle population in the BPF are: parasitic hymenopterans, predatory insects, woodpeckers, parasitic fungi and intra- as well as inter-species competition for the available resources. Generally speaking, after 2-3 years, the spruce bark beetle outbreak is followed by such a high accumulation of antagonistic species (parasites, parasitoids, predators), that the beetle numbers drop precipitously to even below the forage requirements of the parasitoids and parasites (especially those that are highly specialised). This reduction in spruce bark beetles is thus followed by a decline in the numbers of its enemies. For several years following the collapse of an outbreak, there is a gradual increase in the spruce bark beetle population. Wet, rainy years may delay the timing of the next outbreak, but the presence of favourable conditions may accelerate the outbreak towards its peak. It is clear, however, that internal factors of the spruce bark beetle population alone cannot initiate its outbreak. Large numbers of stressed trees capable of being attacked are necessary to start the outbreak, but its end usually depends on biotic factors (parasitoids, predators, fungal pathogens, reduction of stressed trees, etc.).

Observations of natural mixed forests in temperate climates (including the BPF) show that pest control activities do not have a major influence on the duration of outbreaks. Three to four years after the beginning, the outbreak declines both in reserves and in managed forests where intensive spruce bark beetle eradication is applied. 'Pest control' effects may be different in artificial spruce monocultures but that discussion goes beyond the scope of this book.

Spruce bark beetle outbreaks in the BPF and in other semi-natural forests are indispensable processes for the functioning of those ecosystems with a considerable component of spruce. A severe decline of Norway spruce in which the bark beetle plays a critical role is also a system response to prior anthropogenic disturbances, and contributes to the restoration of appropriate forest functions. Outbreaks, therefore, merely eliminate an artefact resulting from direct or indirect human interference. The Białowieża Forest does not exhibit catastrophic die-offs due to spruce bark beetles, as some imply. The existence of neither spruce as a species, nor the BPF as a forest, are threatened by the bark beetle. Norway spruce is only one of numerous species occurring there and it regenerates successfully on suitable sites. A partial retreat of this boreal species in certain communities of the BPF, also observed in other regions of Central Europe, is conditioned by more general factors, such as climatic warming within the last century.

Bark beetle outbreaks are an excellent, selective process that restores and maintains a natural mosaic structure (both spatially and temporally), as well as the species composition and dynamics of the forest. They are also necessary to provide foraging material for saproxylic organisms, which are among the most valuable elements contributing to the functioning of the BPF along with many unique and endangered species (in fact, many unique, endangered species related to spruce in Poland are only known from the BPF, or if still found elsewhere they are in a few, dispersed locations, e.g. *Lasconotus jelskii*, *Pytho kolwensis* (fig. 27), *Bius thoracicus*, *Pityogenes saalasi*, *Orthotomicus starki*). Outbreaks also result in the availability of a larger quantity of food that is important to the diet of various organisms, e.g. birds (mainly woodpeckers), predatory insects and arachnids, and serve as microhabitats for protozoa, nematodes, insects and other organisms.

Pest control carried out according to the 'Forest Protection' regulations in the BPF substantially alters the natural mechanisms of the forest's dynamics and can

Photo 56. Felling and barking this enormous spruce in the Białowieża Primeval Forest has annihilated the habitat, including the area between the bark and wood and deeper within the wood, of many rare species of invertebrates

J.M. Gutowski

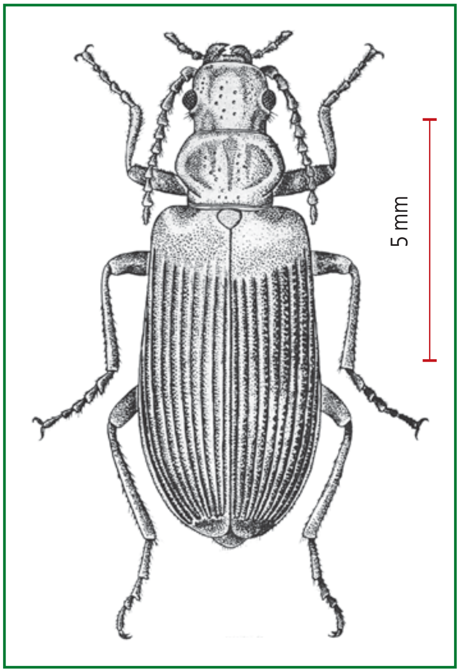


Figure 27. *Pytho kolwensis* – a very rare, boreal species living under the bark of dead spruces (after BURAKOWSKI 1962)

J.Korbel

Photo 57. Felling, barking and burning the bark of spruce is a common 'pest control' method applied in the Białowieża Primeval Forest

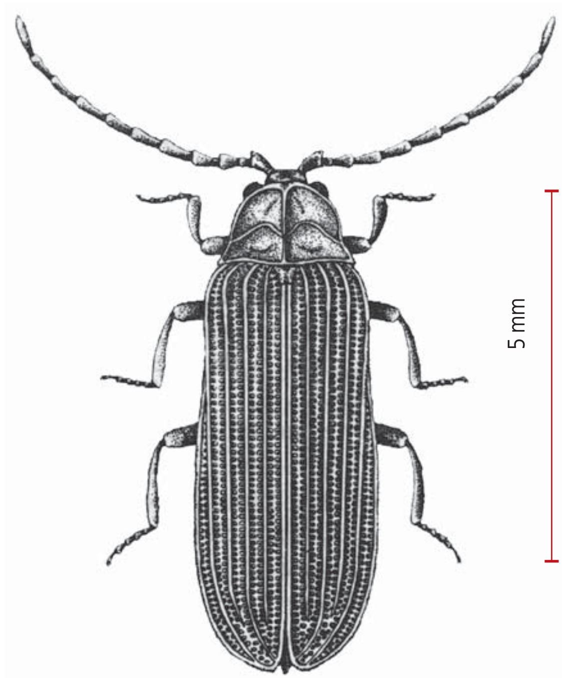


Figure 29. *Lopheros lineatus* (Lycidae), lives in large, wet fallen ash logs and is found only in Japan and the Białowieża Primeval Forest (after BURAKOWSKI 1990)

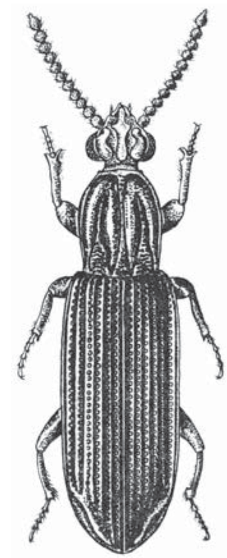


Figure 28. *Rhysodes sulcatus* – a relic of primeval forests; lives under the bark and in the decaying wood of large trees (after BURAKOWSKI 1975)

Photo 59. Piles of marketable timber, the result of 'pest control' in the Białowieża Primeval Forest

J. Korbel

Photo 58. Only memories of the natural forest are left; Białowieża Primeval Forest

J.M. Gutowski

lead to the impoverishment of its unique biodiversity. The most visible aspect of this sort of pest control is the loss of biomass extracted as spruce logs and the burned slash (branches and bark). However, more serious is the loss of the forage and microhabitats of saproxylic organisms. Pest control destroys the eggs, larvae and pupae of many insect species that colonise the dead spruce trees following the spruce bark beetle attacks. Peeling, burning or burying the spruce bark with the eggs, larvae and chrysalises of these insects, as well as removing them with timber from the forest, can lead to the loss of many specimens of rare and very important species (photos 56, 57, 58 and 59). In a single compartment of the BPF, more than 100 rare beetle species and 50 rare fungal species, all associated with the dead wood component, were found.

Summary of Chapter 4.1.2.

Thousands of invertebrate species (e.g. annelids, arthropods, myriapods, insects, molluscs) depend on the presence of dead wood in forests (saproxylic species). Among these animals there are: species living in and under bark, in wood and the rot of woody species; species foraging on decomposing wood fungi and their fruiting bodies; predatory and parasitic invertebrates living on other organisms occurring in this environment; species feeding on the excrement of other saproxylic animals; scavengers eating dead animal bodies found in dead wood or in the cavities/hollows of old living trees; species living in leaking sap; those that utilise dead wood as a construction material for nests; invertebrates seeking refuge from predators or extreme weather conditions or seeking hibernation sites.

A substantial proportion of saproxylic species are rare and endangered. To reduce the risk of their extinction, it is necessary to retain, in forests, an adequate quantity of standing dead trees, lying logs, living trees with cavities/hollows, uprooted trees, snags, dead boughs, branches, etc. Because the specific needs of various species are diverse, the continual presence and adequate supply of all kinds of dead wood is essential.

The most susceptible of these species to extinction are invertebrates inhabiting rot in old hollow trees, thick stumps and lying logs.

Only the establishment of large forested reserves (at least a few hundred hectares in size), where removal of living and dead trees is minimised or eliminated and the functional processes expected are permitted to operate or are restored, can ensure a continuous supply of dead wood and the sustenance of viable populations of saproxylic invertebrates.

The Białowieża Primeval Forest is Europe's most unique forest and its richest reservoir of saproxylic invertebrates.

The cyclical, repetitive outbreaks of the spruce bark beetle are an indispensable element of the functioning of natural forests with a substantial component of spruce in their stands. By killing weakened trees, the spruce bark beetle is an excellent selective process for the restoration and maintenance of a functional forest's mosaic structure. The creation of gaps in the canopy increases the amount of open space, which provides a variety of warm and insolated habitats necessary for those species requiring sunlight, and the accumulated dead wood is necessary forage for a multitude of species, including some that are dependent on spruce and are now endangered and vanishing species.

Rare and disappearing beetle species
living in the dying and dead spruce trees
of the Białowieża Primeval Forest

RHYSODIDAE
Rhysodes sulcatus (fig. 28)
HISTERIDAE
Platysoma deplanatum
Platysoma elongatum
Platysoma ferrugineum
Plegaderus saucius
LEIODIDAE
Agathidium plagiatum
STAPHYLINIDAE
Atheta boletophila
Atheta liturata
Atheta pilicornis
Atheta taxiceroides
Baptolinus longiceps
Baptolinus pilicornis
Bolitochara pulchra
Cyphea curtula
Dadobia immersa
Euryusa castanoptera
Euryusa sinuata
Gyrophaena minima
Gyrophaena nitidula
Gyrophaena pulchella
Gyrophaena strictula
Hapalaraea linearis
Ischnoglossa prolixa
Leptusa fumida
Leptusa ruficollis
Olisthaerus substriatus
Phloeopora angustiformis
Phloeopora nitidiventris
Phloeostiba lapponica
Phymatura brevicollis
Placusa atrata
Placusa depressa
Placusa incompleta
LUCANIDAE
Ceruchus chrysomelinus
BUPRESTIDAE
Buprestis haemhorroidalis
Buprestis splendens
Chrysobothris chrysostigma
Chrysobothris igniventris
EUCNEMIDAE
Hylis procerulus
ELATERIDAE
Ampedus elegantulus
Ampedus erythrogonus
Ampedus praeustus
Ampedus suecicus
Ampedus tristis
Diacanthous undulatus
Lacon conspersus
Lacon lepidopterus
LYMEXYLIDAE
Elateroides flabellicornis
TROGOSSITIDAE
Peltis grossa
NITIDULIDAE
Epuraea angustula
Epuraea fussi
Epuraea muehli
MONOTOMIDAE
Rhizophagus grandis
CUCUJIDAE
Cucujus cinnaberinus
Cucujus haematodes
CRYPTOPHAGIDAE
Pteryngium crenatum
Micrambe longitarsis
BOTHRIDERIDAE
Bothrideres bipunctatus
ENDOMYCHIDAE
Symbiotes latus
LATRIDIIDAE
Latridius brevicollis
Enicmus atriceps
Enicmus testaceus
Stephostethus alternans
Stephostethus pandellei
Corticaria abietorum
Corticaria alleni
Corticaria interstitialis
Corticaria lapponica
CIIDAE
Cis dentatus
Cis quadridens
Dolichocis laricinus
MELANDRYIDAE
Mycetoma suturale
Abdera triguttata
MORDELLIDAE
Curtimorda maculosa
COLYDIIDAE
Lasconotus jelskii
TENEBRIONIDAE
Bius thoracicus
Corticeus longulus
Corticeus suturalis
Hymenophorus doublieri
Mycetochara obscura
PROSTOMIDAE
Prostomis mandibularis
BORIDAE
Boros schneideri
PYTHIDAE
Pytho abieticola
Pytho kolwensis (fig. 27)
CERAMBYCIDAE
Acmaeops angusticollis
Acmaeops septentrionis
Callidium coriaceum (fig. 16, 17)
Evodinus borealis (photo 47, fig. 24)
Lepturobosca virens
Monochamus saltuarius
Pedostrangalia pubescens
Semanotus undatus
Stictoleptura variicornis
Tragosma depsarium
CURCULIONIDAE
Rhyncolus sculpturatus
SCOLYTIDAE
Cryphalus saltuarius
Orthotomicus starki
Pityogenes saalasi
Pityophthorus morosovi
Polygraphus punctifrons
Xylechinus pilosus

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4.1.3. ALGAE, BRYOPHYTES, LIVERWORTS AND VASCULAR PLANTS

The dead tree – an evolving habitat

A dead tree provides a habitat for innumerable organisms, including plants. However, its properties are dynamic and they change drastically during the process of decay. These changes in properties also affect the character and quality of the habitat, and through the habitat, the assemblage of associated or dependent organisms.

When a tree or its fragments fall, they are often covered completely or partially by bark. The bark, whether tightly or loosely attached, forms a barrier to vascular plant rooting. While bark is a good barrier to the establishment of most plants, certain bryophytes can establish and grow on the bark. Epiphytes, (i.e. the plants, mainly mosses and lichens, that grow on the trunks and branches of living trees) are suddenly moved to a different environment with substantially different light and humidity conditions, after the death and fall of the tree. The relatively stable and homogenous vertical site of the trunk is replaced by an uneven mosaic of microsites that develop on the fallen log. The flora that becomes established, through time, on the well insolated and drier tops of fallen logs is very diverse, although subject to trampling by small animals using the logs as movement corridors. The surface of the lower part of a log, which is close to the ground, offers more shade and usually higher humidity. The log's floral composition, originally a fairly homogenous assemblage of epiphytic bryophytes, is gradually transformed into a mosaic of different floral assemblages occupying the newly established niches as the log moves through the decay process.

As wood decay begins (Chapter 3.1 – page 30 and Chapter 4.1.4 – page 107), the plants growing on this substrate face substantial habitat changes. The bark loosens from the wood and gradually falls. The exposed sapwood surface, initially hard and smooth, is slowly but steadily transformed into a slightly compacted material. Mosses adapted to life on bark now begin to be replaced by other species, as the partly rotten wood is now capable of being penetrated by the roots of vascular plants, permitting their establishment.

However, for plants, even very rotten wood, as a habitat, is very different from soil. Rotten wood is "a highly humidified substrate, with very loosely bound particles", according to Hackiewicz-Dubowska, an ecologist who studied vegetation on decaying wood in the BPF in the first half of the 20th century. As such, it cannot offer firm support to the rooting plants, and thus it can be colonised only by certain species. Common characteristics of these species are shade tolerance and stem and root morphologies that allow growth and development on and in the rotten wood. Touch-me-not balsam *Impatiens noli-tangere*, a common plant in the forests of Białowieża, grows additional adventitious roots which penetrate the unstable substrate and support the plants. Other plants, such as herb robert *Geranium robertianum* and wood stichwort *Stellaria nemorum*, support themselves using their lowest leaves.

As CWD decays and creates different and unoccupied habitats to exploit, decaying logs become attractive sites for additional vascular plants. These CWD habitats allow species capable of living on decaying wood to avoid fierce competition in the compact carpet of ground vegetation, and reduce their exposure to ground frost and wet and swampy situations in flooded forests. In certain types of forests, e.g. deep swamps, only the hummocks around the tree trunks and fallen logs provide a suitable habitat for non-hygrophilous plants ■.

Hygrophilous plants:

species favouring wet and boggy conditions.

The fall of a decaying log to the forest floor is merely one consequence of tree death. Tree fall is usually accompanied by the establishment of a canopy gap that modifies local light and thermal regimes, and eliminates inter-root competition, etc., permitting exploitation of the gap by shade intolerant species, at least at first. The progress of wood decay is accompanied by the gradual closing of gaps, either due to the growth of young trees within the gap, or to the expansion of the canopy trees' crowns at the edges of the gap. Closure of the gap also changes the light and thermal regimes of the logs and affects the plants residing on the logs.

If a tree was broken, its debris would consist of the fallen log and the part of the trunk that remains standing – the snag or, if less than about a metre tall, the stump – which are also subject to gradual decay. The soil surrounding the root collar of a decaying snag is locally enriched by the falling particles of bark and wood. This soil enriched by decaying woody material may support an exuberant growth of nitrophilous plants, e.g. in the beech old growth in Pomerania (north-western Poland), characteristic wreaths of nettles *Urtica dioica* surround these snags.

After a fallen tree crown begins to decay, the soil it covers becomes nitrogen enriched due to the rapid decomposition of the thin branches. If this area is exposed to large amounts of sunlight, it can quickly be occupied by abundant nitrophilous and light-demanding vegetation. The rate of decay and establishment of vegetation is quite variable and largely depends on moisture availability in the growing season. Rates seem to be faster in moist, cool forests than in dry, warm forests.

An even more profound diversification of ecological niches occurs as a result of the tree becoming uprooted (photo 60). An uprooted tree creates a characteristic microrelief of the forest floor consisting of a hillock formed from the soil lump connected with the standing root plate, a patch of vegetation that was moved to a new position, a hollow in the place where the roots and soil were lifted, and the fallen log and attached crown. All of these microsites can be colonised by plants (fig. 30). The hollows are often wet, and sometimes filled with water; in many types of forest they are the only reservoirs of hydrophilous and small water plants. Vertical root plates/soil lumps provide microsites for specialised mosses and liverworts. The properties of these sites gradually change as the soil and organic matter is slowly leached out of the hillock formed by the root plate, and down to the bottom of the crater (hollow), slowly filling it up. As these changes occur, there is a gradual closing of the gap by the crowns of young trees and shrubs or the larger trees on the edges of the gap.

J.M. Gutowski

Photo 60. An uprooted spruce in the Białowieża Primeval Forest

Algae – not only water plants

Algae are commonly found in puddles, ponds and lakes. However, there are also algae inhabiting humid spots in forests, such as hollows in the ground and in trees, and in cracks and crevices in the bark of trees, both living and dead. Although algae are still a poorly studied class of organisms, tree cavities containing water are habitats of some very interesting species. For instance, in rain water filled cavities of old willows in the Gorce Mountains (southern Poland), seven species of the family Xanthophyceae (especially *Botridiopsis arhiza* and *Heterotrix bristoliana*), were found with their accompanying flagellates, rotifers and nematodes.

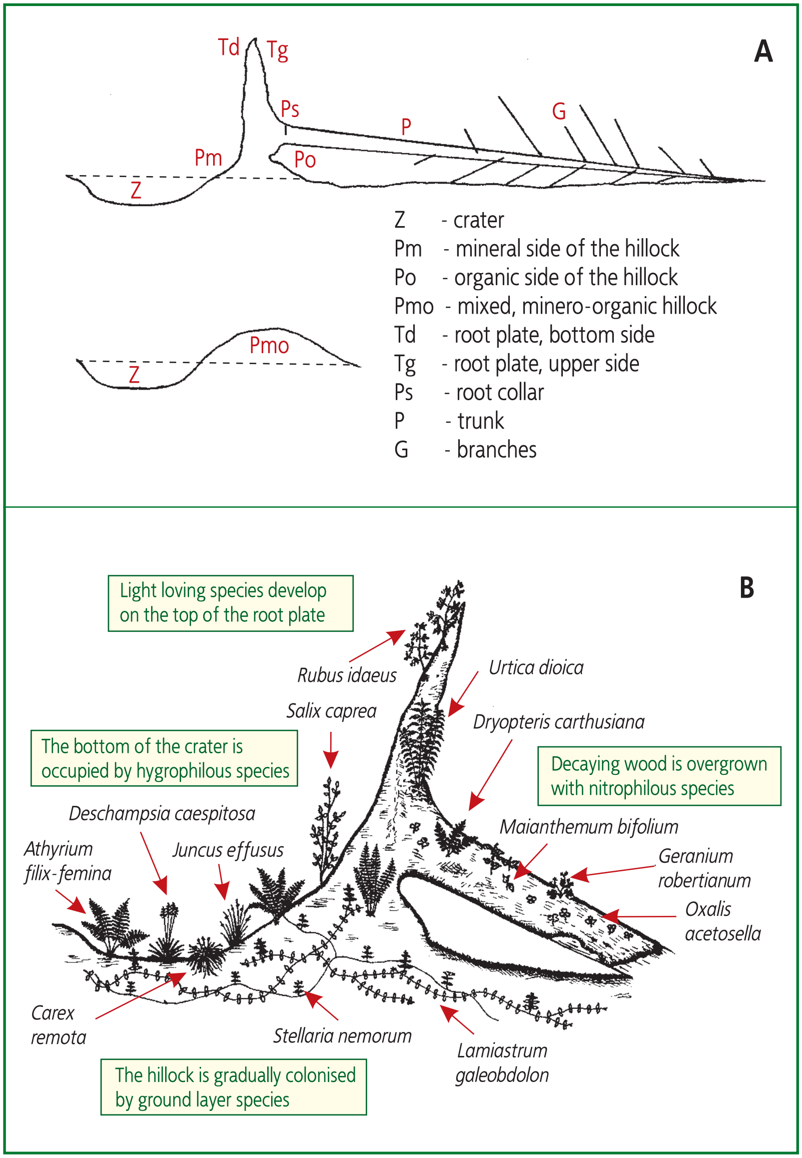


Figure 30. The partition of an uprooted spruce (A); vegetation on the uprooted system in a deciduous mesic forest (B) (M. Bobiec, after MASALSKA 1997, slightly modified)

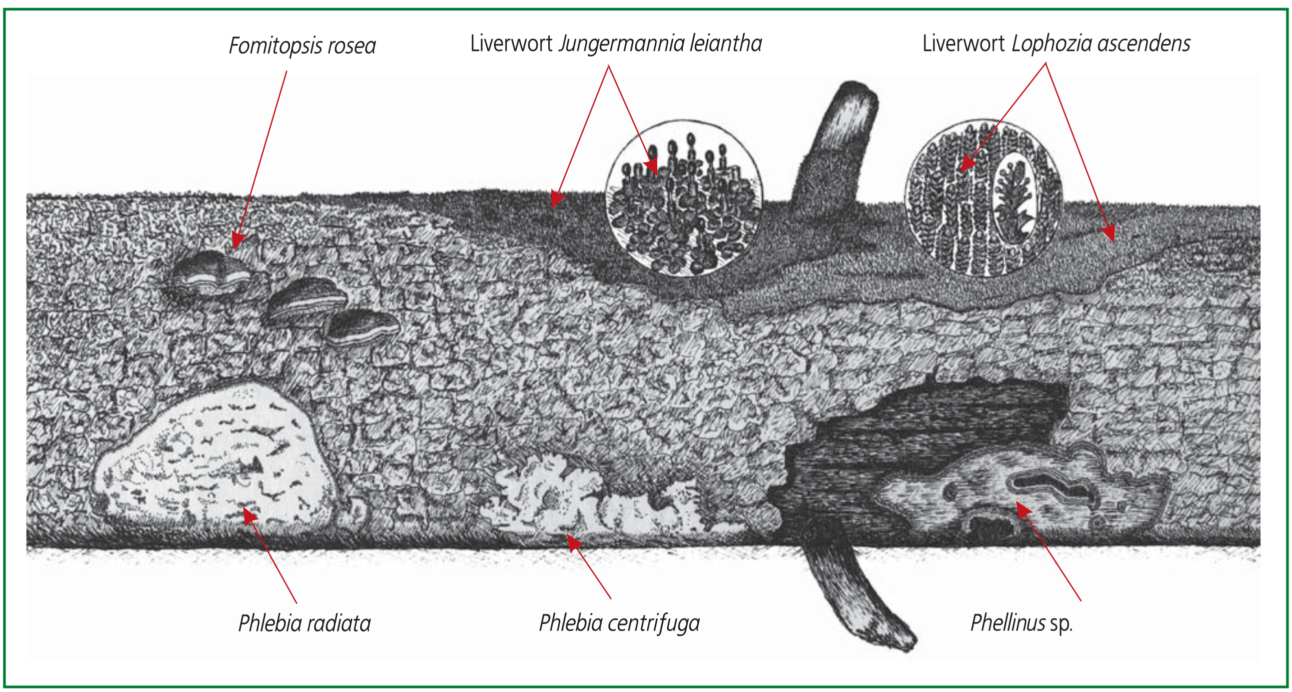
Mosses and liverworts – dead trees decide the occurrence of specialised species

The microsites that emerge following the death of a tree are of particular importance to the richness of the bryophyte flora (photos 60, 61, 62; fig. 31). Generally a few dozen bryophyte species inhabit decaying logs. In a single compartment of the Białowieża National Park, 75 species of mosses and 24 liverworts were found on decaying logs. The species composition of the bryophyte community on dead wood depends first and foremost on the decay stage, then on the species of wood, humidity and light regime, and finally, on the characteristics of the environment surrounding the log.

Shortly after a tree's death, the bryophyte flora on the trunk is dominated by epiphytic species that now have to live under new and less favourable ecological conditions. Along with progressive decay, the vigour of these species decreases, and they are slowly lost from the tree. In the final stages of decay, the woody debris is almost completely dominated by ground bryophyte species.

Besides the two ecological groups (epiphytic and ground species) comprising the bryophyte community at the beginning and final stages of wood decay, there are other more specialised species apparently favouring different stages of decay of CWD habitats. There are distinct bryophyte associations which, though being part of the larger forest ecosystem, are ascribed by botanists to dead wood habitats. As a log decays, it is sequentially colonised by leafy creeping liverworts, e.g. *Novellia* and *Lophocolea* species, followed by the loose leafy mats and erect stalks of *Lepidozia* and *Cephalozia*, and later by thallophytic liverworts (e.g. *Riccardia* spp). In the subsequent stages of succession, various species of mosses begin to dominate.

Figure 31. A log overgrown by lichens, mosses and fungi (M. Bobiec)



J. Walencik

Photo 61. An abundance of moisture in the lower parts of standing dead trunks (here: Norway spruce) supports the establishment and development of mosses and fungi

J. Walencik

Photo 62. Moss growing on the surface of dead wood

Epixylism

Epixylics are organisms (the term is usually applied to plants) that live on the surface of wood. In practice epixylics are considered to be all plants and lichens growing on dead trees representing the various decay stages, regardless of whether occur on wood sensu stricte, bark or rotten wood. As certain species (often mosses) are obligatorily connected with dead wood and do not occur elsewhere, they are referred to as obligatory epixylics. Other species can make use of several optional substrates, including wood when it is available. These are facultative epixylics, and examples are the assemblage of vascular plants occurring on dead wood. In general, obligatory epixylics are rare and stenotopic, i.e. they can tolerate only a very narrow range of variability in their immediate environment. It is not surprising then that their occurrence is often limited to the least transformed elements that reflect forests with intact functions and components.

In the mesic deciduous forests of Wielkopolski National Park (western Poland) the slightly decomposed, barkless logs of pines, and less frequently oaks, are usually occupied by the liverwort *Lophocolea heterophylla*, accompanied by the moss *Hypnum cupressiforme* (a common epiphyte that also grows on dead logs), and several other species that root in the cracks of the wood (photo 61). The moss *Herzogiella seligeri* finds an optimal habitat on the rotting oak bark and well decayed pine wood. A typical epixylic association ■ is shown by the mosses *Aulacomium androgynum* and *Tetraphis pellucida* that form concentrations on well rotted and cracked wood occurring on the surface of the side of logs. The horizontal top surfaces of logs are occupied by bryophyte associations composed of the turf of *Hypnum cupressiforme* and tufts of *Dicranum montanum*; whereas on the sides and undersides of logs there are concentrations of mosses dominated by *Plagiothecium curvifolium* or *P. laetum*.

Similar to Wielkopolski National Park, decaying wood in the forests of Roztocze (south-eastern Poland), is dominated by associations of *Tetraphis pellucida*, *Lophocolea heterophylla* and *Herzogiella seligeri*. Decaying silver fir and spruce trunks in this hilly terrain are occasionally occupied by *Riccardia* species and *Novellia curvifolia*, more typical of mountainous terrain elsewhere in Europe. In shady ravines and in swamp and riparian forests, fallen spruce trunks are occupied by hygrophilous liverworts dominated by *Calipogeia neesianae*. Six other moss communities occur on living trees in these forests.

Lophocolea heterophylla, *Tetraphis pellucida* and *Herzogiella seligeri* are also frequent epixylic associations in the ancient Carpathian forest of Babia Góra (southern Poland). Clusters of the mosses *Dicranodontium denudatum* and *Plagiothecium* species are also commonly found on decaying logs in this area. In high elevation spruce stands, logs are occupied by clumps of *Calipogeia neesianae* and compact cushions of the moss *Mylia taylori*. Detailed studies in Babia Góra National Park revealed more than 40 diverse bryophyte communities associated with decaying wood and dead trees!

In other forests, such as the BPF, the beech forests in Pomerania, the forests of the Sudety Mountains (south-western Poland) and in the Beskid Sądecki mountains (southern Poland), the moss communities on decaying logs are equally diverse. However, generally in most European forests the liverwort and moss components have rarely been studied.

As mentioned earlier, the decaying wood and bark of dead trees are not the only microsites that develop after tree death. Although a complete discussion of the variety of microsites would far exceed the scope of this book, the ground forms created by uprooting (root plates with ground lumps, mounds, etc.) deserve some attention. This kind of microhabitat is often occupied by pioneer bryophyte species, e.g. *Polytrichum juniperinum* and *Pohlia nutans*, or species of the genera *Calipogeia* and *Cephalozia*, before vascular plants become established and come to dominate these sites.

Geobotanical studies in various types of forests have demonstrated that microsites related to dead and decaying trees and their immediate neighbourhood greatly contribute to the diversity of mosses in forests. In numerous Polish national parks and nature reserves, it is on the decaying wood that the most interesting bryophyte assemblages are found.

Epixylic moss communities are inherent components of the forest ecosystem. Although different types of bryophyte associations occurring on dead wood can be related to various types of forest and stand developmental phases, CWD is always the chief habitat.

The importance of dead wood as a habitat for rare bryophyte species is not restricted to forests with intact components and processes. Older pine plantations, occupying former deciduous forest sites, exhibit sufficient amounts of CWD to support some of the rare bryophytes. The best example of this relationship was found in "Pod Dziadem", a nature reserve within Wielkopolski National Park. Here there are a number of artificial pine stands occupying a mesic deciduous forest site. A considerable amount of CWD was deposited after the gypsy moth outbreak in 1975-1982, and after 15 years the CWD developed into a habitat for nine bryophyte associations comprised of a few dozen species. The associations include *Novellia curvifolia*, which was not previously known from the Wielkopolska region, and *Dicranum tauricum* which has been recorded at only seven other locations in Poland.

The abundance of epixylic bryoflora, and the diversity of their associations coupled with the occurrence of rare species are recognised indicators of forest ecosystems that have persisted for long periods with their components and processes intact.

Bryoflora:

flora of bryophytes i.e. mosses and liverworts.

Vascular plants – dead trees provide mosaics of habitats

Unlike the bryophytes, there are no vascular plants that are restricted to dead wood. That being said, the death of trees and deposition and decay of wood have a profound influence on these plants.

Partially or thoroughly rotted wood, though difficult to colonise, is gradually occupied by vascular plants if their propagules find the site. Among the most peculiar sites inhabited by vascular plants, are rotten wood microhabitats situated high on the trunks of old, yet living trees, most frequently willows, maples *Acer* and limes, where touch-me-not balsam, raspberry *Rubus* or even trees such as spruce, mountain ash *Sorbus aucuparia* or birch may germinate and grow. Phenomena like "birch growing out of willow", and pear *Pyrus* trees rooted in old willow stems (that would explain the origin of the Polish saying: "promising pears on a willow") have often been reported. Recently, ash saplings of about 10 years of age were observed growing on an old living oak 12 m above ground in Białowieża National Park.

Much more common and ecologically significant is the colonisation of rotting logs by vascular plants. In Sweden, for instance, 40 species of vascular plants were recorded on decaying logs, while 47 have been detected in the Białowieża Primeval Forest, including 8 tree species. Among the most common species found on logs are wood sorrel *Oxalis acetosella* (photo 63), ground ivy *Glechoma hederacea*, oak fern *Gymnocarpium dryopteris*, herb robert, wood meadow--grass *Poa nemoralis* and nettle (photo 64). Two species that are rather rare in the forests of Białowieża, wall-fern *Polypodium vulgare* and ivy *Hedera helix*, are found more often on decaying logs than on the ground in this forest. Alpine enchanter's nightshade *Circaea alpina* also occurs on this type of site.

J. Walencik

Photo 63. Plants growing in the hollow of a downed lying tree: wood-sorrel, violets and mosses

The species mentioned above are also components of the 'ordinary' ground vegetation found on mineral soil that is lacking dead trees. Colonisation of dead wood can alter the spatial patterns of their populations. In many forests with dead wood, one can observe belts of wood-sorrel highlighting the position of decomposed logs, or glittering clusters of Alpine enchanter's nightshade on dead wood. Without the dead wood that modifies the spatial pattern of these plants' populations, they would be more generally distributed on the forest floor.

Dead wood sites are particularly important in swamps and wet forests, e.g. in black alder swamps. In such environments the fallen logs not only provide dead wood habitats but are among the few kinds of habitats elevated above the water level providing important living conditions for amphibians (photo 65).

Woody vascular plants also colonise logs. Spruce in particular prefers decaying wood in various types of forests. The presence of decaying wood in ecosystems plays an important role in the process of spruce regeneration; this is discussed later in the book (4.2.5. – page 141).

J. Walencik

Photo 64. Plant succession on an uprooted spruce in the Białowieża Primeval Forest

Photo 65. Vascular plants benefit from the humid environment of dead wood, Białowieża Primeval Forest

Although elimination of dead wood does not automatically cause the loss of any vascular plant species, the loss of dead wood does lead to a different species composition and spatial structure, and influences population processes thereby leading to indirect effects. A spectacular example can be seen in the beech forests in Drawieński National Park. In the Radęcin sector, where dead trees are not removed, each canopy gap resulting from the death of an old beech, a mosaic of ground vegetation develops dominated by nettles, clusters of oak fern and other components. Its structure is certainly influenced by the presence of beech logs and branches, although other factors, such as an increase in light, also play an important role. In addition to the nettles and other low lying plants, the openings include abundant beech regeneration and a variety of herbaceous species, e.g. wood melick *Melica uniflora*, bulb toothwort *Dentaria bulbifera* and narrow-leaved bittercress *Cardamine impatiens*, typical in the Pomeranian beech forests (in northern and north-western Poland). In neighbouring forests where fallen trees are immediately removed from the ecosystem, the gap vegetation is much less diverse and dominated by wood small-reed *Calamagrostis epigeios*, with scarce beech regeneration. Similarly, under very different ecological conditions in high mountain spruce forests degraded by air pollution, the retention of dead tree trunks leads to the development of a diverse plant mosaic, in which spruce and mountain ash seedlings and saplings also find favourable growing conditions. In contrast, where dead wood is removed from these high elevation forests, the resulting community inhabiting the gap is completely dominated by the grass *Calamagrostis villosa*.

Summary of Chapter 4.1.3.

Numerous bryophytes live exclusively in dead wood. In most forests, CWD is a key habitat and necessary to perpetuate the diversity of this group of plants.

Increasing amounts of dead wood both in natural and degraded forests usually lead to an increase in bryophyte species richness, often including very rare, interesting species.

Although there are no vascular plant species restricted to dead wood, several species readily colonise decaying logs.

Despite having no direct influence on the presence or absence of vascular plant species, CWD substantially modifies the population structure of these species and affects their regeneration processes. The lack of dead wood may disrupt regeneration processes and make it difficult for many plants, including trees, to regenerate.

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4.1.4. FUNGI

Fungi are among the most important and underestimated components of the forest ecosystem. They play two basic roles. They co-exist with living trees in a very close symbiotic relationship called mycorrhiza, and they decompose animal and plant debris, wood in particular. In addition, these organisms participate in numerous other ecosystem processes, such as the accumulation of nitrates or the reduction of populations of certain insect species. The paramount role of fungi in the forest ecosystem derives from their wide-spread occurrence, species diversity and great variety of life forms.

The BPF is rich in fungal species and it is thought that some 5,000 species exist there. In a single compartment covering 1.5 km^2 of the BPF, 1380 species have been identified. Many among them are related to dead trees and shrubs, both standing and fallen, as well as to their fragments comprised of fallen boughs and branches. As many as 119 out of 338 (35%) randomly collected fungal species shown at the annual mushroom exhibitions in Białowieża are connected with CWD.

Fungi

The kingdom of Fungi, according to HAWKSWORTH et al. (1995), embraces five classes:
Ascomycota – sac fungi (spore-shooters)
Basidiomycota – club fungi (spore droppers)
Deuteromycota – imperfect fungi
Oomycota – water moulds
Zygomycota – conjugation fungi (pin moulds)

Project CRYPTO

Most of the data presented in this chapter have been collected by the team of experts involved in the long-term project CRYPTO (1987-1996) carried out in a 144 hectares compartment of Białowieża National Park and aimed at analysing relationships between spore organism diversity and variability of the forest environment.

Neither plant nor animal – why fungi make up a separate kingdom of beings

For many years, fungi were considered to be plants despite calls from mycologists to create a separate systematic group. Their immobility and the apparent similarity of some of their parts (fruiting bodies with 'stems,' root-like rhizomorphes, etc.) meant that they were thought of as peculiar plants. However, there is a wide range of characteristics specific only to fungi. First of all, cell walls are made of a substance similar to chitin – a compound found in the bodies of insects. Secondly, and without exception, fungi are heterotrophic organisms. Also, the compounds produced and stored in fungal cells resemble those produced by animals, like glycogen, and not plants. There are also a plethora of anatomical features and ways of regeneration that are exclusive to fungi. Thus, it is no surprise that the fungi were eventually elevated to a separate kingdom* on the same level as plants and animals.

Fungi, because they are heterotrophic, do not require the light necessary to support photosynthesis in plants, and are therefore able to live in situations where light is lacking, such as in dense forests. High humidity and large concentrations of organic matter are also factors contributing to the fact that more than 80% of the world's species of fungi live in forests.

Mycologist:

a biologist whose expertise is in fungi.

Heterotrophs:

living creatures can be divided into the autotrophic and heterotrophic categories; autotrophic organisms (or producers) are primarily plants photosynthesising organic compounds in their cells which contain photoactive pigments, in most cases chlorophyll; heterotrophic organisms (or consumers) are all other organisms unable to photosynthesise and dependent on the organic matter synthesised by producers.

* This is certainly an oversimplification because the systematics of the living world are far more complex when organisms without cell nuclei, viruses or prions are included.

Necessary partnerships – mycorrhizae...

While discussing fungi and their roles in the forest, one cannot avoid the mycorrhizae, a symbiotic relationship exclusively found with living plants, especially trees, which plays a paramount role in the forest ecosystem. Every species of forest tree and shrub, at a certain stage of its life, gains a symbiotic relationship with fungi. They are often species specific relationships (exclusive to a given species) e.g. elegant larch boleta *Suillus grevillei* grow only under larches. It is not a coincidence that, to find rough-stalked boleta, we go to aspen and birch stands, whereas other boletus species are found under pines or oaks. The mycorrhizae enormously increase the absorption surface of tree roots, permitting better supplies of water and minerals to reach the tree or shrub than if they relied only on their roots. The trees 'pay' their partners back by providing them with carbohydrates produced by photosynthesis as well as other compounds including growth substances. Enzymes produced by the fungi enable trees to use substances present in the soil that would otherwise not be available to them. Equally important is the protective function of mycorrhiza. The hyphae densely wrap tree roots and thereby protect them from parasitic fungi that would stress and could eventually kill the tree. Mycorrhizae are particularly important for seedlings and young trees initiating growth. Reforestation of open ground or land long without forest cover is often very difficult because the reservoir of mycorrhizal fungi or their spores are no longer present or nearby to invade the new forest. Studies carried out in the USA have shown that rodents can play an important role in the transmission of the spores of mycorrhizal fungi.

...and dangerous relationships – disease- and death-causing fungi

In addition to the saprophytic (developing on dead organic matter) and symbiotic fungi there is a large group of parasitic fungi. They attack seeds, seedlings, leaves and needles, and infect the trunks and branches of living trees and shrubs. Fungi rarely infect completely healthy trees growing under favourable environmental conditions. Fungal infections are most often associated with a prior stress (weakness) related to drought, air pollution, high temperature or an otherwise unsuitable site. Such stress factors weaken trees' resistance and permit parasites to penetrate the trees' defence.

While stressed trees are most often attacked, some fungi are capable of attacking healthy trees; these include members of the genus *Phellinus* (bracket fungi), e.g. *Phellinus pini* attacks pine, and willow fomes *Phellinus igniarius* attacks mainly broad-leaved species. Certain species of *Phellinus* specialise on specific species of trees and shrubs, e.g. *P. robustus*, *P. hartigii*, *P. hippophaecola* or *P. ribis*. Another common species that may attack healthy trees is chicken of the woods *Laetiporus sulphureus* (photo 66), with its impressive yellow fruiting bodies. However, this species develops mainly on dying and dead trees.

Considerably more fungus species colonise weakened trees, contributing to their death. They are, among others, the tinder polypore *Fomes fomentarius*, the oyster mushroom *Pleurotus ostraetus* (photo 67), the red banded polypore *Fomitopsis pinicola* (photo 68) and the birch bracket *Piptoporus betulinus*.

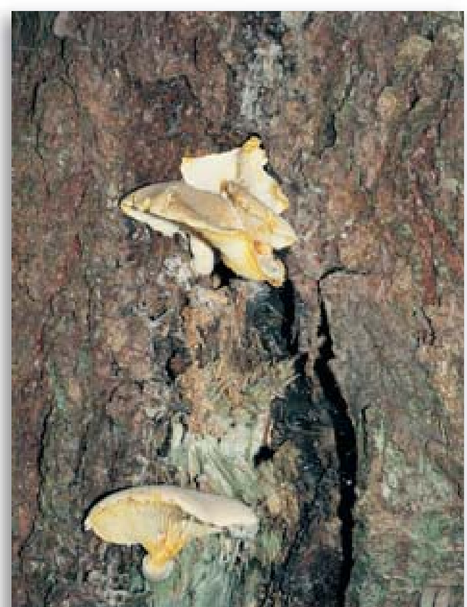
J. Walencik

Photo 66. Chicken of the woods *Laetiporus sulphureus* on a dying oak

Photo 68. A red banded polypore *Fomitopsis pinicola* on a spruce stump

J.M. Gutowski

Photo 67. Oyster fungi growing on a dead standing spruce



J.M. Gutowski

A number of moderate parasites may invade, develop, and produce fruiting bodies for a few decades on the same tree, weakening but often not killing the tree. There are rare and protected species among these parasitic fungi, e.g. the cauliflower fungus *Sparassis crispa*, a parasite occurring on pine roots and *Polyporus umbellatus* (photo 69), developing on the roots of oak. Other weak parasites are the beefsteak fungus *Fistulina hepatica* that grows on the trunks of oaks, and the northern tooth fungus *Climacodon septentrionalis* that grows on maple trunks.

K. Zub

Photo 69. *Polyporus umbellatus* growing on hornbeam roots

J. Walencik

Photo 70. Beef-steak fungus at the trunk's base

Cleaning-up the forest: saprophytic fungi

As mentioned earlier, wood consists of cellulose, hemicelluloses and lignin, totalling about 96-97% of its dry mass; waxes, fats, tannins etc., contribute to the remaining 3-4% of the dry wood mass. Both coniferous and broad-leaved species contain similar amounts of cellulose, but they differ in the hemicellulose/lignin ratio. In general, the former have less hemicelluloses and more lignin compared to the latter. These differences affect the rate of wood colonisation by various organisms and the characteristics of decomposition specific to various tree and shrub species. The presence of such substances as flavonoids and terpenoids (terpenes) may inhibit the growth and development of decomposing fungi. The wood building compounds (cellulose, hemicellulose and lignin) cannot be directly utilised, and only a few organisms have the ability to decompose them and then use the decomposed products. The carbon bound in cellulose, hemicellulose and lignin is only available to organisms producing enzymes (ligases and carbohydrases) that decompose these compounds. Compared to the green parts of plants, wood contains only a small amount of nitrogen. Only fungi belonging to the basidiomycetes can manage without nitrogen. However, enzymes produced by many fungi are catalysts that initiate the decomposition of wood cell walls, and for these species, the nitrogen deficit is partially compensated by coexisting microorganisms.

The visible results of the activity of both parasitic and saprophytic fungi are rots, i.e. "decay of the wood substance caused by chemical decomposition" (according to MAŃKA 1981). There are many classifications of rot, but the one based on decay symptoms is among the easiest systems. According to that classification, we distinguish brown rots, white rots and white pocket rots.

Another kind of rot is ring rot, which separates the rings of annual increments in trees; ring rot is caused by fungi such as *Phellinus pini* which attack the faster growing spring wood layers. Other fungi, mainly sac and imperfect fungi, but not basidiomycetes, under conditions of high air humidity, cause the mould (or grey rot) that is the result of wood 'weathering.'

Fungal activity changes not only the structure of wood (photo 72), but also its chemistry. Fungi infected wood contains 1.5 times more water and nitrogen than uninfected wood. Fungi exude various sugars, acids and proteins that can be utilised by other organisms. The fungal features that we usually observe on trunk surfaces, called 'bracket fungi,' are merely the fruiting bodes that disseminate spores and spread the fungus. The principal part of the fungus is hidden from sight within the wood tissue. In Sweden, an old spruce log lying on the ground for seven years was colonised by 15 species of fungi, but only three produced

Rot classification

Rot classification according to WAŻNY (1968), after MAŃKA (1981):

- Brown rot (often called red rot), makes wood colour darker than the original colour; mainly decomposes cellulose while the untouched lignin is the source of the red hue (photo 71); the disappearance of cellulose causes cell disintegration and a break-up of wood into prismatic blocks; the brown or red rot is caused by chicken of the woods (photo 66), birch bracket and beef-steak fungus (photo 67), among others.
- White rot causes a lighter hue compared to the original wood colour; it results in an even decomposition of all of the wood's compounds, but because of a dominating amount of cellulose in wood, the remains of this compound give the rot a light hue; white rotted wood crumbles and falls apart into fibrous fragments; the white rot is caused by members of the genus *Phellinus* on broad-leaved trees, tinder polypore and oyster mushroom (photo 67), among others.
- White pocket rot (called spotted or pocket rot) can be distinguished by regularly distributed white pockets of cellulose within a dark matrix; it is caused by *Phellinus pini* and root fomes (*Heterobasidion annosum*), among others.

J. Walencik

Photo 71. A decaying spruce – an example of dark brown rot; Białowieża Primeval Forest

J. Walencik

Photo 72. The peculiar structure of decaying spruce wood visible fruiting bodies. The lack of the production of observable fruiting bodies by other species is caused by one or more of the following:

- certain fruiting bodies are produced only for a specific and short period of time in the year,
- for some species the mycelium needs to reach an appropriate size before the fruiting body will be produced,
- some species do not create fruiting bodies.

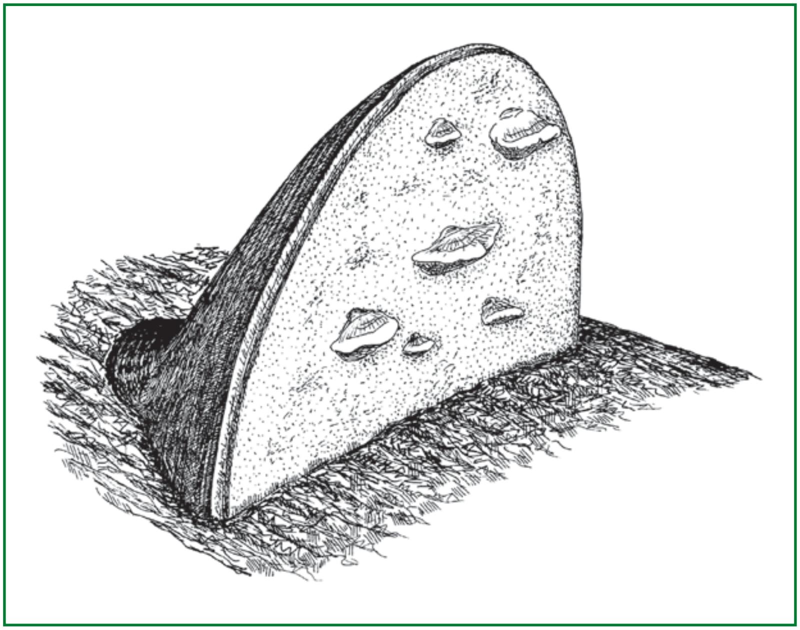
Besides the typical parasites, many fungi that generally live a saprophytic life may 'take a liking' to considerably weakened trees and shrubs and colonise still living trees. This display of opportunism is exhibited by species such as tinder polypore, *Ganoderma applanatum* (photo 73), varnished polypore *Ganoderma lucidum*, *Bjerkandera adusta* and *Stereum* species (genus *Stereum* – photo 74). After the death and fall of an infected tree, these fungi become full saprophytes. One can commonly observe the old fruiting bodies, placed perpendicularly to the trunk before the tree fell, with the new, smaller ones, placed parallel to the tree trunk with their bottom sides oriented toward the ground (fig. 32).

Dead wood is a very specific habitat. Because of the small amount of readily available nutrients, it is a substrate suitable to only specialised species able to secure the nutrients locked up in the woody structure of the tree. Thus the inter-specific competition between epixylic species is fairly limited and their number is not high.

K. Zub

Photo 73. *Ganoderma applanatum*

Figure 32. The fruiting body of a bracket fungus that originally grew on a standing tree and adapted to life on a fallen log after the tree fell (M. Bobiec)



K. Zub

Photo 74. A *Stereum* species of fungi

Relations of fungi with diverse forms of dead wood in the forest

Dead wood can exist in a variety of sizes and forms, from small, easily movable fragments (fragments of bark platelets, thin branches, parts of boughs and logs), to large fallen logs and standing trunks, snags and stumps. Each of these forms offer different conditions of humidity, insolation, durability, etc. to fungi. Therefore, these microenvironments are colonised by different fungal species, creating different associations.

Fine woody debris is usually derived from the bark and the rate of its decay is relatively fast. In this type of substrate, 84 fungal species were identified in the BPF, among which 43 species were obligatorily connected with fine woody debris. Most of them are basidium fungi (54 species), e.g. *Collybia* species, *Mycena* species, *Oudemansiella longipes*, *Peniophora laeta* and the artillery fungus *Sphaerobolus stellatus*. Among the 30 species of sac fungi, three are obligatorily connected with fine woody debris: the scarlet cup *Sarcoscypha coccinea* (photo 75), *Hyaloscypha stevensonii* and *Tapesia minutissima*. Two species of sac fungi – the orange wood cup *Bisporella citrina* and the eyelash cup *Scutellinia scutellata*, often occur on fine woody debris, though they are mostly found on bark and trunks.

C. Bystrowski

Photo 75. The scarlet cup *Sarcoscypha coccinea* – a beautiful fungus, whose fruiting bodies can be seen even in winter

The bark of recently broken branches and snapped trunks offers more nutritious substances in addition to cellulose and lignin. Fungi growing on bark may penetrate into deeper layers of wood, reaching even heartwood. Bark, and the cambium and sapwood beneath, are suitable microenvironments for primary saprophytes, i.e. organisms that cannot decompose cellulose and lignin but can utilise sugars, starches and proteins in the tissues of recently dead trees. These fungi include the sac fungi *Diatrype stigma*, *Diatrypella favacea* and *Hypoxylon howaenum*. Also, occasional parasites such as coral spot (*Nectria cinnabarina*, photo 76), use this type of substrate. The easily absorbable, nutritious substances are quickly utilised, and wood is subsequently colonised by other species with the ability to decompose more complex compounds. In the Białowieża National Park, 142 species, including 83 sac fungi and 59 basidium fungi, have been recorded on the bark of fallen dead trees and branches. Among the sac fungi, black bulgar (rubber buttons, *Bulgaria inquinans*, photo 77) and *Holwaya mucida*, similar to numerous species of flask fungi (Pyrenomycetes), show a strong associa-

Photo 76. Coral spot *Nectria cinnabarina* on the trunk of black alder

J. Walencik

tion with this type of substrate. Ten species of basidium fungi occur exclusively on the bark of fallen dead trees and branches.

Fallen logs are a typical habitat for fungi (photos 78, 79, 80 and 81), where, in the Białowieża Primeval Forest, 282 species were found, including 109 obligatorily dependent on fallen logs. Because of the high water content, far more fungal species reside on fallen logs in contact with the earth, than on elevated logs (logs with parts not in contact with the ground such as those extending from root plates or lying on rock outcrops). Among the 90 species of sac fungi found in the BPF, 38 occur exclusively on such logs. The most common, among other species, are *Hypoxylon multiforme*, *H. rubiuginosum*, *H. serpens*, dead moll's fingers *Xylaria longipes*, eyelash cup, *Peziza micropus* and brittle cinder *Ustulina deusta*, often growing in the mossy environment on the large trunks of broad-leaved trees. The basidium fungi are also very common residents on fallen logs; 192 species were found on fallen logs in the BPF, and of these, 67 were restricted to fallen logs. The remaining four species that are restricted to fallen logs

Photo 77. Black bulgar *Bulgaria inquinans* on a dead hornbeam log; Białowieża Primeval Forest

J. Walencik

Photo 78. The cross section of a broken, decayed spruce; the tree rings are visible

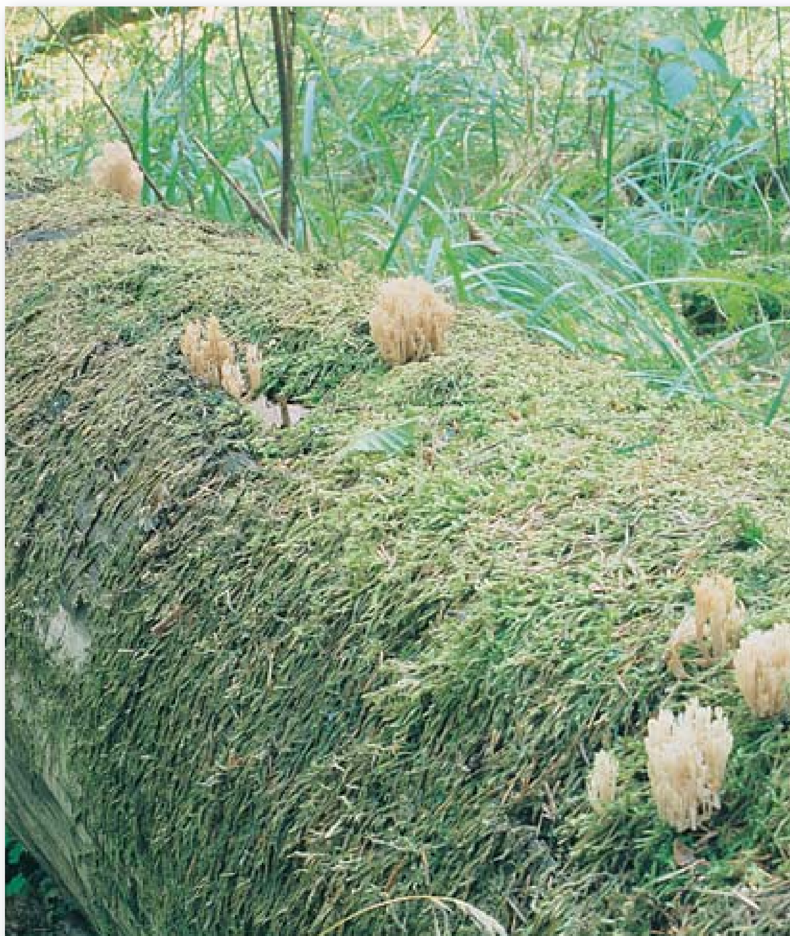


Photo 79. Fungus on a decaying log: *Artomyces pyxidatus*

J. Korbel

Photo 80. Fungi emerging from beech logs sometimes reach amazing sizes and fantastic shapes; southern Poland

Photo 81. Fruiting bodies, such as these ink caps on an uprooted spruce, sometimes occur abundantly on fallen trees; Białowieża Primeval Forest

J. Walencik

Photo 82. Golden pholiota *Pholiota aurivella* at the base of a maple trunk

Photo 83. *Trametes* species

belong to other systematic groups. The basidium fungi have a decided competitive advantage over other organisms when it comes to colonising dead wood. They have the ability to use cellulose and lignin, permitting many members to colonise and resulting in a high species diversity. The non-gill fungi (Aphyllophorales) are fairly numerous; they produce annual fruiting bodies that appear on dead trunks. Other species of this group are *Funalia gallica*, the blushing bracket *Daedaleopsis confragosa*, *Dentipellis fragilis* and *Trametes suaveolens*. Members

K. Zub

Photo 84. Dead man's fingers *Xylaria polymorpha* growing on woody debris

K. Zub

Photo 85. Candlesnuff *Xylaria hypoxylon* on a hornbeam stump

of the Agaricales also colonise fallen logs, and they include numerous species belonging to the genera *Pluteus* (11 species), *Pholiota* (5 species, photo 82), *Lentinellus* and *Crepidotus* (3 species each). The most frequent are those species that produce perennial fruiting bodies, and among these numerous genera are: *Chondrostereum*, *Stereum* (photo 74), *Ganoderma* (photo 73), *Hymenochaete*, *Schizophyllum*, *Trichaptum*, *Fomitopsis* (photo 68), *Gloeophyllum*, *Daedalea* and *Trametes* (photo 83).

Snags with broken tops offer far less favourable conditions to fungi than fallen logs. This is the result of low humidity (in particular in the upper parts) and intensive insolation. The fungi found on this substrate include 10 species of sac fungi as well as 58 basidium fungi, among which 6 occur exclusively on this type of substrate.

Equally difficult conditions for fungal development occur on the trunks of standing dead trees or snags. The trunks of spruces are most frequently colonised, followed by alders and birches. Besides a few sac fungi, only 18 basidium fungi occur on standing dead trees, but most of the common saprophytic fungi can be found on this substrate. They include tinder polypore, red banded polypore (photo 68) and dryad's saddle fungus *Polyporus squamosus*.

The relationships of fungi with dead wood range from strong to weak. As was discussed earlier, certain parasitic species may function as saprophytes after tree death. Similarly, many species growing on heavily decayed wood may also grow on forest litter, e.g. eyelash cup and bird's nest fungus *Cyathus striatus* (photo 86). About half of the flask fungi found in the forests of Białowieża (83 species) are epixylic, but only 34 are obligatory epixylics. Discomycetes have a much stronger affinity with dead wood, as 44 out of 56 species grow exclusively on woody substrates. Most epixylic species are basidium fungi (227), among which 85% are obligatory dead wood dwellers.

According to studies from Sweden, the species richness of fungi related to dead wood is positively correlated with dead trunk diameter and their group (or cluster) distribution in forests.

J. Walencik

Photo 86. The shell-like fruiting bodies of the bird's nest fungus *Cyathus striatus* sometimes emerge on fallen wood debris

The relationships of fungi with various tree species

Fungi prefer specific tree species. Among the 11 tree species considered, birch trees host the largest number of fungi (68 species) and mountain ash the lowest (only 5).

The number of epixylic fungi species occurring on given tree species in the Białowieża Primeval Forest (according to CHLEBICKI et al. 1996; modified)

Tree species	Total number of epixylic fungi species	Species occurring exclusively on the given tree species	Number of rare fungal species
Black alder *Alnus glutinosa*	59	7 (+ 4 species showing strong preference)	53
Birch *Betula pendula* + *B. pubescens*	68	9	59
Hornbeam *Carpinus betulus*	54	5	45
Norway spruce *Picea abies*	54	18	50
Pedunculate oak *Quercus robur*	61	7	55

The most prominent species occurring on birch wood are the primary saprophytes belonging to the flask fungi. This strong relationship is probably related to the weak vigour of these trees growing in natural stands and their vulnerability to decay. The birch bracket and *Lenzites betulina* are among the species typically found on birches, and they occur exclusively on these trees.

The most frequent fungi on oaks are those associated with the bark of fallen trunks and branches. On other types of oak substrate (small fragments of wood, stumps and snags) club fungi, usually rare species, are the major occupants. Among them are blood-stained bracket *Daedalea quercina* and beefsteak fungi (photo 70). On trunks of standing dead oaks, one can also spot *Phellinus robustus*, usually living as a parasite but switching to a saprophytic life after its host dies.

As hornbeam wood quickly decays, it is mainly colonised by secondary saprophytic sac fungi. Except for a few specific saprophytes, hornbeam wood hosts numerous common fungus species such as *Hypoxylon howeanum*, brittle cinder and dead moll's fingers.

Photo 88. *Gloeophyllum odoratum* occurs only on spruces

J.M. Gutowski

Most of the monophage species associated with alder are sac fungi. Only one basidium fungus, *Entoloma euchroum*, is restricted to this tree species. There is, however, a group of species that strongly prefers alder, such as *Inonotus radiatus*, *Stereum subtomentosum* (an indicator species of primeval forests) and black witch's butter *Exidia glandulosa*.

Spruce is characterised by the largest number of fungi species exclusively residing on a tree species. They are dominated by basidium fungi, such as *Fomitopsis rosea* (photo 87), *Gloeophyllum odoratum* (photo 88), *Lentinus adhaerens*, *Mycena viscosa*, jelly tongue (*Pseudohydnum gelatinosum*, photo 89), *Tremella encephala*, *Postia caesia* and *Xeromphalina campanella*. Spruce also hosts one of the most common fungi of the Białowieża Primeval Forest, red banded polypore (photo 68), that like *Armillaria* species (photo 90) and *Fomitopsis rosea* (photo 87), is a facultative parasite living a saprophytic life after the death of the tree. A very rare species, *Ischnoderma benzoinum* (photo 91), most frequently occurs on spruce wood.

Eighty to ninety per cent of fungus species that commonly occur on particular tree species in the BPF are found at only a few or sometimes only one location outside that area.

Photo 87. *Fomitopsis rosea* on a spruce log, Białowieża Primeval Forest

K. Zub

Photo 89. The forms of fungi are sometimes intriguing – a jelly tongue *Pseudohydnum gelatinosum*

J.M. Gutowski

J. Walencik

Photo 90. Honey fungi on a birch

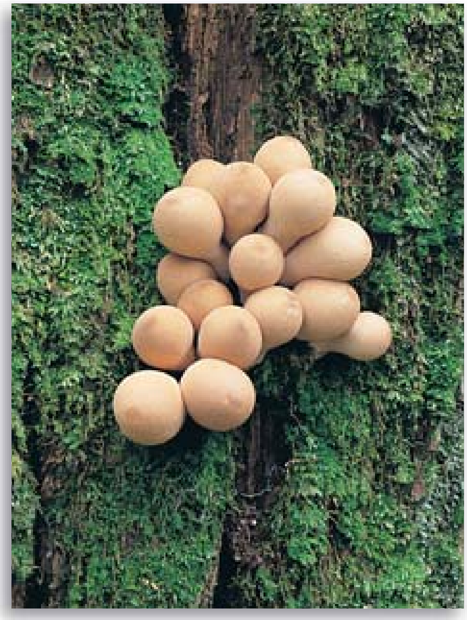
J.M. Gutowski

Photo 91. Sometimes fungi create 'multi-storey' fruiting bodies – *Ischnoderma benzoinum*

Basidium fungi colonise the widest habitat spectrum of any fungi – from thin fallen branches to barkless lying logs. However, flask fungi, with almost equally universal life strategies, show a clear preference for branches and logs with the bark attached. Sac fungi tend to colonise conifers less frequently than hardwoods. This pattern is related to the different chemical compositions and structures of and amount of growth inhibiting compounds in the two kinds of substrates. These differences also explain why the association of fungi living on hard wood is much larger than that living on conifers, e.g. spruces, that are largely occupied by basidium fungi.

Fungal affinity to given species of tree and certain types of substrate results in variability in fungal richness among different forest types (photos 92, 93). There are also substantial differences in humidity and light regime between various forest environments. It is no surprise, then, that richer sites have a greater diversity of epixylic fungi. However, local accumulation of a large amount and variety of CWD may substantially increase fungal diversity even on poorer forest sites.

Photo 92. A stump puffball *Lycoperdon pyriforme* – one of the few puffball species that grows on trees



J. Walencik

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Photo 93. Fruiting bodies of a fungus growing on a decayed log, attacked by a fungal parasite

Dead wood colonisation by fungi

It is difficult to identify the moment fungal colonisation of wood is initiated. It is tightly connected not only to the physical and microclimatic conditions of the given environment, but also with the successional sequence of other epixylic species, such as lichens, mosses, liverworts and vascular plants. In numerous instances, the colonisation of wood by fungi starts many years before the fall of a tree, and for many trees, about 50 years may pass between tree death and fall. Data from the BPF indicates that about 45% of falling trees are already dead. Thus, two types of colonisation can be distinguished: a parasitic one, beginning when the tree is still alive and led by facultative saprophytes and facultative parasites, and a saprophytic one, beginning after the tree or shrub dies and led by typical saprophytes.

In the initial successional stages, flask fungi play an important role, colonising mainly the branches and trunks still covered with bark. They are primary saprophytes, as they utilise simple sugars, starches and proteins contained in the fresh wood. Importantly, these fungi inactivate the phenolic compounds that inhibit the growth of basidium fungi. Through the destruction of the outer wood layers, flask fungi expose the deeper wood strata. Colonising thin branches, these fungi may successfully compete with other species, thereby increasing the rate of desiccation of the wood. The Aphyllophorales and Agaricales are the fungi that play a decisive role in the decay of the woody substance. Their succession is facilitated by the prior activity of other groups of fungi and epixylic plants. The facilitating function of bryophytes is key to the establishment of these fungi: they retain substantial amounts of water, modify microclimate, filter sun radiation, regulate gas exchange between the wood and the atmosphere, and moderate temperature amplitudes in the neighbourhood of fallen logs. The very last stage of wood decay permits colonisation by the fungi that grow on the forest litter, e.g. the eyelash cup and bitter boletus *Tylopilus felleus*.

4.1.5. SLIME MOULDS: MYXOMYCETES

Slime moulds (photo 94) are organisms that bridge fungi and animals. Although their anatomy resembles the former, they reveal numerous animal characteristics. In the same way as the *amoebae*, with or without *flagella*, they are mobile in the juvenile or reproductive stages of their lives. *Plasmodia* are conglomerates of the multi-nuclei crawling plasma. At this stage, the slime moulds may absorb bacteria, fragments of mycelium and even small fruiting bodies. In the forests of Białowieża, 118 species of slime moulds have been recorded (in Poland slightly more than 200 species have been discovered so far). During the project CRYPTO, carried out in Białowieża National Park, 44 species of slime mould were found, among which 38 are connected with dead wood. Their preferred substrate is strongly decayed wood, and the slime moulds' fruiting bodies usually emerge in CWD previously occupied by fungi. In unfavourable periods (e.g. drought, winter), slime moulds can survive in a latent state as spores, or so-called *sclerotia*. Therefore, certain species may change into their "active" form only once every several years. Among the most common slime moulds occurring in the Białowieża Primeval Forest are the reddy-pink, sometimes brown, with light beige spores, *Lycogala epidendrum*, the lemon yellow scrambled egg slime (dog vomit slime, *Fuligo septica*) and the white *Ceratiomyxa fruticulosa*.

J. Walencik

Photo 94. A slime mould

Summary of Chapters 4.1.4–4.1.5.

Most fungi occur in the forest environment. The fungal richness of the Białowieża Forest is estimated to be at about five thousand species. This large number results from the preservation of large fragments of natural forest and large amounts of dead wood.

Fungi play two very important roles in the forest ecosystem. Because of their symbiosis with trees (mycorrhiza), they improve the tree's growing conditions, whereas saprophytic species decompose organic matter including wood, hence recycling nutrients for plants.

Fungi are among the few organisms that can decompose the wood components cellulose and lignin. This particular ability is characteristic of the fungi from the Aphyllophorales group.

Fungi occupy fine fragments of dead wood as well as the trunks of fallen and standing trees and shrubs at various stages of decay.

The majority number of fungus species occur on fallen logs.

In the BPF, most fungi are associated with birch, oak, black alder, spruce and hornbeam.

Fungi colonise wood in a defined sequence. The process is often initiated by parasitic fungi that, after tree death, become saprophytic. This is followed by primary saprophytes utilising simple compounds from fresh wood tissues, and then those that decompose more and more complex compounds (cellulose and lignin). At the final stage of decay, those species that can also grow on soil colonise the residual woody material.

Dead wood is the substrate utilised by a number of rare, often legally protected fungi, e.g. the scarlet cup, ***Hericium clathroides***, ***Fomitopsis rosea***, ***Stereum subtomentosum*** and ***Xylobolus frustulatus***.

Most forest slime moulds are connected with dead wood.

Photo 95. Lichens (mainly cup-mosses) on a spruce stump

K. Zub

4.1.6. LICHENS

Among the 400 lichen species found so far in the Białowieża Primeval Forest, only 121 are epixylic. Of these, only a dozen or so species, including an interesting mountain lichen, *Icmadophila ericetorum*, are restricted to dead and decaying wood. During the survey carried out in Białowieża National Park, as part of the CRYPTO program, 86 epixylic lichen species were found, of which 15 were found only on dead wood. Many of the lichens that usually grow on the ground are also found growing on dead trunks. These include *Cladonia silvestris*, reindeer moss lichen *C. rangiferina*, *C. mitis* and *C. bacillaris* (photo 95). Species with a preference for dead wood are *Micarea elachista*, *Trapeliopsis granulosa*, *T. flexuosa* and *Calicium glaucellum*.

Most lichens colonise standing dead trunks and fallen logs. Among the 72 lichen species found on fallen logs in the forests of Białowieża, 13 occur exclusively on this substrate. Lichens on logs are dominated by fast growing foliose species (44), such as *Cladonia* species (photo 95), *Hypogymnia physodes*, *Parmelia sulcata*, *Platismatia glauca*, *Pseudevernia furfuracea*, *Parmeliopsis ambigua* and *Imshaugia aleurites*. In addition to those lichens found exclusively on dead wood, this substrate also hosts lichens that are generally found on the ground, mainly cup-mosses, but also dog lichen *Peltigera canina*, a rare and endangered species (photo 96). The trunks of standing dead trees are occupied by 55 lichen species (photo 97). Unlike logs, the crustose species found on trunks are rarely accompanied by cup-mosses. Most of these lichens occur on the lower parts of trees due to more humid conditions. Among the most common ones that show a distinct preference for tree trunks are *Calicium glaucellum*, *Micarea elachista* and *M. melaena*. Several species, e.g. *Chaenotheca xyloxena*, *Buellia schaereri*, *Lecanora saligna* and *Lecidella elaeochroma*, occur exclusively on standing dead tree trunks. Their companions are epiphytic lichens, usually growing on living trees, that can also colonise the bark-covered surfaces of logs.

K. Zub

Photo 96. The lichen *Peltigera canina* on the moss covering a dead trunk

J. Walencik

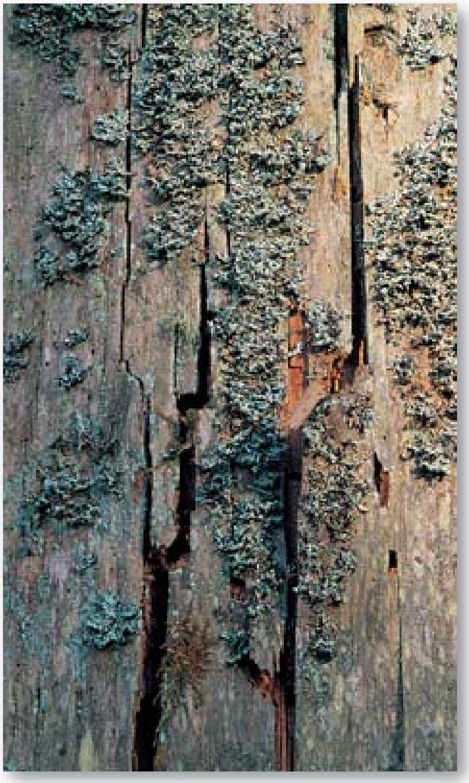

Photo 97. Lichens on a dead spruce trunk

Studies on lichen colonisation and succession on pine stumps in dry sites of Bory Tucholskie (northern Poland) revealed four distinct stages: 1) initial, 0-4(5) years after felling, mainly non-specific epiphytic and terrestrial lichens, such as *Lecidea humosa* and *Hypogymnia physodes*; 2) intensive colonisation, 4(5)-10(11) years; 3) optimal growth and development, 10(11)-15(16) years; and 4) regression, after more than 15(16) years. After the fresh stumps are colonised by the primary colonisers (stage 1), the intensive growth of mainly crustose species *Placynthiella oligotropha* and *Trapeliopsis granulosa* follows (stage 2). The third stage, dominated by crustose species and cup-mosses, is characterised by the highest diversity; 39 lichen species were found occupying pine stumps in the research area. While *Cladonia botrytes* occurred exclusively on the stumps, *Placynthiella oligotropha*, *Cladonia cenotea*, *C. floerkeana*, *C. digitata* and *C. macilenta* showed a clear preference for this substrate.

Lichens are pioneer organisms, colonising very poor environments, e.g. wood of low and fluctuating water content. The acids secreted by lichens can, on the one hand, efficiently inhibit the development of fungi, while on the other hand they accelerate wood decay. Lichens can successfully compete with other epixylic organisms in strongly insolated sites. Best predisposed to these warm, sunny sites are foliose lichens, such as *Hypogymnia physodes*, *Parmelia sulcata*, *Platismatia glauca* and *Pseudevernia furfuracea*. Because of their susceptibility to sulphuric and nitric compounds, lichens are considered indicator organisms for air quality monitoring. Less well known is that they have been successfully used in Great Britain and Sweden as indicators of forest continuity (e.g. tree lungwort – *Lobaria pulmonaria* and *Gyalecta ulmi*). Most of these indicator species grow either on dead wood or on old trees.

Summary of Chapter 4.1.6.

Most lichens are epixylic organisms, but many of them also occur on dead wood.

Among the lichens growing on CWD, most species colonise the trunks of fallen trees; this substrate hosts most of the typical epixylic lichens, mainly foliose species.

Stumps and strongly decayed logs are mainly colonised by terrestrial species, chiefly cup-mosses and crustose lichens.

Standing dead trunks are mainly inhabited by epiphytic lichens.

Certain dead wood-related lichens are used as indicators of forest continuity.

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4.2

FROM FOREST FUEL TO STREAM COURSE MODIFICATION

4.2.1. FOREST 'FUEL'

Forest fires, ignited by lightning or indigenous peoples, are among the chief factors underlying the dynamics of boreal forests in Siberia and Scandinavia, and coniferous forests in North America. Under historic conditions, the frequency and intensity of fires depended on the amount of accumulated fuel, including dead wood, as well as topography and weather conditions at the time of the fire. The techniques of efficient detection and suppression of small and moderate fires, mastered during the 20th century, have contributed to an accumulation of such immense quantities of CWD that once accidentally ignited they may fuel uncontrollable fires. Such catastrophic events forced the managers of flammable forests to implement measures to reduce the amount of fuel. The most interesting and ecologically acceptable approach is the use of 'prescribed fires,' simulating natural dynamics of the forest communities. Prescribed, controlled fires have become the 'bread and butter' used by the U.S. Forest Service in pine forests, and are being tested in Sweden. Forest fires create habitats that permit the occurrence of certain specialised animal species (mainly insects) and the regeneration of some plants, e.g. jack pine and lodgepole pine.

Pyrophylous insects

In Sweden, beetles representing as many as 50 families (about half of the families occurring in the country) prefer forests subject to natural fires. For instance, the jewel beetle *Melanophila acuminata,* which also occurs in Poland, is attracted to smoke and fire from great distances (in excess of 20 km).

In Central and Eastern Europe, the mostly non-flammable character of the forest ground vegetation, as well as a relatively high humidity and large number of saproxylic organisms preventing CWD accumulation, substantially reduce the frequency of natural fires. Therefore there is no need to apply prescribed fires in these forests.

4.2.2. STOCKING ORGANIC MATTER

In natural forests, where fire is an infrequent visitor, dead wood sequesters huge stocks of organic matter (photos 98, 99). Depending on the geographic location, the type of forest site and the phase of stand development, an average CWD volume may range from 100 to 200 m^3/ha, or even more. In the natural boreal forests of Northern Europe, a mere 20 m^3/ha is accumulated, but in the mixed beech-fir-spruce forests of East-Central Europe, CWD deposition may total 500-1000 m^3/ha. Certain forests in North America (California, Oregon, and Washington states, Vancouver Island and British Columbia), containing giant sequoia, Douglas-fir, western hemlock, red cedar or Sitka spruce, may stock as much as 1100-1400 m^3 of dead wood per hectare; so too may wet eucalypt forests in Tasmania. The CWD input rate varies from 0.5 to 2.5 (exceptionally 7.0) tons per hectare per year, and is less in broad-leaved than in coniferous stands.

The amount of CWD retained in managed forests is often very small. In the pine stands that replaced most of the original forest communities of Central Europe, the CWD volume hardly exceeds 3 m^3/ha, and very often is under 1 m^3/ha. Such a small amount of dead wood cannot provide a sufficient habitat for many saproxylic species, nor is it likely to have the full array of decomposition classes at appropriate scales. Thus, the saproxylic species diversity of these forests is very limited and these limitations also reduce the overall biodiversity. The plantation-type forest management, which includes intensive sanitation and the salvage of dying and dead trees, has led to the extinction of numerous saproxylic species of invertebrates in vast portions of Europe (see Chapter 4.1.2, page 62).

Volume vs. weight

It relates to the weight under natural conditions; the average weight of 1 cubic meter of dry wood equals about 0.5 tons. However, it may vary substantially, depending on species and the local microenvironment.

Photo 98. Huge oak logs such as these can only be observed in only a few places in Europe; Białowieża Primeval Forest

J.M. Gutowski

Nutrient content in 1 m³ of wood:

(after PROSIŃSKI 1969)

Pine:
0,1743 kg potassium (K)
0,0371 kg sodium (Na)
0,0965 kg magnesium (Mg)
0,5218 kg calcium (Ca)
0,0437 kg phosphorus (P)

Oak:
0,3155 kg potassium (K)
0,1113 kg sodium (Na)
0,0904 kg magnesium (Mg)
2,0086 kg calcium (Ca)
0,1004 kg phosphorus (P)

When a tree or shrub dies, the macro- and micro-elements accumulated in its tissues during its lifetime begin to return to the soil. The organic matter, through the activity of saproxylic organisms, decays and releases its nutrients, which are then reabsorbed by other plants. This release does not happen immediately, but takes place over years, providing the plants with a steady supply of minerals. This gradual release also prevents mineral loss during heavy rains and subsequent run-off (as often happens after artificial fertilisation). It also helps stabilise natural processes, particularly following massive disturbances (e.g. hurricanes and fires) that cause an immediate and overwhelming supply of CWD.

Studies in North America show that a mass of 215 tons of large CWD accumulated on one hectare of forest contains 14 kg of phosphorus, 330 kg of calcium, 46 kg of potassium and 7 kg of sodium.

In commercial forests, every harvest rotation or commercial thinning removes nutrients from the soil.

Photo 99. Dead wood in an alder swamp, Białowieża Primeval Forest

J.M. Gutowski

Assuming that during one tree generation (about 100 years) we extract about 300 m^3 of wood from one hectare of pine forest and 400 m^3 from oak woods, the quantity of nutrients removed from the ecosystem is immense. In the case of pine forests, accepting PROSIŃSKI'S (1969) conversion rates, more than 52 kg of potassium, 11 kg of sodium, almost 29 kg of magnesium, 157 kg of calcium, and more than 13 kg of phosphorus are removed from one hectare. In oak forests, we lose more than 126 kg of potassium, almost 45 kg of sodium, more than 36 kg of magnesium, more than 803 kg of calcium and 40 kg of phosphorus. So much from only one hectare! And if these losses are extrapolated to an entire district or other administrative unit, the amount of nutrients lost will total many tons. A forest cannot sustain such losses in perpetuity. In fact, such losses of nutrients will eventually lead to serious reductions in tree growth.

4.2.3. CARBON AND NITROGEN ACCUMULATION

Nitrogen is essential for plant growth and survival, and the nitrogen deficit – its limited amount and, more commonly, limited availability – is an important factor inhibiting plant growth in many types of forest. There are two ways of incorporating nitrogen into wood. First, during the tree's lifetime, nitrifying bacteria inhabiting the mycorrhizal fungi twisted around or penetrating tree roots and also living close by in the soil, transform unabsorbable ammonia into absorbable nitrates. Among the nitrifying bacteria inhabiting roots are the Actinomycetales that fix free atmospheric nitrogen into nitrates that can be absorbed and used both by fungi and trees (more topical information can be found in the Chapter devoted to fungi – 4.1.4, page 107). These symbiotic fungi and bacteria are frequently transmitted to new seedlings through soil infected by rodent excrement. Second, nitrogen is also fixed by bacteria in decaying wood after tree death. These nitrogen fixing and transforming bacteria are transmitted to the recently deceased or dying trees by insects. In a North American study, 215 tons of large dead wood (> 10 cm in diameter and > 1 m in length), accumulated on one hectare of forest, contained almost 300 kg of nitrogen.

Carbon accumulation occurs only during photosynthesis in a tree's lifetime. An average annual carbon accumulation rate in Central European forests is about 1.4 tons per hectare. It is estimated that the overall amount of carbon sequestered in one hectare of forest in the temperate climate zone totals about 150 tons (with two thirds stored in soil), and 220 tons in tropical forests. After the death of a tree or shrub, the decay process slowly releases carbon back into the soil so that it can be reused. However, the long years that carbon is stored in dead wood reduces the amount that could be 'stored' in the atmosphere (carbon in the atmosphere contributes to the so-called greenhouse effect). In a natural forest, where a balance between the rate of dead wood accumulation and carbon release through decomposition may exist, the process of carbon sequestration is relatively steady. In temperate zone forests, perhaps as much as $10\text{-}68\times10^{12}$ kg of carbon is stored in large dead wood. Available data do not permit an estimation of the amount of carbon sequestered in dead wood throughout the world but we can guess that the quantity is immense. Some assessments suggest that forests (including forest soil) contain 2-3 times the carbon present in the Earth's atmosphere. According to recent studies, all the terrestrial ecosystems together store $1{,}0\text{-}2{,}5\times10^{12}$ kg of carbon per annum. On a global scale, deforestation increases overall carbon emission to the atmosphere by 20-25%, the second largest source of anthropogenically released carbon dioxide after the burning of fossil fuels (coal, petroleum and gas).

Burning slash

Wood burning causes a sudden release of carbon to the atmosphere. According to the *Instruction of Forest Protection*, the regulations which forest managers in Poland must implement, all the slash should be collected after felling, piled and burned. Burning the green slash is intended to prevent the proliferation of insects that foresters consider to be pests. There is a substantial difference between natural fires in our moist and cool forests, and artificial slash burning. In the case of the former, only a small portion of wood is burned; besides standing trees both living and dead, larger logs and stumps are generally not burned. This is different from forests in drier climates where wildfires are or were quite frequent (e.g., in the pine forests of North America, or the eucalypt forests of Australia), consuming large amounts of the existing CWD (including stumps and major roots where fires are intense). Despite the removal of CWD, such fires often create new CWD. In pine and many eucalypt forests, for instance, natural fires facilitate the regeneration of trees by consuming organic litter and opening up an area of the ground to more sunlight which permits establishment of these shade-intolerant trees. In addition, some insects require burned stands to complete their life cycles.

Slash burning could be tolerated in certain coniferous forests where lightning is the primary cause of natural fires (but in central Europe, lightning fires only occur sporadically). However, such operations should not be conducted in broadleaved and mixed forests. Even in pine forests, not all of the slash should be burnt post-felling as there is a need for dead material to retain a habitat for saproxylic organisms.

Slash burning following a one-hectare clear-cut in a pine forest releases about 7.5 tons of carbon monoxide to the atmosphere that, under suitable conditions, can be transformed into 44 tons of carbon dioxide. In Poland, the slash burning operations performed in 1998 released 280,000 tons of carbon monoxide and more than 1,600,000 tons of carbon dioxide to the atmosphere. Considering only this environmental aspect, slash burning should not be applied in these cool moist forests where natural fires are a rare event. Slash burning can have a negative effect on various components of the ecosystem, such as neighbouring trees and stands, ground vegetation, soil and micro-fauna and -flora. These concerns need to be evaluated and should be taken into consideration when deciding whether or not to burn the slash. But the most negative effect of slash burning is its environmental impoverishment; a sudden mineralisation of large amounts of organic matter that is the habitat of many saproxylic species.

Recently, certain forestry districts, instead of burning, process slash into chips that are spread over the felled area. While this technique eliminates certain disadvantages of burning, it is still inconsistent with natural processes, as it still removes the structure of the dead wood which is key to the establishment and development of many dead wood-related organisms.

4.2.4. DEAD WOOD AS A WATER RESERVOIR

The water holding capacity of a fallen log generally increases with time. However, the capacity varies with tree species and climate; in some tree species (e.g., firs) and in more humid climates, the moisture content is generally greater than in other tree species (e.g., some pines in western North America) growing in Mediterranean or even drier climates. There are two sources of water in dead wood: precipitation, and the release of water through the processes of chemical decomposition of woody tissues led by bacteria and fungi. Within a few years to a decade after the fall of a tree, the water content in a log can be so high that it can be wrung out like from a sponge. Therefore, logs lying on the forest floor should be considered an important reservoir for water storage in the forest and a factor moderating the microclimate under the tree canopy. Such logs, especially the larger ones, become favourable 'well-watered' beds, where tree seedlings can easily become established. The ability of water retention and microclimatic modification abilities of logs is particularly important in rocky areas, on ground with shallow soils, and in arid locations. The water storage capacity of logs is substantially improved with a covering of bryophytes, lichens and vascular plants.

Summary of Chapters 4.2.1.–4.2.4.

Dead wood is an exceptional, very rich store of energy and chemical substances – indispensable factors in the proper functioning of forest ecosystems. The solar energy 'captured' and fixed by leaves in the process of photosynthesis is accumulated in the organic compounds building the wood tissues. These substances contain great amounts of carbon derived from carbon dioxide absorbed from the atmosphere. Gradual metabolic oxidation of these compounds yields energy supporting the life processes of both plants and saprophytic organisms unable to directly utilise carbon dioxide.

Natural forest fires (e.g. ignited by lightning) are also a way in which certain types of forests use the dead wood energy and nutrient residues to initiate tree renewal.

Though smaller in relative content to that of leaves, the total content of nitrogen and minerals in dead wood is enormous because of its much larger total volume.

Dead wood, due to its slow rate of decay, stabilises the nutrient function of ecosystems.

With a porous, sponge-like structure, dead wood in many forests is a very capacious reservoir of water supplied both by precipitation and then retained as well as that produced in the wood itself by the metabolic processes of bacteria and fungi. It is a very important function during periodical droughts or in ecosystems permanently exposed to dry conditions.

4.2.5. ROLE OF DEAD WOOD IN TREE REGENERATION

Forest 'nannies'

How do trees regenerate in swampy forests, where surface water becomes stagnant for several months each year (as in alder swamps) or in forests regularly flooded by brooks in the spring (as in riparian communities)? Tree seedlings germinating in places that are later flooded are subject to suffocation or death caused by freezing. Under such conditions, all places above the water level are important for tree regeneration. Hummocks are typical places that remain above the water level in alder swamps. Hummocks are formed around the trunks of old trees that once had once germinated on rotting 'nurse logs' providing a 'dry' substrate for young trees and other plants (photo 100). Straight rows of young trees are commonly observed in natural alder swamps and riparian communities; they are usually 'the charges' of the same 'nurse.' To access the soil, the sapling roots twist around and gradually overgrow the decaying log. Thus, each 'nurse' 'teaches' the young generation of trees 'an appropriate posture,' suitable to survive high water levels. The young trees gradually develop the root system that forms the skeleton for a new alder hummock (fig. 33). Although single (sometimes more numerous) examples of "nurse logs" can be seen in other kinds of forest, those found in wet, boggy environments are fundamentally important to the dynamics of the whole community. The importance of the above described mechanism in the Białowieża Forest has been emphasized by PACZOSKI (1930).

Various types of natural spruce stands also exhibit an analogy to the processes observed in alder swamps and riparian forests. The relation between spruce regeneration and decaying wood is almost spectacular. Dense aggregations of spruce saplings and seedlings entirely covering decaying logs are very characteristic of high elevation forests in the Alps and Carpathians, as well as at lower elevations in the Scandinavian taiga and forests of Białowieża (photo 101, 102, 103). This relation of young trees to decaying logs is of great importance to the regeneration of these forests (fig. 34). In a nature reserve in Lapland, 40% of the young and small spruce trees occur on decaying logs that cover merely 6% of the ground. And in the high mountain forest of Babia Góra National Park (southern Poland), almost 50% of the spruce regeneration is found on logs covering only 5% of the ground surface.

Log diameter is an important attribute of a log's role as a regeneration bed. Studies from the mountains of Poland show that logs less than 20 cm in diameter are rarely colonised by young trees, but logs greater than 40 cm in diameter are regularly colonised. A lack of CWD, especially of larger sizes, would severely limit natural spruce regeneration.

In the mesic deciduous, mixed and coniferous Białowieża assemblages, young spruces can often be seen growing on top of the stumps of their ancestors. This utilisation of stumps as microsites frees the young spruces from competition with herbs and dwarf shrubs, secures an abundant supply of water and permits close association with mycorrhizal fungi permitting establishment of that essential symbiotic relationship. Trees growing in these locations develop a specific stilt-like form (photo 104).

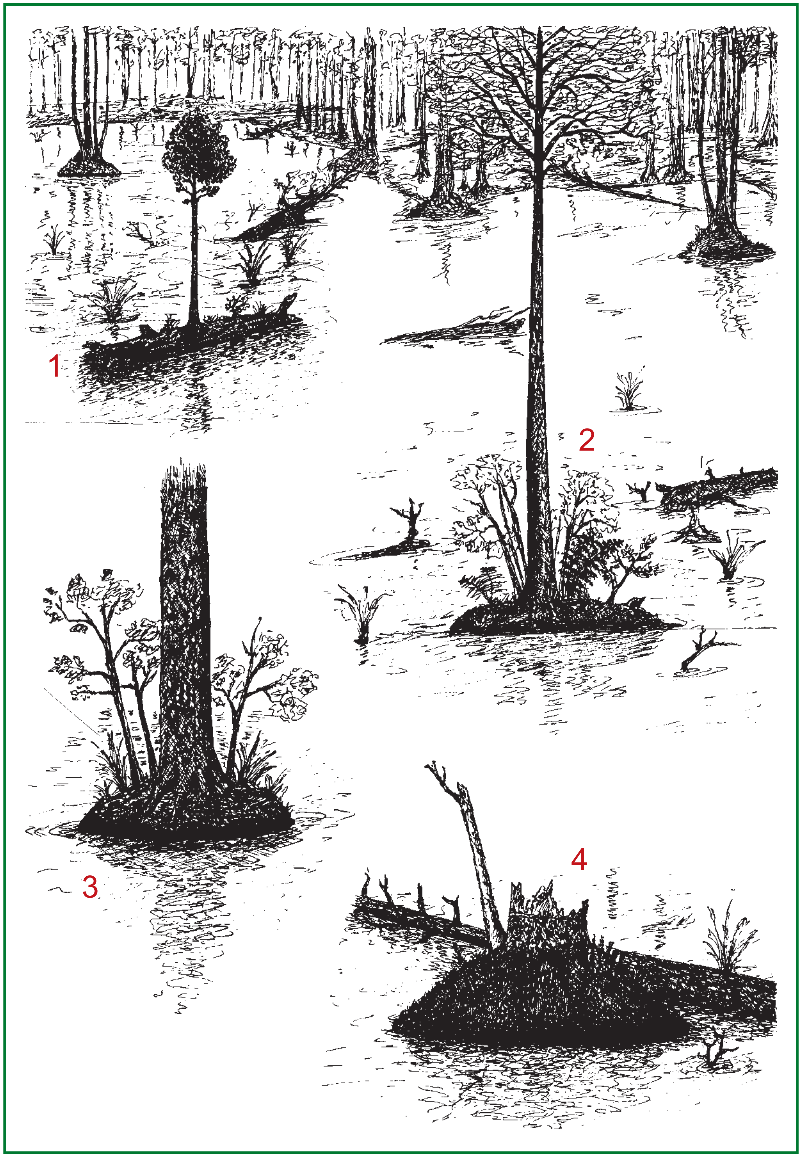

Figure 33. Tree development on a nurse-log or the formation of a hummock: 1 – The emergence of seedlings and young trees on the decaying log; 2 – the formation of the new hummock: gradual disintegration of the nurse-log and accumulation of organic matter around the roots of young trees; 3 – the matured alder on the developed hummock; 4 – a 'vacancy hummock', ready for occupation by a new tree (M. Bobiec)

A. Bobiec

Photo 100. 'Nurse logs' and their 'charges' in an Alder swamp in the Białowieża Primeval Forest

Photo 101. Spruce seedlings on a decaying log

J. Walencik

Photo 102. An old snag used as a growth substrate by the new generation of trees

J. Walencik

J. Korbel

Photo 103. Young spruces growing on a decaying log

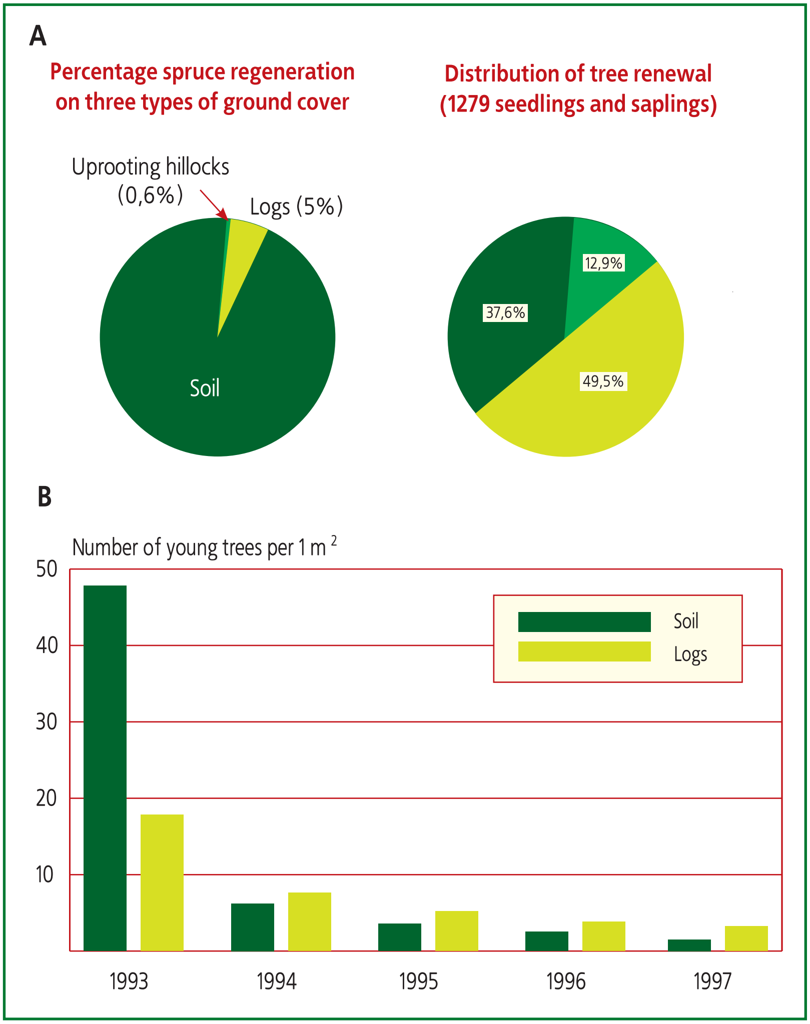

Figure 34. The importance of decaying logs for spruce regeneration in the subalpine forests of Babia Góra; A – the distribution of spruce undergrowth on various types of sites depending on their relative richness, B – Changes in seedling numbers of a cohort established in 1993, depending on site type (after HOLEKSY, DANIELEWICZ and PAWLACZYK 1998; modified)

In dry forests where fire is a frequent process, burned out stump holes may serve as good places for young pines to become established. These sites tend to hold moisture longer and their limited area does not permit occupancy by many seedlings, thus limiting competition (unlike in other locations where many seedlings attempt to establish).

Animals too may play an important role as active carriers of seeds to decaying wood. Certain birds, such as the nuthatch, transport tree seeds to logs where they are covered and hidden from other potential consumers and then often ‘forgotten.’ These seeds are in a more advantageous situation for germination and establishment than seeds randomly dropped onto the dead wood or elsewhere.


J. Walencik

Photo 104. This stilted spruce used to grow on dead wood; Białowieża Primeval Forest

Forest protection issues

'Damage from game' is a concept that has recently joined the canon of forest management. 'Damage from game' is mainly the damage to and loss of seedlings and young trees in forest plantations and pole-aged stands caused by ungulates (red and roe deer, elk and bison). These animals cause damage by eating shoots and buds, peeling young bark and cambium, and rubbing maturing antlers against trees. Measures taken to correct such damage require human labour to replace the damaged trees and tend the plantations. Diminishing the damage may require a substantial reduction of ungulate numbers, or the application of expensive measures such as the erection of ungulate-proof fences or the protection of each planted tree.

In natural forests, where herbivores behave in the same way as in managed forests and cause the same kinds of tree injuries, this concept of 'damage' does not apply. These same species of trees and animals have coexisted for centuries and the forest continues to persist. The destiny of most young trees, from the stages of seed to seedling, is to become forage for herbivorous organisms. Losses may start with birds feeding on seeds. The loss of foliage or bark may be due to a range of organisms, from foliophage caterpillars to deer scraping their antlers and damaging bark and perhaps even killing the tree. Only a small portion of young trees (regeneration) survive to maturity and achieve immense size. Ungulate populations in Poland's unmanaged forests are substantially higher than those in managed forests and yet no protective measures are needed to prevent ungulate 'damage.' Why then are they needed in managed forests?

In Białowieża National Park the red deer population is 2-3 times greater than in the managed part of the ecosystem. These unmanaged forests still have efficient mechanisms that maintain a balance between the components of the ecosystem, including mechanisms between trees and the foraging pressure of herbivores. Fallen logs and other fallen woody material provide protective entanglements that prevent penetration and browsing by ungulates in some areas of the forest. Those areas protected from browsing are 'used' as regeneration sites, where young trees may safely grow and exceed the browse line before the protective CWD completely decays (photos 105, 106). Fallen spruces provide a particularly effective form of protection, acting like colossal barbed wire 'bristling' with hard, pointed and enduring branches. Belts of dense regeneration of broad-leaved trees commonly find 'asylum' along spruce logs in natural forest communities. Complex systems of a dozen to a few dozen fallen trees enabling the

A. Bobiec

Photo 105. Fallen spruces efficiently protect a new generation of trees from deer browsing; Białowieża Primeval Forest

simultaneous development of a new generation of trees over entire gaps (usually from 500 to 1500 m^2) are even more common. Groups of dying trees, mainly caused by fungal infections followed by insect 'terminators' and strong herbivore pressure, can prevent continuous and even regeneration. These are among the leading factors responsible for the dynamics and exceptionally high spatial diversity in the natural mixed and deciduous Białowieża forest assemblages.

A. Bobiec

Photo 106. Remnants of spruce 'entanglements' that protected young trees from browsing animals and thus facilitated the regeneration of broad-leaved trees, Białowieża Primeval Forest

Summary of Chapter 4.2.5.

In swampy forests (e.g. alder swamps) and riparian communities that are regularly flooded, young trees successfully develop only on microsites elevated above the water level. Such sites are commonly established by decaying 'nurse logs.' The young trees develop root systems that twist around and overgrow the 'nurse' so that after its decay, they are capable of independent life in that difficult environment. A similar phenomenon can be seen on a larger scale in mountain and taiga spruce forests. In these cases, the logs serve as seed beds free from severe competition from herbs and dwarf shrubs.

Fallen trees, limbs and other parts are capable of protecting developing seedlings and saplings from herbivorous mammals (e.g. deer). Such natural entanglements provide regeneration areas where young trees can quickly grow above the browse line.

4.2.6. STABILISATION OF STEEP SLOPES BY DEAD TREES

Human activities are increasingly being credited as the cause of cataclysmic avalanches and landslides. Analyses of these events often point to the deforestation of mountainous areas as the culprit. In mountainous terrain, dead trees play a role as important as that of the living ones. The roots of living trees hold soil and rocks in place on slopes, whereas fallen logs either lying across slopes or anchored on living or dead trees or on rocks, do the same. Under many circumstances, they resist avalanches (photo 107). The removal of dead trees and other CWD on steep slopes or in mountainous forests (near the tree line in particular, e.g. complete harvesting, including the soil disturbance caused by dragging trees to the landings), at scales exceeding several hectares, causes erosion, intensifies land slides, and heightens the risk of cataclysmic soil movements.

J. Korbel

Photo 107. On slopes, logs substantially reduce soil erosion; southern Poland

CWD plays a role in the maintenance of mountain ash or rowan *Sorbus aucuparia* in mountainous terrain. Studies from Gorce National Park (southern Poland) show that dying spruce stands (decline may be caused by air pollution, hurricanes, spruce bark beetle outbreaks or fungal infections) are quickly replaced by mountain ash dominated thickets which effectively limit soil erosion. Mountain ash seeds are mainly spread by birds that perch on dead trees, and the removal of these birds would make the mountain ash's expansion far more difficult.

4.2.7. THE ROLE OF DEAD WOOD IN SURFACE WATER RETENTION AND STREAM COURSE MODIFICATION

Dead wood contributes to water retention in forests, commonly in riparian communities and in wetter areas of mesic deciduous communities. In these places, fallen trees dam water and cause local floods or form new 'relief' streams that are routed away from the existing stream bed. The dynamics of ephemeral streams are particularly instrumental in shaping the land and restoring soil. Frequent changes of stream beds caused by falling trees modify the ground micro-relief and 'rejuvenate' the soil locally.

Trees falling into streams and rivers lead to considerable changes in the local stream-bed morphology (photo 116, fig. 35). Changes in current patterns and velocities cause spatial shifts where the bottom is scoured out relative to where sediment accumulates. The resulting changes in the depth and character of the bottom are utilised by various aquatic organisms. Many fish find safe refuges under logs and branches that have fallen into streams and rivers, and anglers seek out such locations knowing that fish can be caught there. On the Trzebiocha river in Pomerania (northern Poland), trees are purposely felled into the stream to improve spawning conditions of the rare lake trout. The removal of logs from a stream can result in reductions in fish populations. Fifty years ago, many fallen trees were removed from rivers and creeks in the north-western United States to facilitate salmon migration; however, after the work was completed, fish numbers greatly declined.

J. Korbel

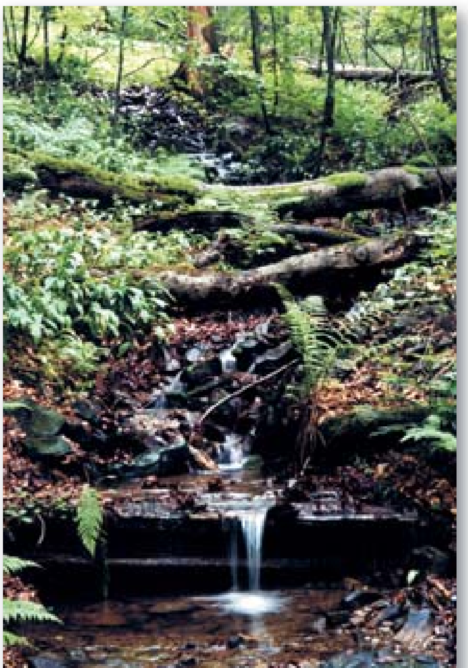

Photo 108. Dead trees slow down the flow rate of stream currents especially when seasonal flows are particularly high; southern Poland

Logs blocking small brooks locally impound water and contribute to its retention in the forest. These impoundments retard or even prevent the massive flows that follow torrential rains and would lead to floods (photo 108). Beavers also contribute to the retention of water in the forest and the reduction of water flows by constructing their dams on streams; these dams are mainly built from the limbs and stems of trees (photo 29). CWD deposited on the forest floor impounds melt water, delaying its outflow and reducing the potential of flooding downstream.

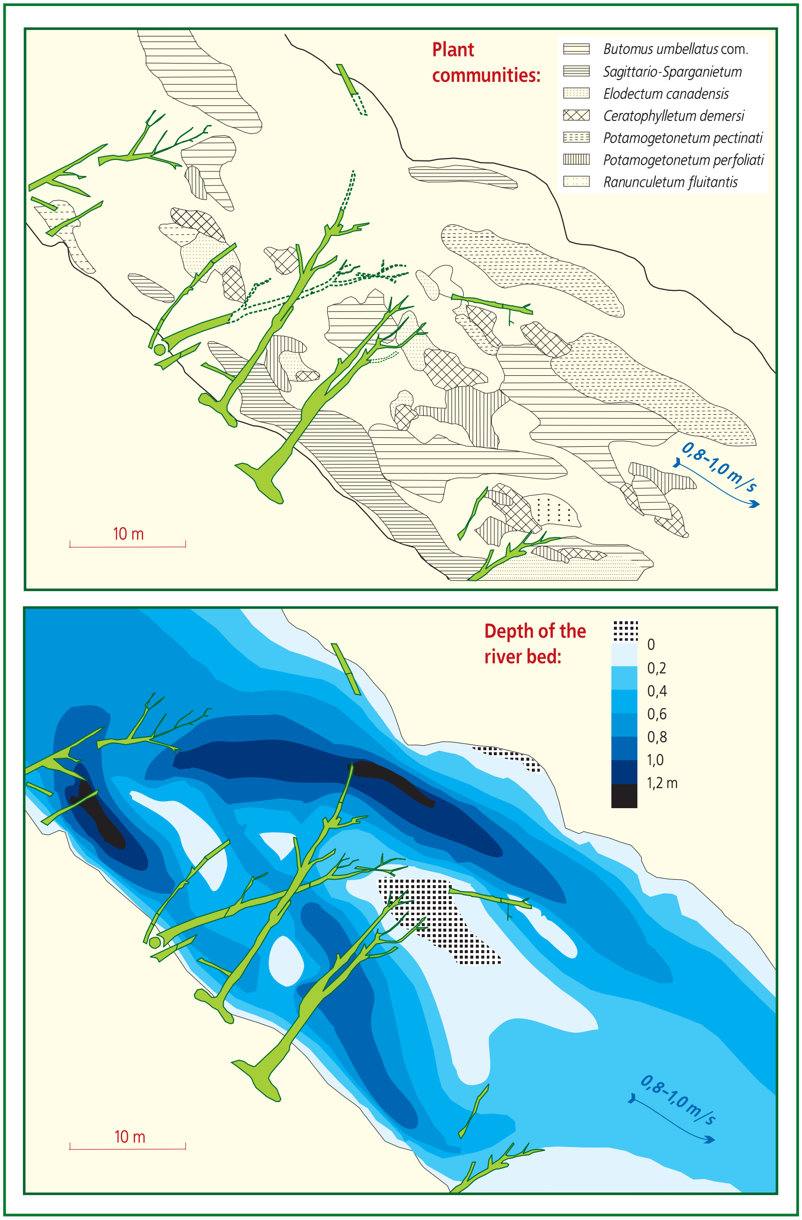

Figure 35. The change in river bed relief influenced by dead trees falling into the stream, the Drawa river in Drawieński National Park (after PAWLACZYK 1995)

To recapitulate, the wood accumulating in rivers and creeks, particularly in mountainous areas, is an important feature. CWD disperses the energy of flood flows, improves the transportation and accumulation of sediments, and diversifies current speed and bed depth. Fallen trees alter the pattern and structure of rivers and brooks providing, among the other things, additional microhabitats, forage for a variety of aquatic organisms, and a physical structure to the stream channels.

4.2.8. THE ROLE OF UPROOTED AND DEAD WOOD IN SOIL PROCESSES

Uprooting – a forest 'orogenesis'

Uprooted trees (i.e. trees that have fallen with the roots still attached but now exposed above the soil surface) are very important to forests. In Central and Eastern Europe, the most frequently uprooted trees are spruces. Spruce trees have superficial root systems, and are therefore especially vulnerable to strong winds (photo 109).

A falling tree, especially if still alive, retains large portions of its root wad including soil and rocks attached to the so-called root plate. These root plates create microrelief at a small scale in the landscape comprised of craters and hillocks composed of the material continually falling from the root plates (fig. 30).

Photo 109. The presence of large fallen trees makes it easy to perceive the forest's primeval character

J. Walencik

Uprooting exposes layers of soil that often differ in degrees of coarseness, proportion of organic matter, and other such properties (in the forests of Białowieża, the heavy, water-tight layer of loam is covered by light sands); thus structures created by uprooting offer a greater variety in site characteristics. The hillocks, comprised of sand and organic matter (e.g. the mor type humus and spruce needle litter), are dryer and more acidic than the undisturbed soil, whereas the 'water-proofed' craters function as long-lasting pools or puddles. Thus uprooting, a phenomenon inseparably connected with the death of trees and CWD production, is a process that diversifies and rejuvenates forest sites. Falling trees cause temporary disturbances that permit species of a variety of ecological requirements to coexist in a very small area (fig. 31).

Humus:

organic matter, mainly plant debris in various stages of decay (humification, mineralisation), accumulated in soil (called the "ectohumus" when found on the soil surface in forests); forest humus can be classified into 'mor' type – of low degree decomposition, 'moder' – of intermediate decomposition, and 'mull' – with the greatest degree of decomposition.

Forest management, minimising the 'risk' of uprooting, reduces or prevents this process which leads to the homogenisation of forest stands. When windblows do occur, they are considered "catastrophic" events, and their effects, as in the case of other catastrophic events in managed forests, are quickly removed. Removal is achieved by cutting the fallen trees from their root plates and removing the logs from the forest. After removal of the log, the now unbalanced root plate often falls back into the hollow created by the uprooting, wiping out the newly created microhabitats. Soils are also commonly "prepared" in managed forests. Such preparation, either manual or mechanical, does not remotely resemble the dynamics and soil structures exposed by the uprooting of trees.

When a tree turns to dust

Dead wood, as it decays, is gradually covered by litter and vegetation and blends into the forest floor. The dead wood, at this point, has not yet been returned to the soil. Often, the red-coloured lignin will remain recognisable as components of *moor* ectohumus. Thus, the uppermost soil layers in a functioning forest exhibit a great deal of variability both horizontally and vertically. Acidic coniferous sites are generally characterised by a thick ectohumus layer whose depth ranges from 0 cm (in places where uprooting recently occurred) to a few dozen cm where a decaying trunk is rotting into the forest floor. In the mesic deciduous forest, where the ectohumus is generally lacking, decaying logs supply thick organic layers. The rot substrate differs substantially from the surrounding mineral soil. The retention of large amounts of moisture in the rot-ectohumus provides an ideal environment for pteridophytes: ferns, horsetails and club-mosses. On the other hand, ramsons *Allium ursinum*, a species that in springtime forms vast and beautiful swathes in the deciduous Białowieża assemblages, avoid the ectohumus, leaving non-colonised patches corresponding with the decomposed logs. However, the almost totally decayed wood is inhabited and penetrated by many representatives of the soil fauna, including mites, springtails, myriapods, earthworms and other species.

Recent studies show that a few decades after the cessation of wood extraction from coniferous forests, deposits of CWD have substantially enriched the site, resulting in changes in the ground vegetation including a greater presence of species typically found in richer sites. These species include broad-leaved trees characteristic of mesic deciduous communities, such as hornbeam. Besides enrichment, dead wood decomposition leads to improvements in soil structure. Lignin, a major component of decaying wood, provides many of the basic elements found in humus; humus enhances the air-water ratio, absorption capabilities and thermal conditions of the soil substrate.

Summary of Chapters 4.2.6.-4.2.8.

Dead wood substantially influences the quality of forest sites. In the mountains, dead wood can reduce the potential or intensity of avalanches and soil erosion, and facilitates the regeneration of trees after windblows. In wet and riparian communities, fallen trees may change the channels of streams, rivers and brooks.

Uprooting plays a very important role in the ecosystem, creating crater-hillock land microforms. This process converts relatively uniform sites into a variety of microenvironments. Forest management, however, leads to the loss of these forms and to the homogenisation of forest sites.

The decayed logs, blended with the soil, form belts of thick layers of ectohumus, which are favoured by certain organisms and avoided by the others.

Dead trees alter the character of streams and rivers and their presence and abundance is necessary to maintain the biodiversity of forest rivers and brooks.

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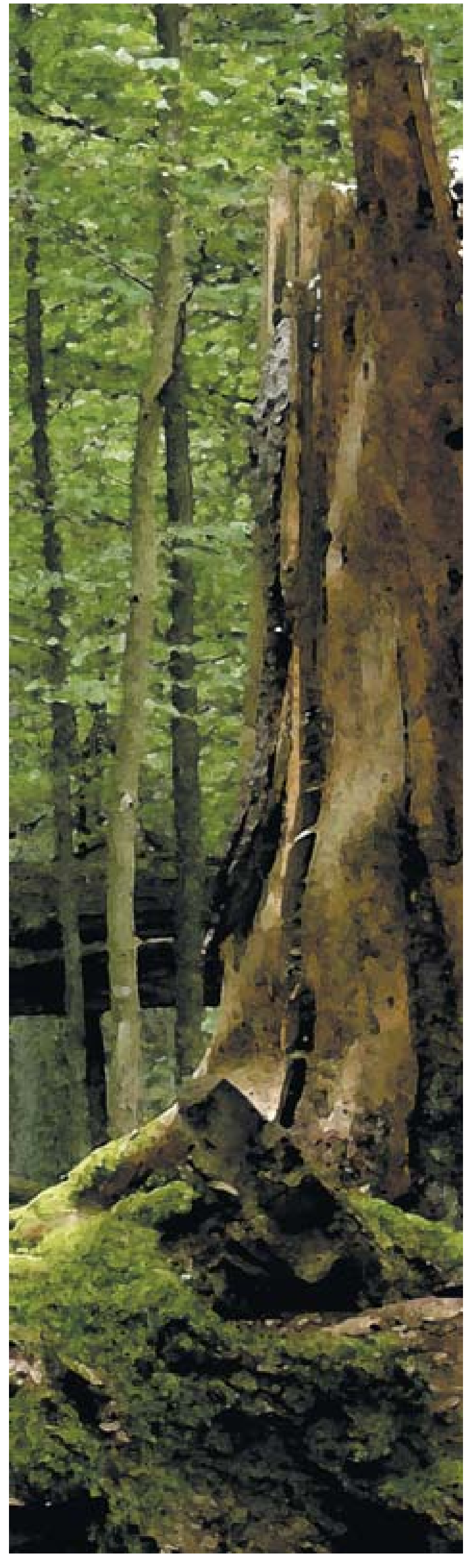
Chapter 5



DEAD WOOD IN FOREST MANAGEMENT AND NATURE CONSERVATION

5.1

DEAD WOOD IN FORESTS – TIME TO RETHINK THE PARADIGM

Good taste and bad habits

Dead wood, in particular dead and fallen trees, has long captured peoples' attention, focusing reflection on the power of nature and the inevitability of mortality and decay, phenomena that eventually affect every living thing (photos 98, 101, 109). Such reflections result in romantic descriptions of primeval forests, of which dead trees are a key element. We find such descriptions in the beautiful verses of *Pan Tadeusz,* by Adam Mickiewicz (see the Introduction), in the drawings of Michael E. Andriolli, and even in the tune of the *Peer Gynt* suite by Edward Grieg. Dead wood symbolises an untamed and mysterious primeval forest. Our sense of aesthetics favours a natural, wild, 'chaotic' landscape over the orderliness of a 'well managed forest.' With the freedom to choose decorations such as photo calendars or wallpaper representing either the wildness of an unmanaged forest full of dead wood and fallen trees, or a properly tended and managed forest, we usually request the former.

European bison in the primeval forest: an illustration to *Pan Tadeusz*, by Adam Mickiewicz. MICHAEL E. ANDRIOLLI, 19th century

Such an intuitive, 'innate' view of the untamed primeval forest has given way to that of a managed forested landscape modelled on intensively managed agricultural fields. Since wood has become a valuable commodity, the practice of forestry to produce wood products has become dominant, in many cases deliberately controlling and preventing anything that would reduce the commercial value of the timber. The ancient protection of royal forests, usually understood as protection of habitats for game animals, has been replaced by 'forest protection' or the fight against tree pathogens and 'pests.' The profitability of forest products is dependent upon the liquidity of the supply of a commodity of an acceptable quality, and to meet this objective, foresters have modified species composition and limited the maximum ages of trees to optimise the production of lumber and reduce the risk of waste. Natural tree mortality resulting from old age, fungal infection, insect infestation or abiotic natural factors is perceived as a waste of the commodity. The swift removal ('salvage') of trees which exhibit traces of spruce bark beetle infestation is intended to reduce timber wastage, and removal of "threatened trees" ('sanitation') is intended to prevent further spread of the 'pest.' Such a forest no longer includes the complete and natural life cycle of trees from the seedling stage through to tree death and the decomposition of the wood tissue. Burning piles of slash is commonly used in many European forests as a preventive measure against 'pest' dispersal. Alas, such techniques are also being applied in the Białowieża Primeval Forest (photo 56). The stereotype "dead wood = pest hatchery" dominates European forest management and has resulted in a regime of forest hygiene that removes all pieces of dead wood regardless of their importance to and use by dependent species.

'Forest protection' is among the deepest-rooted practices of forestry management, and its objectives are to fight tree 'pests' and pathogens. In some European countries, these practices are strengthened by legislative inertia and requirements for forest managers to apply forest protection practices. Those forest managers who permit trees to die and decay in the forest and do not keep the forest 'clean' risk rebuke for failing to apply the 'appropriate hygiene standards.'

However, even in times when most foresters thought dead wood to be a deadly threat to forests, some did recognise the ecological role of CWD. In 1885, the forestry superintendent Tschepske in Pieńsk (in Lower Silesia) wrote about the necessity of retaining old, decaying oaks (200-300 years old) in some parts of the forest so that "insectivorous birds had places to nest."

Dead Wood: Fad or necessity?

Decaying wood has long been a focus of the naturalist's interest as a habitat for a wide variety of fungi, slime moulds, arthropods and other organisms – many of them very rare. However, it took the agreements to protect biodiversity, made by states attending the Earth Summit in 1992, to bring the biological richness associated with dead wood to the attention of decision makers. Since then, a widespread educational campaign has been undertaken in many countries to illustrate the incredible diversity of the dead wood 'microcosm.' The goal of such an activity is to educate people about the values of 'messy' forests, and the variety of species that inhabit dead wood which enrich the ecosystem and increase the potential for sustainability. A good example of this sort of educational campaign is the Scandinavian *A richer forest* programme, developed in the early 1990s (PERSSON (ed.) 1990). A richer forest has led to a common recognition that the quantity of dead wood is a major criterion of forest 'naturalness.' In Sweden, for instance, when a forestry district applies for the international certificate of the Forest Stewardship Council, it has to set aside and retain without intervention at least 5% of the area considered and all fragments of the forest harbouring any red-listed species. Such fragments are called "key habitats." German forestry policy suggests an average of 10 m^3 CWD per hectare, whereas in France, an average of 15 m^3 is recommended. While such recommendations are commendable, under natural conditions one could expect well above 100 m^3/ha – i.e. far more than the recommended CWD levels. In the USA, dead trees are sometimes retained even on golf courses to provide habitats for saproxylic fauna, thus educating both players and spectators. In the north and west of Poland, a dozen or so forest superintendencies decided to co-operate with a conservation NGO, The Naturalist Club, to develop a network of "xylobiont reserve," areas within forests where CWD would be permitted to accumulate. Current forestry regulations in Poland (*Principles of Silviculture*, *Instruction of Forest Protection*) suggest a gradual improvement in the policy concerning CWD. For the last few years, the forest practice rules recommend leaving several trees following harvest operations until they eventually die, and the Polish forestry administration usually recommends leaving up to 5% of the stand volume in harvested units for this purpose. The new edition of the Polish *Principles of Silviculture* recommends that hollow trees be retained in forests and that they should receive protection. Recently too, a rule to retain the so-called 'sterile' woody debris (CWD that is not used by 'pests') is to be applied, although in practice, the logs and larger CWD are often removed and sold as fire wood.

There are also attempts to apply some of the natural phenomena related to dead wood in forest management. For instance, it is well known that the removal of dead trees retards the regeneration of high elevation spruce stands. It is now being recommended that dead trees be left to complete the decay process and that new spruces should be planted next to the retained logs and stumps.

However, despite these regulations that are intended to conserve much more CWD than in the past, they are often applied inconsistently in Polish forests. For instance, while there is now tolerance for, and even encouragement of the retention of "sterile dead wood" in forests, the regulations still emphasise the necessity of removing "active dead wood" (CWD colonised by 'pests'). The maintenance of "an appropriate state of forest hygiene," comprising an adequate application of 'pest control' (e.g. burning slash, pealing the bark off of stumps) is still one of the primary priorities of forest managers (photos 56, 57).

However, any dead wood classified as "sterile" was "active" at some time or another. Any suitable fragment of 'healthy' wood, standing or lying, is sooner or later colonised by organisms considered as 'pests.' The 'terminator' species (those that ultimately kill weakened trees or shrubs) are necessary to initiate the trajectories of the microsites to be used by the thousands of species associated with the successive stages of wood decay. The natural functioning of the forested ecosystem is impossible if such an important element as CWD is removed or substantially reduced! Simply leaving slash or wood chips in the forest is not sufficient to conserve the biodiversity of organisms related to dead wood, because many of them require the presence of large logs.

The lack of an efficient and universal system for monitoring the quantity and dynamics of dead wood, as a standard forest survey procedure, shows that we are far from a proper recognition of the role and importance of CWD in a functioning forest. Studies carried out in Polish forests indicate that the amount of dead wood that is recommended for retention or that currently exists in most forests is several times less than the minimum necessary to maintain the organisms that are dependent on it.

The Instruction for Forest Protection states that:

§ 4
(...) The amount of active dead wood must not be higher than 0.5 m^3 per hectare in spruce stands, 1 m^3 per hectare in remaining coniferous stands and 2 m^3 per hectare in deciduous stands.

§ 360
1. Any wood with bark attached that originated from windblows and windbreaks, autumn-winter felling, slash, and dying trees should be removed from the zone endangered by pests. It must be completed:
1) before 1 March in lowland and upland areas
2) before 1 April in mountainous areas

2. After this term is met, the coniferous wood left in the forest risk zone should either be submerged or sprayed with water, barked, or, under exceptional circumstances, treated chemically.

§ 361
(...) 2. During thinning operations the trees occupied by cambiophages should be removed (...)

§ 362
1. Barking is one of the most efficient methods to prevent wood from being infested by secondary pests. Barking destroys larvae and pupae, particularly of species which forage under bark.

(Instrukcja Ochrony Lasu [Instruction for Forest Protection]. 2004. Państwowe Gospodarstwo Leśne, Lasy Państwowe, Warszawa, 276 pp)

Spruce bark beetle outbreaks – an unwanted gift of nature

In the midst of an intensifying spruce bark beetle outbreak in Bavarian Forest National Park (BFNP, ca. 25,000 hectares) in the early 1980s, the authorities responsible for nature conservation in Bavaria decided not to attempt to control the outbreak by employing 'sanitary cutting.' This decision was heavily criticised by those working in forest management and extraction as well as the local authorities. "Why waste so many trees?" they asked. The decision, however, while it dramatically changed the area's character, also resulted in a very quick renaturalisation of the BFNP ecosystem. When the park was designated in the mid 1970s as the first national park in Bavaria, its forests resembled those of other well managed mountain forests – well maintained, artificial spruce monocultures. Now, thirty years later, thanks to the unconstrained course of the outbreak, the BFNP ecosystem is much more "natural," now comprised of a variety of patches of different forest structures at a variety of scales and with an abundance of CWD. Mother Nature reorganised a forest that was managed and intensively utilised for hundreds of years. After the spruce bark beetle outbreak, BFNP became the most popular natural attraction in Germany, visited annually by more than 2 million tourists. According to calculations from 1995, the profit gained by tourism in that area was four times greater than the loss of income from the elimination of timber sales and the costs of park administration.

Unfortunately in the Białowieża Primeval Forest, detection of a spruce bark beetle outbreak automatically intensifies sanitary cutting, which then halts the renaturalisation process. However, the spruce bark beetle outbreaks could quickly restore the primeval character of the ecosystem, both from an ecological point of view (improvement of the dead wood balance, natural exchange of tree species), and from the viewpoint of visual attractiveness.

The short-term benefits achieved by intensive sanitary cutting cannot compensate for the long-term losses to the forest's composition and processes and the damage to the scenic quality that is especially appreciated by tourists. At the time of production of this book, decision makers on both sides of the Polish-Belarussian border appear to have ignored the numerous appeals of ecologists to reduce sanitary cutting, and do not appear to understand the tragic consequences of intensive sanitary cutting to the critical components of the primeval forest that their policies, in the name of 'pest control', promote. The application of intensive sanitary cutting does not appear to be limited to the Białowieża Primeval Forest; this policy is also being implemented in other rare and valuable natural areas in Europe, including Šumava National Park, neighbouring BFNP.

Decay and rot outside of forests

For over 300 years, the intensive management of most of the European forests has led to an almost complete elimination of their dead wood. Organisms depending on a sustainable supply of dead wood, those relics of ancient forests, are sometimes even found in vegetation outside of forests! This paradox results from the sharp division of land into forests and pastures in many European countries, which has been ongoing for centuries. Before the Middle Ages, there was not a great demand for large-sized timber. At the time, the Western European societies were capable of meeting their commodity and energy demands by coppice woods and wood pastures. The harvested wood was cut from young sprouts on the top of untouched, pollarded trunks. ■ As the demand for large-sized timber increased, pastures were separated from the forests and left for livestock production. Since then, the forests have been intensively managed for the production of tall trees. The resulting forests did not have a place for old, irregularly shaped, or wide-crowned trees characteristic of former wood pastures. These beautiful spreading and now quite rare, legacy trees were only

Coppice, pollard

Coppice – an area of trees cut near ground level and left to regenerate from the stool. Pollard – a tree cut once or repeatedly at a height above that at which grazing animals could reach the regenerating shoots. Usually cut on a semi-regular basis, with the whole or a part of the crown removed. (Read 2000) preserved in farmland, the parklands of mansions, or in royal forests, where they are a unique remaining component of the historical landscape, e.g. in England or Southern Sweden (photos 110, 111). The decay and rot in these often very old field 'veterans' retain the valuable biological legacy once found throughout the ancient forests. Thus, these trees are such a crucial component of the landscape that they require protection and management to permit them to persist as long as possible. However, in addition to maintaining the old trees, continuous efforts need to be taken to develop a reservoir of replacement trees through the successional sequence. But, might it already be too late? Will the younger rotting trees that will replace the hundreds-of-years-old veterans as they eventually die be capable of supporting the array of organisms found in the old trees?

A. Bobiec

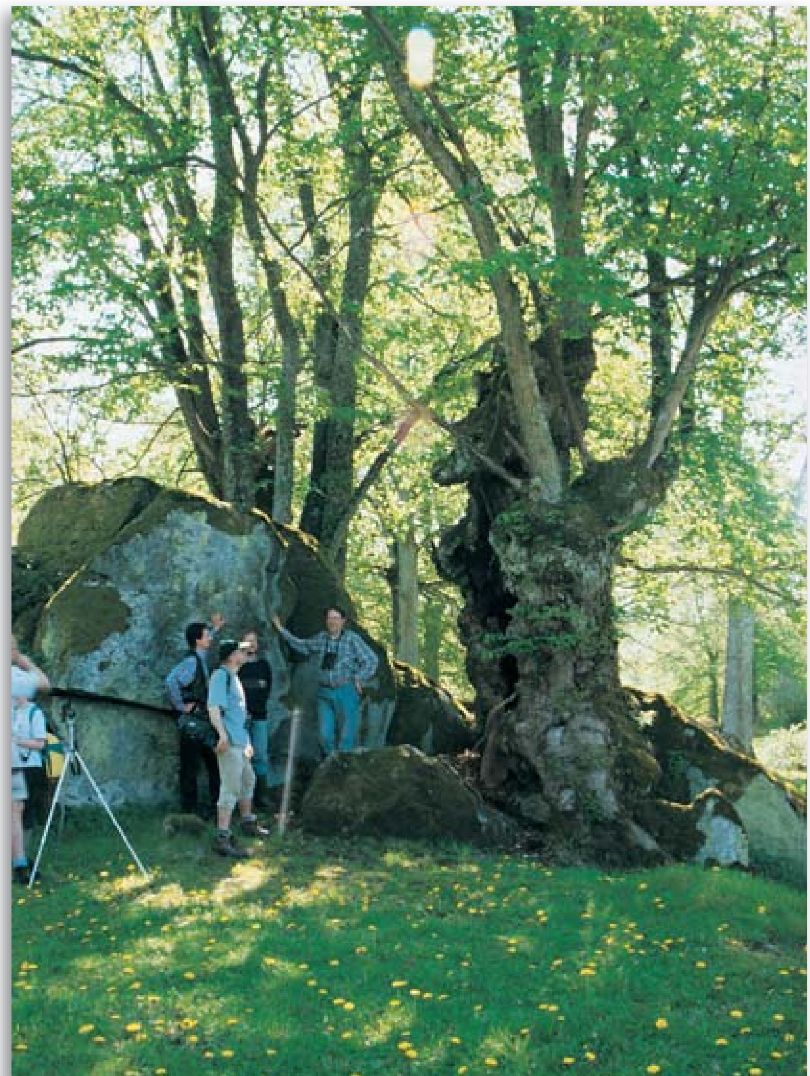
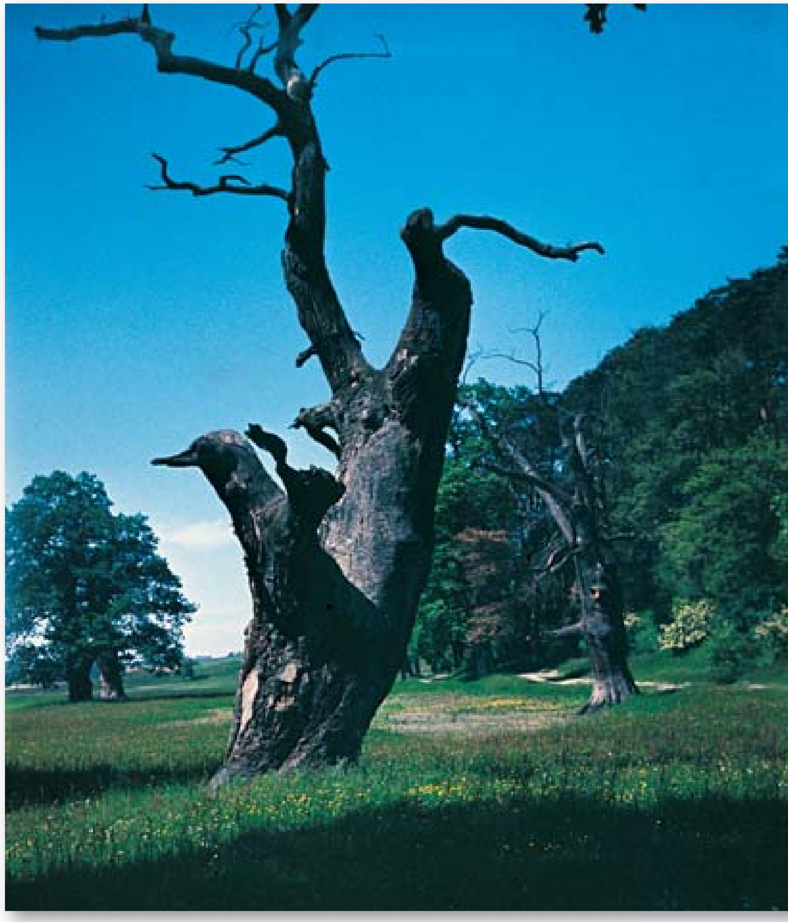


Photo 110. Rot and wood decay beyond the forest boundaries – a mountain elm, a Swedish 'veteran'

Photo 111. A dead oak in Rogalin; western Poland



J.M. Gutowski

"Management for decadence"

"Management for decadence" is an approach intended to enrich the variety and quantity of CWD in forest ecosystems. Ecological studies, in particular those that have examined the population dynamics of rare invertebrates, often show that even immediate cessation of dead wood removal does not maintain the natural biological diversity. Diminishing quantities of dead wood result in greater distances between each piece of debris. A particular piece of dead wood inhabited by insects and other organisms does not provide a suitable habitat forever. This home, that serves simultaneously as the forage base, is gradually used up, and looses the very qualities that made it suitable for its inhabitants. New occupants requiring 'older' dead wood move in, and the former ones leave and find a less decayed substrate. This temporal change in occupants is called succession, and their movement in search of a suitable habitat is called dispersal.

What would be the fate of an amphibian population inhabiting a disappearing pond if there is no alternative habitat within a distance that sufficient numbers are capable of traversing? The same challenge is posed to the occupants of dead wood. Many among them, especially those highly specialised and strictly dependant on certain sorts of decaying wood, are also characterised by very low mobility. These include, among others, many of the insects incapable of flight; the arachnids, nematodes, molluscs, fungi and slime moulds. Extension of the distance an organism must travel beyond its ability results in death. If a species requires only the largest decaying logs, e.g. in excess of 40 cm in diameter, then in a forest managed as the strict nature reserve of Białowieża National Park, it may encounter an average of 7 linear m of such substrate within a radius of 5.6 m. Once the overall CWD quantity is reduced ten fold proportionately in each diameter class, then a ten fold larger area would be necessary to find an equal amount of suitable substrate. Usually, however, the average quantity of dead wood in managed forests is far less than 12 m^3/ha (10% of the average CWD volume found in the natural forest of BNP), and is seldom greater than 3 m^3/ha. Moreover, the slash generally retained after harvest or thinning operations is comprised almost exclusively of branches rarely attaining diameters exceeding 40 cm. Under such circumstances, would a small, slow, dead wood dweller be able to find its way to a new suitable microsite?

In such instances, intervention may be necessary to help CWD-dependent species, especially those that are endangered, to colonise new substrates. Usually, such intervention consists of providing a more continuous supply of dead wood, decreasing its spatial dispersion and shortening the distances that dispersing organisms have to cover. Intervention eventually leads to the establishment of shorter and more reliable links among elements of the populations. At the sight of a decaying hornbeam log covered with numerous fungal fruiting bodies in BPN, Ted Green, a prominent advocate of veteran trees in the UK, said "we could not afford such waste." Asked what was meant by that statement (did he, perhaps, regret the "wasted" timber?), he explained that he meant "the wasted opportunity of direct infection transmission to living trees." Such a decaying log would, in English forests, be undergoing a renaturalisation programme, like yeast in bread making, but would not be an end in itself. If forest renaturalisation is not to be limited to a 'green' slogan intended only to help those with forest extraction interests acquire subsidies, it should involve revitalisation of all forest components and processes that have been extirpated, or elements marginalised by intensive forestry for the sole purpose of timber production. The exemplary activities occurring under "management for decadence" (currently being implemented by the USDA Forest Service in Washington state) include inoculating artificially scarred trees with infected wood, felling trees and leaving them in the forest (increasing the amount of CWD), girdling trees (enrichment of the ecosystem with snags), and creating nesting cavities in living trees. Note, however, that other work from the western United States suggests that girdled ponderosa pines do not function as completely as dead trees, as far as the insects and foraging birds are concerned, as do those pines killed by bark beetles which use attractant pheromones.

The installation of nest boxes to support populations of cavity nesting birds, considered to be useful in stands where "high hygienic standards" are applied, does not equate to renaturalisation. The nest box approach is analogous to the Dutch programme of establishing white stork breeding centres within landscapes dominated by intensive agriculture. In Denmark, where people are equally eager to restore storks to their landscapes, proponents wished that the return of the birds should result from the restoration of their original ecosystems. In the Dutch model, an almost immediate increase of the stork population was achieved without changing the industrial model of agriculture, whereas in the Danish approach, the addition of each pair of white storks would indicate a progressive revitalisation of the historical landscape with traditional rural communities and using traditional farming techniques. Similarly, a spontaneous recolonisation of forests by species related to the amount and quality of dead wood suggests that the function of the forest ecosystem has been improved.

If we truly desire to maintain the populations of certain species at levels which ensure their persistence, increasing the number of dead trees is important in these dead wood limited forests. Increasing the number of dead trees also needs to be applied outside of Białowieża National Park. Species that will especially benefit from increased numbers of dead trees are woodpeckers. The minimal population density of woodpeckers in BNP is 6 individuals encountered along a 1 km long transect, where, on average, 17 dead trees are found per hectare. In the managed part of the Białowieża Primeval Forest, there are only about 6 dead trees per hectare (and far fewer are retained until they fall), therefore it is necessary to at least triple the number of dead trees to reach the dead tree levels that should support the minimal population density of woodpeckers. Because of the long time spans required for trees to grow to an appropriate size and then die (those preferred by woodpeckers tend to exceed 20 cm DBH), one should consider girdling or otherwise killing selected trees to increase the number of dead trees.

Artificial infection of trees by introducing the mycelium of a saproxylic fungus *Laricifomes officinalis*, has been tested in central Poland, but only on the experimental scale of a few healthy trees. This work is a part of a series of studies on the protection and perpetuation of this rare, endangered fungus that is associated with weakened and dying larches.

Decay and rot in a forest

Despite the great importance of semi-rotten old trees growing in open landscapes to the conservation of biodiversity, it is the forest that has always supplied the richest resource of decaying wood. Isolated, solitary old trees, even if subject to intensive care, are not able to provide the diversity of dead wood (in terms of species, size, degree of decay) comparable to the CWD available in natural forests, nor are the organisms found there able to easily disperse to another isolated tree or to the nearest fragments of forests. A natural forest guarantees sustainable amounts of dead wood and resilience of the remainder of the forest components as well as the entire forest. Such forests are extremely rare today. The Ministry of Forests of British Columbia (Canada), in a recent (1993) monograph on dead wood, concludes that the BPF is the only 'natural' forest remaining in Europe.

5.2 DEAD WOOD AND CONSERVATION

The presence of organisms associated with dead wood, in particular the specialists that cannot exist without dead wood, is, as has been mentioned before, a reliable indicator of the 'naturalness' of forest ecosystems. Many of these species are rare and endangered, so their conservation is of paramount importance in the maintenance of the biodiversity of forests. Therefore, from the viewpoint of maintaining all of the species in forests, the more decaying wood in the forest, the better. Studies in Bavaria showed that forest species richness is positively correlated with the number of dead trees, and that areas with greater amounts of dead wood supported more species listed in the red book of endangered species than areas with lower amounts.

Contemporary plans for the protection and management of most natural areas now tend to consider the need for dead wood, and some action plans actually set targets for acquiring and maintaining adequate stocks of CWD. In the Abernethy nature reserve in northern Scotland, the tops of selected old pines are shot off to produce a suitable number of snags to improve the breeding habitat of the crested tit. In nature reserves in Great Britain and the Netherlands, girdling and felling living trees and leaving the logs in place have become common techniques to increase the amount of dead wood. While these examples address quantities of dead wood, there is an increasing awareness that the "quality of decaying dead wood may be even more important than its quantity," and the successful conservation of biodiversity requires planning and management for the diversity of forms and sizes and degrees of decomposition of wood, including large logs and standing dead trees. While this premise is gaining support in many countries, it has not yet been accepted in Poland. Policies relating to conservation in the protected forests of national parks and nature reserves are still constrained by the concerns that dead wood is a threat to the forest.

The forests of national parks remain subject to the procedures stipulated by the *Instruction of Forest Protection*, which are applied to all managed forests. The only exceptions are the forest fragments that are designated as strict protection areas (where interference with natural processes is not permitted) or 'passive protection' areas (where intervention has not been permitted in the 20 years following the initiation of the protection plan). However, 'moderate pest control' is still practised as part of 'reserve management' in Polish national parks. Such control is applied through 'protective activities,' described in the *Instruction of Forest Protection* and recommended by the Forest Protection Taskforce, a group responsible for developing adequate 'hygienic standards' for managed forests. Passive preservation, precluding the extraction of dead wood, is applied to a mere 22% of the acreage of Polish national parks, and is still perceived as "a risky scientific experiment". Similar activities are taking place in numerous nature reserves (only 2.6% of the acreage of Polish reserves is designated for strict preservation); removal of dead and dying trees, snags and uprooted trees is often considered part of the standard measures of 'active nature protection.'

Fortunately, the attitudes about retaining dead wood have been undergoing a slow positive shift and more positive regulations concerning the management of dead wood in protected areas are beginning to appear. Although it is not yet a universal rule, plans for protection now include recommendations for retaining certain or all of the cut trees throughout their decomposition process. This policy approaches that of active protection or restoration management. Despite this change in management philosophy, there are still many national parks whose managers continue to thoroughly remove dead and dying trees, thus eliminating those components of the ecosystem that perhaps are most deserving of protection.

In some countries, most of the educational trails in protected forests already contain information describing the function and importance of dead wood to the forest. However, in other countries, this topic is often ignored even in the nature education programmes conducted in national parks. As a result, the understanding of the ecological role of decaying wood by many societies is very weak and the sight of snags and uprooted trees is still often perceived as "a mess in the forest" and "a proof of improper and wasteful management."

Gaps in conservation education and a low level of ecological awareness in society are closely connected. Is it possible to expect to have accurate and reliable nature education in a society where natural phenomena are nearly always prevented from operating in the forest and fought using 'pest control' remedies? Should we be surprised when the strict nature reserve of BNP – the greatest example of nature conservation in Poland and the largest and oldest protected forest in Europe – is often still called "a graveyard of trees?"

The way in which dead wood is perceived by the public focuses, like a magnifying glass, on their general perception of nature and its overall protection and perpetuation. We acknowledge that nature, together with all its components, processes and dynamics (including tree death and decay), has great value and deserves protection. It is not appropriate to speculate on the number of trees that ought to be left to die 'naturally' and to decay completely in the protected area. Our task is to conserve NATURE, as a whole, and nature then 'decides' how the natural processes play out and numbers and kinds of properties which emerge. If such a vision is to be successful, it is crucial to identify the acreage necessary to permit the processes to function properly at the appropriate temporal and spatial scales in order to restore a dynamic equilibrium in the forest. As a system becomes more complex and spatially variable, a larger area will be needed for the system to function properly.

Experience shows that we are much more eager to ASSESS nature and apply utilitarian criteria, than to ACCEPT the properties that emerge from the interactions of the forest and the natural processes that evolved over millennia. Therefore, we EXPECT the natural forest to grow 'high quality' trees, to have no 'pests,' and for its stands to accurately reflect the compositional norms defined by the *Principles of Silviculture* or the *Protection Plan*. If a given stand differs from our expectations, we conclude that "nature cannot manage," or that "it needs our help," especially today, with the evident magnitude of human-induced environmental changes (air and water pollution, climatic warming, etc.) that affect forests. And yet, the spontaneous changes in forest stand composition (e.g. expansion of broad-leaved species at the expense of spruce) in the regions of Europe that are most heavily impacted by industrial development and resulting pollution, is proof of the great resilience and robustness of nature! Is the stress of modern atmospheric contamination currently influencing the forests of northeastern Poland more severe than the stresses produced by climate change during the so-called 'Little Ice Age' of the 17th and 18th centuries and its subsequent decline?

The booklet *National Parks in Poland* (published by the State Board of National Parks, Warsaw 1999; also later editions), mentions among "the major threats to the national parks" the erosion of the sea coast (two intended national parks are supposed to protect the natural Baltic coastline), game overpopulation (22 out of 23 NPs), poor forest health caused by abiotic and biotic factors (8 NPs), and insect outbreaks and windblow. What has created the shifting sand dunes and formed the high coastal cliffs if not the erosion of the sea coast by wind and water? How does one diagnose "the overpopulation of game animals" if not from observations of "damage from game" in plantations, which is largely an artefact of management? How do indigenous insects and windblow, two fundamental processes that contribute to the dynamics of natural forests, threaten national parks?

Similar 'threats' are traditionally listed in both the provisional, annual protection tasks and the long-term protection plans for national parks (prepared for a period of 20 years). "Removing dead, uprooted and broken trees" is still perceived in many parks as a tool to reduce or prevent the threats to forests, despite attempts to allow foresters to retain some of the dead trees as long as they do not threaten the stand's viability.

With such a limited view of the necessary components of forests and the obvious concern about the economic value of stands, the suggestion to retain a limited number of dead trees in a forest is not enough.

In summary, it is critical that the amount and quality of dead wood (species, diameter, degree of decay) and the continuity of its input become recognised as some of the most crucial elements in forests which must be retained. The amount and quality of dead wood should also become criteria for the evaluation of the degree of success in protecting forests, and monitoring dead wood should become a standard procedure used by the conservation service (APPENDIX I). The monitoring of CWD dynamics as a surrogate for the dynamics of a stand may become a basic source for information about the processes, trends and progress of succession either in natural stands or managed stands where intensive management is terminated.

Species protection of animals, plants and fungi

The list of protected species in Poland, based on the Species Protection Act of 2004, covers slightly more than 1% of the Polish fauna. Only one fourth of this list represents invertebrates, mainly insects.

As many of the protected species are dependant on dead wood, the regulations could provide a legal basis to enforce the protection of their habitats, including the dead wood component. For instance, many endangered and beautiful beetles develop in decaying wood. These include the hermit beetle, *Ceruchus chrysomelinus*, lesser stag beetle *Dorcus parallelipipedus*, *Buprestis splendens*, *Phryganophilus ruficollis*, *Tragosoma depsarium*, *Ergates faber* (fig. 36), *Pseudogaurotina excellens*, *Stictoleptura variicornis*, *Leptura thoracica*, great capricorn beetle (photo 51), capricorn beetle *Cerambyx scopolii* and *Leioderus kollari* (fig. 37). Further species are the rare *Cucujus cinnaberinus* and *C. haematodes*, *Pytho kolwensis* (fig. 27) and *Rhysodes sulcatus* (fig. 28), all of which live under the bark of large, standing or lying trunks. The ground beetles (more than 30 species, photo 36) and *Calosoma* (5 species) winter in the partly decayed wood of stumps and logs. Several species of amphibians (spotted salamander, photo 20, and newts) and reptiles (lizards and snakes) find temporary refuge in logs and stumps under bark still slightly adhered to rotting wood. Finally, dead standing or fallen trees and shrubs provide forage, refuge, hideouts, and nesting and breeding sites to numerous birds and mammals, many of which are on the protected list, including all of the species of woodpeckers (photo 22), owls (photos 23, 24 and 25), shrews, bats, squirrels and dormice.

Figure 36. *Ergates faber* occupies insolated stumps, snags and the lower parts of large dead pines (M. Waszkiewicz)

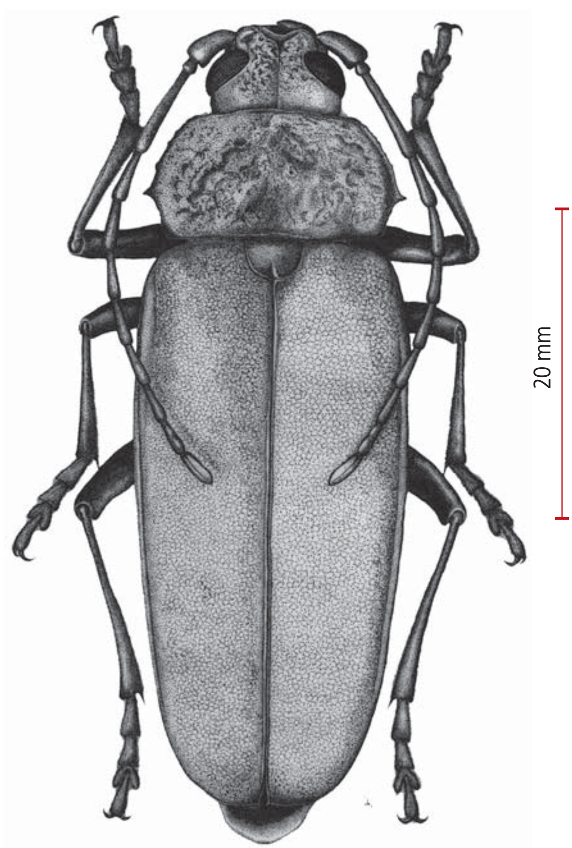
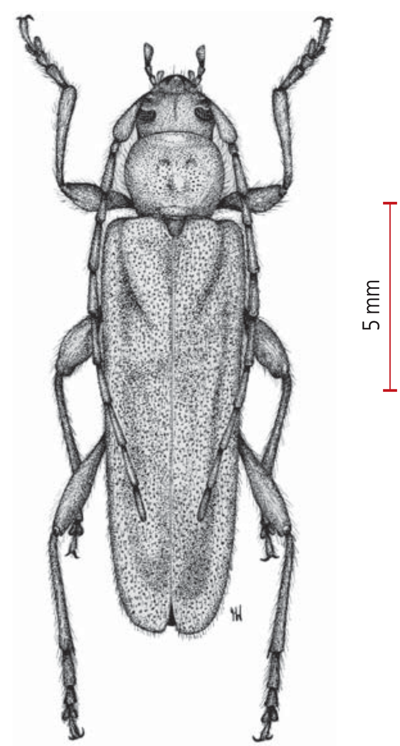


Figure 37. *Leioderus kollari* – a very rare species associated with old maples (after GUTOWSKI 1988)



It is worth mentioning that the hermit beetles, *Boros schneideri, Rosalia alpina* and *Pseudogaurotina excellens*, the stag beetle *Lucanus cervus*, *Buprestis splendens*, *Cucujus cinnaberinus* and *Pytho kolwensis* are not only protected in Poland, but are also recognised in other parts of Europe as species of importance. The presence of these species, as well as the status of their populations, are the criteria considered when designating areas for the pan-European network of Natura 2000. The hermit beetle, *Rosalia alpina* and *Pseudogaurotina excellens* are considered to be priority species, meaning that any landscape where substantial populations of these species are found will be required to join the network. The Network and its protection of species and their habitats is promulgated by the European Union, and the conservation of these species' habitats has priority over any activity except the protection of human life and health.

The list of protected animals in Poland is relatively short and does not include many of the endangered and declining species of invertebrates. Such species are, however, listed in the 'red books' of endangered species. In many groups of invertebrates, 30-40 percent of the species are sufficiently endangered or declining to appear on the red lists, and should be provided legal protection. Among the taxonomic groups comprising the saproxylic species, the percentage of endangered animals is even higher, therefore protection of dead wood should be of the highest priority among the activities designed to conserve forest biodiversity.

Many fungal species that are considered rare in Poland, are dependent on dead wood. They include the scarlet cup (photo 75), *Fomitopsis rosea* (photo 87) and *Pycnoporellus fulgens*. For certain rare species, such as *Schizopora paradoxa*, *Stereum subtomentosum* and *Xylobolus frustulatus* (photo 112), the Białowieża Primeval Forest is either the only location where they are found or a unique location where they are locally abundant.

K. Zub

Photo 112. The fungus *Xylobolus frustulatus* on an oak log

K. Zub

Photo 113. *Grifola frondosa* at the base of a living oak

Of the fungi living on trees, there are a number of strictly protected species including *Grifola frondosa* (photo 113), *Hericium clathroides* (photo 114), *Hericium coralloides*, the hedgehog fungus *Hericium erinaceum*, *Lariciformes officinalis*, the giant polypore *Meripilus giganteus* and *Polyporus umbellatus* (photo 69). All other fungi in Poland, including species related to decaying wood, are subject to partial protection, meaning that neither their fruiting bodies nor their biotopes are permitted to be destroyed. Interestingly, picking mushrooms for culinary purposes (except for the strictly protected species) is not legally considered to be destructive.

K. Zub

Photo 114. *Hericium clathroides*, a strictly protected species in Poland

Witnesses to the past – relict species in the Białowieża Primeval Forest

A number of non-vascular plants and fungi are found only in the primeval forests of BPF, especially in the national park. We call them relics or relict species because they are species that used to be widespread throughout the European lowlands, but have become rare and endangered as their habitats declined. The rare and endangered status of these species was determined by CRYPTO, the project focused on fungi and sporophytes and concucted in the BPF. These organisms were classified into the relics of the primeval forest (bryophytes and lichens) and apparent primeval relics (fungi)*. There are sixty-three species of relics and many of them are closely associated with dead wood.

Bioecological groups of the primeval forest relics in the BPF (after CIEŚLIŃSKI et al. 1996, modified)

Taxonomic group	Total number of species	Primeval forest relics		Epixylites	
		Number of species	Percentage of species	In general	Exclusively on dead wood
Liverworts	41	7	17	6	2
Mosses	104	13	12	7	-
Lichens	164	43	26	15	6
In total	**309**	**63**	**18**	**28**	**8**

The liverworts are strongly associated with dead wood. One liverwort, *Anastrophyllum michauxii*, is known only from the BPF in the Polish lowland.

Of the 35 relics, 13 fungus species are unquestionably relics of primeval forest. Almost half of them are fungi associated with dead wood (a total of 16 including 7 relics of primeval forest). This group includes *Fomitopsis rosea* (photo 87), *Hericium clathroides* (photo 114), *Exidia pitya* and *Phleogena faginea*. In addition, the fungus *Tubaria confragosa* is associated with the dead wood of deciduous trees, and *Rhodotus palmatus,* which occurs on elms in riparian forests, should also be numbered among the relics. Both appear to be quite rare; *T. confragosa* was recently discovered and in Poland, is only known from the BPF, whereas *R. palmatus* was recorded in the area surrounding Elbląg (northern Poland) a century ago but is now found only in the BPF.

The fauna of the BPF includes numerous saproxylic species that are also considered to be primeval forest relics. Most of these relics are animals that depend on dead wood rather than those that live on living, healthy trees or on herbs. A listing of these species for the BPF has not been made. However, we can safely say that among the 119 longhorn beetle species found in the BPF, 46 are relics

* The current status of mycological knowledge does not allow us to describe the ecological character of many fungi with certainty.

of primeval forests, e.g. *Tragosoma depsarium*, *Evodinus borealis* (photo 47, fig. 24), *Acmaeops angusticollis*, *Alosterna ingrica* (photo 46), *Pedostrangalia pubescens*, *Stictoleptura variicornis*, *Leptura thoracica* and *Lepturalia nigripes*. Similarly, among the 45 species of jewel beetles living in the BPF, 13 are considered relics. These include *Dicerca berolinensis* and *D. moesta*, *Eurythyrea quercus*, *Buprestis splendens*, *Chrysobothris chrysostigma* and *Agrilus pseudocyaneus* (fig. 18).

As nearly all vertebrate animals can adapt to modified environments to some extent, it is difficult to distinguish the true relics of the primeval forest from other species existing there. However, the behaviour of a number of animals indicates that they are well adapted to the environment of the primeval forest. Examples include some of the many birds that nest in the BPF. Many species that are commonly found in open environments, such as the buzzard and wood pigeon, feed almost exclusively under the forest canopy in the BPF. The swifts, typically known in Europe as urban dwellers, build their nests in the hollow cavities of tall trees in the deep forest. Many species that usually build open nests can also utilise cavities where they are available, especially in the natural forest. These birds include the blackbird, robin and dunnock. Another behaviour that is usual in natural forests is using uprooted trees and snags as breeding sites. A typical species that nests on the tops of tree snags is the great grey owl, which generally occurs in Northern Europe, but is regularly observed in the BPF.

Some mammals also exhibit characteristics that could be considered 'relict.' Racoon dogs in managed forests winter in dens dug in the soil, whereas, in the BNP, they usually winter in large fallen logs with hollows large enough to contain the animal. Similarly, pine martens, polecats and weasels often use standing dead trees, snags and fallen logs as hideouts. In North America, many members of the weasel family also use dead trees and fallen logs throughout the year. When the forest floor is covered with snow, exposed logs and branches provide an entry point to openings beneath the snow where prey species can be found. One of the bat species, *Myotis brandtii*, generally thought to exclusively inhabit buildings, has been seen using tree hollows in the BPF.

Obviously, the white-backed woodpecker, pygmy owl and European bison should definitely be numbered among the relics of the ancient forest and woodland landscapes. Both the woodpecker and owl use cavities or hollows in old or dead trees that are rare to non-existent in managed or younger forests. The European bison is characteristic of a historical landscape mosaic that contained patches of closed forest mixed with other patches of more open woodland and herbaceous vegetation. This sort of mosaic, perpetuated by the natural disturbance processes acting on the landscape, is not generally part of the modern managed landscape.

5.3

FIRE: AN ALTERNATIVE MECHANISM OF REDUCING DEAD WOOD TO ITS COMPONENTS

Dead wood is a natural and essential part of a functioning forest, however gaining an understanding of how much dead material is necessary depends on the actual processes that mineralise dead wood to its constituent parts and the rates at which these processes operate. Forests appear to be arranged along a continuum from those where decay is the primary process that reduces wood, to those where fire is the dominant process. Our intent here is to briefly discuss where these different forests are found, describe some of the differences in historical management that have led to the dead wood levels that exist today, and explore how dead wood resources may differ in quantity and quality in forests operating under these two radically different processes.

Decay and reduction by invertebrates, fungi and micro-organisms is a key process that reduces dead wood. The rates at which decay reduces dead wood vary with temperature and humidity; if conditions are warm and humid, decay moves at a much more rapid rate than if conditions are cool and dry. Fire is another key process that reduces dead wood albeit in a very different manner than does decay (photo 115). The rate at which fire reduces dead wood is also dependent on humidity and temperature variables; fires are more likely to burn when conditions are warm and dry than when they are cool and moist. For fire to be a player in the dead wood process, ignition also needs to take place.

Decay driven forests are scattered throughout the world in areas where rainfall tends to be relatively high or relatively well distributed throughout the year especially in summer. Such forests can be found along parts of the west coast of North America, much of eastern North America, large parts of Europe, the rainforest zones of South America, Africa and Asia, and in the temperate southern zone, including Tasmania and New Zealand. A good example is the coastal mixed coniferous forest in western North America, dominated by Douglas-fir. These forests tend to remain moist throughout much of the summer, promoting decay and reducing the potential for fires to ignite and spread. Fire driven forests are rather more typical of Mediterranean climates which tend to have hot, dry summers, such as areas around the Mediterranean Sea, the Pacific coast of northern Mexico, California in North America, parts of the Chilean coast of South America, and parts of Australia, or places in the interior of continents where summers are very dry either due to rainfall patterns or rain shadow effects from mountains, like much of the western part of the North American continent. A good example of a fire driven forest is the eastside pine forest of western North America. These forests tend to have frequent fires that consume much of the existing dead wood yet also create new dead wood. Thus, fire truncates the decay process but the length of time wood decays until it burns seems to be quite variable and is to this day not well understood as historic fire

A. Bobiec

Photo 115. The post-fire landscape in Yellowstone National Park

regimes have been substantially altered. It must be recognised, however, that these are simply generalisations and that the decay vs. fire relationship is likely to be a continuum rather than discrete classes into which forest types may fall. Furthermore, these relationships are likely to change with changes in topography, elevation, soils and climate.

Dying and dead trees, and the various forms of logs that are derived from these trees, have been, are, and will always be a controversial subject. Their value to functioning forests and organisms such as fungi, insects and vertebrates is unquestioned. However, dying and dead trees and logs can also be a hazard, provide fuel for fires, and provide a habitat for organisms whose activities may conflict with some management objectives. Given these trade-offs, the issue today is not so much whether or not dead wood should be left in the forest, but rather how much should be left or maintained and where.

Historically, dead wood was used as a fuel, removed from the forest if it was still merchantable, or burned in place. In some U.S. forests, there were targets for the removal or burning of dead trees. In others, dead trees were simply dropped and left as logs. Dying and dead trees, when still suitable for lumber, were often removed singly to preserve their value. In U.S. National Parks, dead trees were generally left unless they were a hazard (e.g., standing close to roads or buildings) and then removed.

On many managed lands, both privately and publicly owned, dead wood has become one of the legitimate objectives in forest management along with the retention of large trees and certain other forest values including plant and animal species of concern. Today, on private lands, some dead wood is often left on intensively managed sites and even more is left in areas where companies do not wish to remove it or are prevented from doing so by regulations. On most Federal forest land in the United States, the majority of the dead wood is left unless it was created from a massive mortality event covering many hundreds if not thousands of hectares. Then, the salvage of many of the trees is often permitted, but what is thought to be a sufficient number of dead trees is still left in place. In some locations where dead wood volumes are considered excessive, homeowners are often permitted to remove dead wood for heating fuel, and campers often use dead wood within and adjacent to campgrounds for their campfires. In many parklands, most dead trees are still left in place. These shifts in perception, from that of not too many decades ago when dead trees were thought to be bad for the forest, and when science was responsible for managing woodland based exclusively on tree establishment and growth research, are a very positive step forward. While still not all forest managers embrace this management philosophy, the trend is a positive one. However, while the direction is indeed positive, additional research is needed on dead wood processes to support this change in management philosophy.

There is still great debate about how much dead material ought to be left in the woods. Many snag and log guidelines have been prepared, but they tend to be based on our knowledge from today's forests which appear to be generally free of fire, at least for long periods of time, and thus depend largely if not entirely on the decay process to reduce dead wood. As such, these guidelines may not reflect what is sustainable in forests where fires were historically much more frequent and tended to reduce dead wood at times long before the decay process was complete. The guidelines also seem to believe that snag and log numbers are independent of the living components of the forest, rather than regarding them as products of a tree's existence: becoming established, growing, and dying across spatial and temporal scales. Some current snag and log targets seem not to be sustainable in many forests, that is if all of the forest processes are operating as they did historically.

In forests where decay is the primary wood reduction process, and in fire-driven forests where the forest structure has not been excessively altered by decades of fire suppression and climate shift, removing dead trees because they are going to waste or harbouring insects that may injure the forest is largely inappropriate. Such mortality, degradation and decay of trees is to be expected and ought to be permitted in forests that are designated to remain in a more or less natural condition. The risk related to CWD removal is evident from the analyses presented in the former sections of this book.

However, in forests that were historically frequently visited by fire, fires may since have reoccurred as frequently as once a decade. In these forests, the increasing number of trees and the resulting cascading increases of dead wood (caused by episodic drought coupled with stand densities in excess of what can be sustained) in the absence of fire for long periods may be largely unnatural. This large fuel base may contribute to larger and more contiguous areas of nearly 100% tree mortality when a fire does return (photo 115), whereas under the historical fire regime, areas of such high mortality are thought to have been rather small and distributed relatively widely through the burned area where the severity of the fire was generally much lower.

Under these conditions, it may be appropriate to remove many of the dead trees to reduce the potential of a very large and possibly catastrophic wildfire. Unfortunately at this time, our understanding of how much dead wood should remain in these fire frequent forests is very limited and much more research is needed. Furthermore, the resulting answer will be highly dependent on variables including forest composition, soil characteristics and geo-topographic variables such as elevation, prevailing wind direction during the fire season, slope, aspect and proximity to water.

Another critical issue in the management of dead wood is the distribution of the material, both in terms of quantity and quality, over space and time. The existing dead wood guidelines generally do not recognise the spatial variation in the forest's capability to sustain dead wood quantities, nor the nuances between forests that are generally dependent on decay for reducing dead wood to its constituent minerals and forests where fire historically has truncated the decay process.

In fire-prone forests, prescribed fires burning at the "proper time" of year consume much of the dead material, and wildfires are also successful at removing dead wood. But fires, whether prescribed or wild, often create new dead wood. Generally there are some hot spots in most fires where some trees are killed. In forests that have gone long without fire, the build-up of fuel, both in the form of snags and logs, and the deposit of duff and other material (e.g., needles and exfoliated bark) conspire to kill trees, and sometimes these are some of the oldest trees in the area (in some instances, the mortality of old trees does approach 100%, albeit in relatively small scales of up to a few hectares).

The future of forests is also part of the debate. Following large mortality events [e.g. large forest fires over large areas (in 1,000s of hectares) of high tree mortality], leaving all of the dead material on the site could easily, in the next burn, jeopardise all or large parts of the re-established forest. Furthermore, large amounts of burned CWD often change the structural and perhaps chemical composition of the soil, rendering it water repellent, increasing erosion, and not permitting water to recharge the soils in such areas for years if not decades.

So the debate continues. Today it is not so much whether dead wood ought to be left or removed in the forest, but more about the amounts and distribution of what ought to be left relative to the natural processes that drive the reduction of dead wood (whether decay or fire is the dominant wood reduction process), and the rational balance of the competing values (e.g. biodiversity, lumber, safety, reducing the potential of catastrophic wildfire) on the local or regional scale.

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Summary of Chapter 5.

Dead wood is inseparably associated with the primeval forest. However, the basic tenet of forest management is still 'forest protection,' interpreted as the protection of trees against harmful abiotic and biotic factors, including natural biotic agents such as spruce bark beetles. The retention of dead wood and dying trees is still considered to be a threat to the life and health of living trees, reducing their commercial value.

Despite the increasing interest in dead wood and its crucial importance to ecological processes and organisms, both the Polish forestry commission and a substantial part of the Polish national parks administration perceive dead wood as a threat to the health of forests.

Ignorance of the importance and crucial role of dead wood in the forest ecosystem makes the 'concessions for biodiversity' symbolic and incapable of stopping the degradation of forests and their important components.

In many countries, special measures are undertaken to increase the amount of dead wood in forests. These measures are intended to perpetuate the presence of dead wood in the ecosystem, which is in turn necessary to perpetuate the processes inherent to dead wood and the many species that are dependent on it.

The restoration of the biological richness of natural forests, which has been lost in large areas of forest now managed without dead wood or old trees, will not be possible unless effective protection is extended to all remnants of primeval forests.

Because of the crucial role of dead wood as a basic and irreplaceable component of forest biodiversity, the protection of the patches of remnant natural forests needs to be considered as inseparable from the efforts towards protection of dead wood and restoration of the forest's natural stock.

The volume and quality of dead wood (species, diameter, degree of decomposition) and perpetuation of its "supply" is an important criterion when assessing the efficacy of nature conservation in forests.

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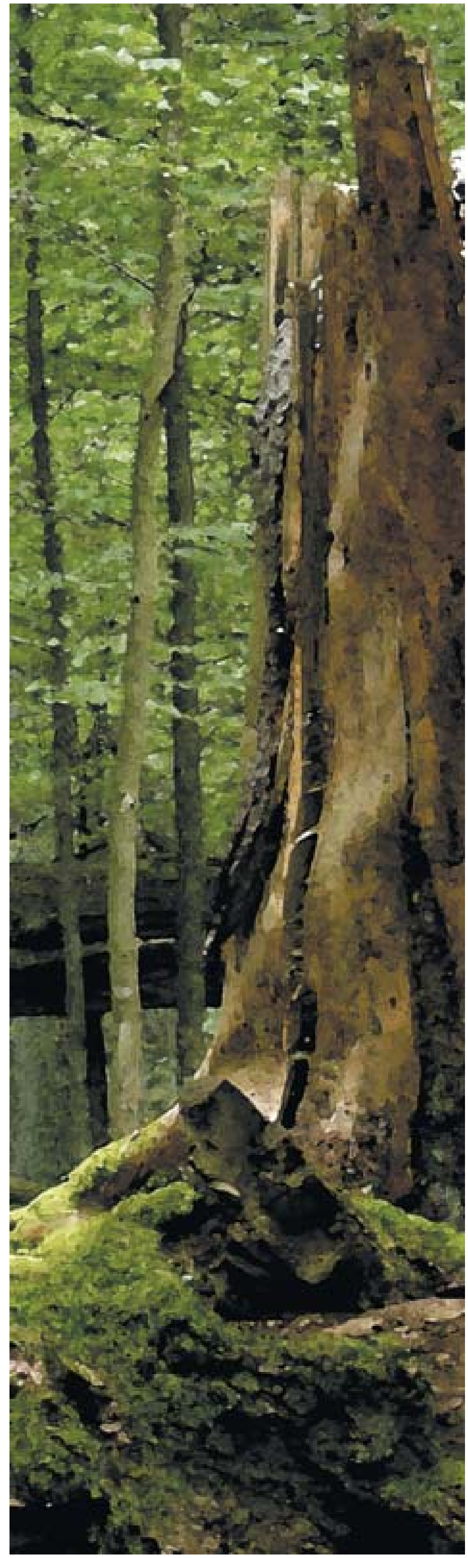
Chapter 6



DEAD WOOD IN SCIENCE AND THE ECONOMY

An object of scientific studies

Even a decade or so ago, hardly anybody cared about dead wood or its role in the ecosystem. As wood was mostly considered a commodity, 'wood science' was focused on ways to process and use wood and on its value to the economy and society. In recent years, however, scientific interest in decaying wood has been increasing. Numerous studies have been carried out to develop the most suitable procedures for the assessment of quantities and the various kinds of CWD, to detect its spatial patterns at local and larger geographic scales, to understand its association with forest type and developmental phases of stands, to learn about its dynamics both temporally and spatially, and so on. In addition, research focussed on the role of decaying wood as habitats for various groups of organisms is skyrocketing, and is reflected by the hundreds of new publications emerging annually in both scientific and popular journals. Many researchers devote all of their time to study the puzzles associated with dead wood. In addition to saproxylic organisms, numerous B.Sc., M.Sc. and Ph.D. dissertations cover CWD. We could say that after many years of underestimating or even disregarding dead wood, a new era has come into being; an era of proliferation of studies on dead wood and the application of results to land management and conservation issues.

We would like to outline one of the many subjects studied in this field. There are strong reasons to expect that research on saproxylic fauna could provide crucial information that would help improve our understanding of the processes underlying these animals' evolution. It is well known that the most primitive groups within numerous taxa (tribes, families, orders) are saproxylic. If we want to track the course of development of primitive characteristics within particular evolutionary lines, we should focus our attention on the animals living in CWD.

Wood, particularly that found in higher latitudes and elevations, should be perceived as indispensable 'chronicles' of environmental change that are recorded in the 'code' of tree rings. Environmental changes that can be inferred from tree ring patterns include global patterns such as climatic shifts, and local dynamics driven by disturbances. Dendrochronology, the science of detecting and interpreting common patterns in tree ring sequences, allows inference of environmental changes back to the Middle Ages or earlier. Dendrochronology can be applied to both living and dead trees as well as to old wooden artefacts, such as rafters, timbers and other wood in old buildings or even specific woodwork in old churches. The wood of both living and dead trees in forests affected by fires can record accurate data on the years and frequency of fires occurring in those forests. For instance, the studies of well preserved fire scars in pines and other trees can help us understand the disturbance regimes driving coniferous forest ecosystems in Scandinavia, taiga ecosystems and western North America.

The pharmacological exploration of dead wood and the organisms associated with it may result in the development of useful medicines. The possibilities of exploiting unusual bioactive capabilities in fungi living on dead wood are being thoroughly tested by the pharmacological industry and hopefully, new and powerful therapies will be developed.

Dead wood as a 'commodity'

A survey recently carried out in the Białowieża Primeval Forest showed that, among the seven purposes of tourist visits (social, recreational, seeing the natural forest, encountering bison, learning about forestry, scientific, other), "seeing the natural forest" was the primary objective for an overwhelming majority of respondents (*Tourists in the Białowieża Primeval Forest: Who are they, why do they come, how do they perceive us?* TOPB, Białowieża, 1999). This result supports the need to provide nature education in the Białowieża National Park (APPENDIX II). Visitors are eager to experience what is most valuable and most available in the BPF – the natural forest. It means that we do not need to 'create' the focus of interest, because most tourists expect to see the forest and its constituent parts. Thus the major task of education in the BPF is to provide an adequate display to 'sell' the naturalness and 'primevalness' of the forest that are the primary reasons for visits to the area. Primevalness is a commonly recognised, intuitive attribute of the forest, even if the actual characteristics of 'primevalness,' such as the uprooted trees creating impenetrable 'jungles' or the huge decaying trunks, hiding the mysteries of the primeval forest in their hollows, themselves are not noticed (photos 3, 15, 109).

In addition to the European bison which is a symbol of the forest and of the national park, the major attraction that must be seen while visiting Białowieża is the Jagiełło Oak, a powerful symbol of Poland's history and culture which can be found only a short hike into the forest. Many of the visitors when actually at the famous oak, are convinced that it is but a heavily decayed log. People appreciate the embellished stories told to them by local guides about the brave king (Władysław Jagiełło) who rested in the shade of the tree in 1409. If the oak had grown outside of the national park, it would have shared the fate of so many other old oaks and would have been cut and sold for a good price. But would that have been a better 'deal' than leaving the famous 'rot' so it could keep 'producing' for tourists decades after its death? How many groups and individual tourists beheld 'Jagiełło' standing in front of that dead log? What was the contribution to the income and perhaps profit of tour operators, travel agencies, etc.? How many pictures portraying the oak have been published in books, booklets and postcards? And yet, this is only a single log, and not even the largest one in BNP.

However, its romantic story and linkage to Poland's history and culture makes it a sight worth visiting. How many other equally interesting legends could make trips to the Białowieża Primeval Forest and other natural areas more exciting for people with little interest in the natural world!? Since Jagiełło, almost every succeeding Polish monarch hunted in the BPF. In the 19th century, the BPF was a focus of the military activity of Polish insurgents against Russian rule. Could the atmosphere of those days be well portrayed without a large amount of dead wood? And yet, it is not only about 'decoration.' In fact, in these values we are 'buying' only the external 'packaging' of dead wood, painted with our own sense of aesthetics and imagination. But what about its very content? What about the genuine 'product?'

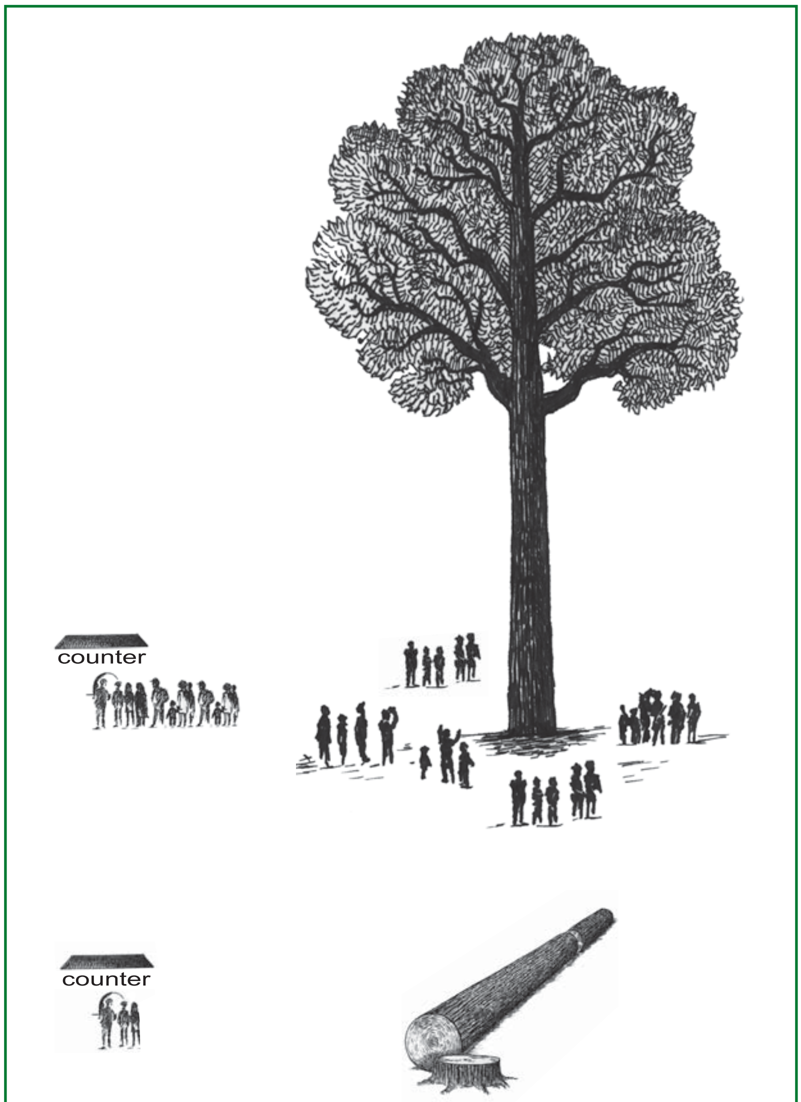


Figure 38. Sell the tree once or let it continue to 'earn'? (M. Bobiec)

M. Czasnojć

Photo 116. Trees falling into the beds of forest streams alter the channels and flow rates of stream environments, The Płociczna river in Drawieński National Park

Photo 117. Amazing forms of fungi are often found on dead wood

J. Walencik

M. Czasnojć

Photo 118. One of the last locations in Poland where one can still observe the processes of death and decay of old trees in beech forests, Radęcin reserve in Drawieński National Park

Photo 119. Dead wood improves the aesthetic appeal of a forest

J. Walencik

J. Walencik

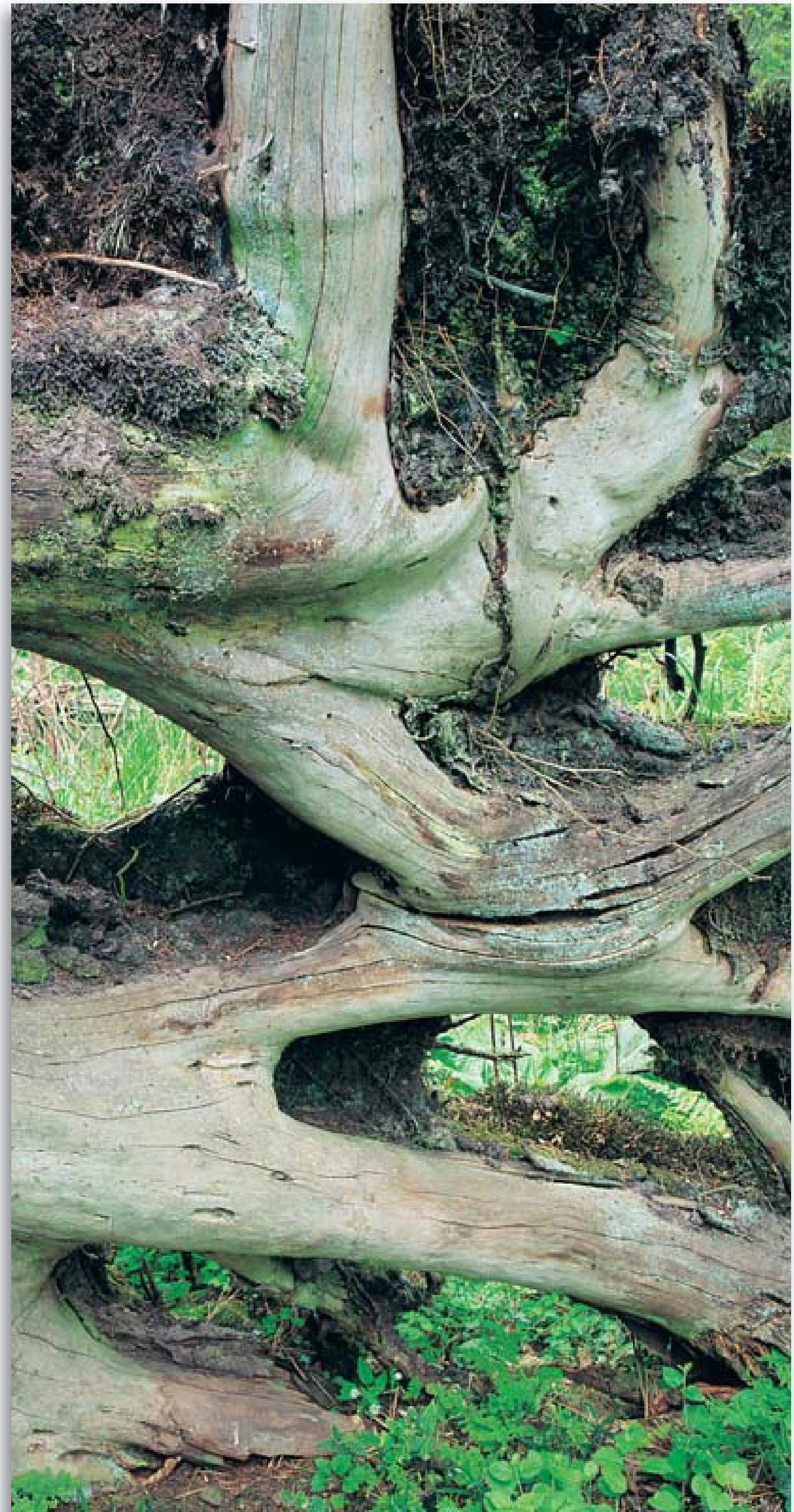


Photo 120. Dead wood improves the aesthetic appeal of a forest

A. Bobiec

Photo 121. "A dead wood museum" – the cheapest museum

Dead wood, as with other sophisticated, luxury goods, requires a suitable form of presentation and very knowledgeable and professional advertisements to entice a demanding and sophisticated 'customer.' Successfully 'selling' dead wood (fig. 38) means fully displaying its species and microenvironmental richness and presenting the functions it provides to the ecosystem. There may well be a variety of ways to 'sell' dead wood. Has anybody thought of constructing an interpretative dead wood trail (photos 117, 118, 119, 120, 121); a living 'museum' of dead wood? A paradox? Not at all, because dead wood is not truly dead, but is in fact more alive and dynamic than the wood of living trees (much of which is scarcely either alive or dynamic)! Such a 'museum' might include a special trail leading between examples of the various phases of decay, showing some of the variety of CWD functions in the ecosystem. Trail brochures and signs at the stops along the trail would interpret the different decay phases displayed and provide the visitor with insights into the decay process and its value to the forest. What an inexpensive museum in terms of maintenance, where the collection maintains itself and the exhibits need not be preserved nor can they be preserved. What rewards one would reap from 'selling' and 'bying' tickets to such an exhibition!

Summary of Chapter 6.

The increasing interest in dead wood has generated numerous studies focusing on the ecology, biology, biochemistry, pharmacology and other aspects related to dead wood. The already existing, rich literature illustrates the depth and breadth of dead wood studies. Some may result in discoveries that will cast new light on our understanding of the forest ecosystem or even on species evolution. Others, those involved with pharmacological exploration of the CWD associates, provide a hope that some members will contribute to the synthesis of much-needed medicines.

The unique aesthetic values of dead wood, expressed through the intuitive perception of a primal 'wild forest,' are a major and necessary attribute of the forest being 'sold' to visitors as a 'primeval forest.' Large amounts of dead wood reinforce the forest's appeal to an increasing number of people eager to experience traces of untamed nature. At the same time, decaying wood and its myriad of associated fungi, flora and fauna, is poorly displayed and insufficiently used as a valuable 'product' by nature educators and tourist operators. However, with little cost, excellent 'museums' that interpret dead wood and the decay process could be established.

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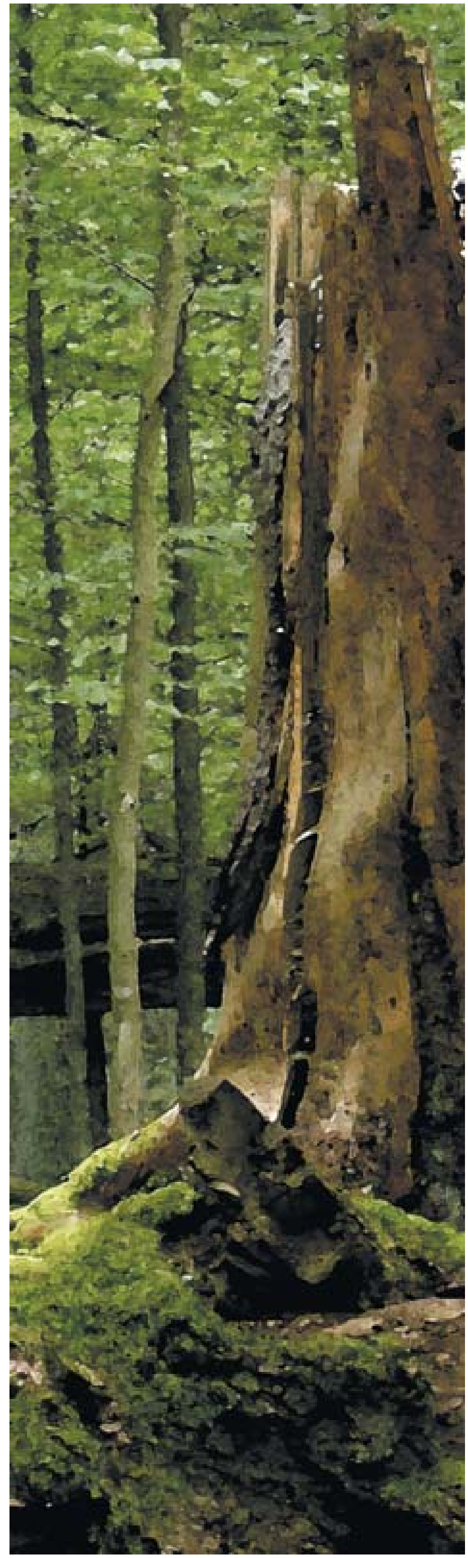
Chapter 7



WOOD AS A RAW MATERIAL

Wood as fuel:

In 1995, 3.35 billion m^3 of wood were extracted throughout the world, including 2.1 billion m^3 (63%) for fuel. Poland extracts 26 million m^3 of large-sized wood (more than 7 cm in diameter) on an annual basis, of which 10% is utilised in energy production.

Despite the values of dead wood to a functioning forest, we cannot forget that wood is an important renewable commercial commodity, irreplaceable in numerous applications necessary for society's development, e.g. in construction, mining, railways, telecommunication, the furniture industry and the chemical industry. In addition to such industrial uses, wood is a valuable and renewable fuel. ■ The purpose of this book is not to call for the termination of wood extraction and use. We only want to point out other values of wood that are usually underestimated or ignored. We want to show that in many cases, the commodity value of wood (photos 59, 122, 123, fig. 38) is less than its many other values. Moreover, the importance of wood in the construction, paper or furniture industries is so widely recognised that it is not necessary to consider these uses here. We cannot, however, neglect the importance of wood in art, including traditional wood crafting, sculpting, and souvenir-making (photos 125, 126).

The demand for wood as a raw material or fuel can partly be met by plantations of fast growing trees or shrubs, e.g. willows. However, wood extraction in forests should also take into account the other objectives of the forest. Obviously, wood should not be harvested in forests that still retain much of their natural character; such forests are very rare in Europe and the industrialised world. Indeed, such forests are the sadly limited remains of our natural heritage which are too precious for us to permit the extraction and consumption of their wood. The only functions that should be assigned to such ecosystems are the perpetuation of the ecological processes and emerging properties inherent to these forests; it is the interaction between the natural processes and the forest that leads to the conservation of biological diversity.

J.M. Gutowski

Photo 122. A pile of alder timber in the Białowieża Primeval Forest

J.M. Gutowski

Photo 126. A wooden wayside shrine on an old dead pine in Biebrza National Park

A. Bobiec

Photo 125. Dead wood as a focus for reflection and meditation: a confessional box carved from a single segment of an old hollow log from a lime tree – a Roman Catholic church in Białowieża

K. Zub

Photo 123. Old oaks felled in the Białowieża Primeval Forest


J.M. Gutowski

Photo 124. Charcoal pit. Though picturesque, charcoal production in Bieszczady (south-eastern Poland) destroys the habitats, eggs and larvae of the rare, protected longhorn beetle *Rosalia alpina*

It is critical to preserve these forests as models where natural processes can operate, be observed and studied; places where we can learn from nature – the oldest, most experienced and successful 'forester' – about how the ecological systems that we perceive as forests function together. Without this knowledge, without that teacher, our discussion about renaturalisation of European forests and restoration management, and the application of that information to other highly altered forests, would remain a trivial academic pursuit. For the same reasons, one should stop harvesting wood in other areas that have been set aside for 'protection' and are sufficiently large to permit the forest to function as a whole, that is in national parks and nature reserves.

An appeal to foresters

In managed forests, the management of the crop should be based on a compromise between the demand for wood products and the requirements necessary for resource and species conservation. Such compromises need to meet effective conservation goals, but also need to be flexible to reflect the variation in forest characteristics driven by variables including geographic location, the type of site and its characteristics, species composition, the structure of the stand and other factors. It is also very important that commercial forests retain a certain number of dead trees (both standing and fallen), including large specimens, until they completely decay. Commercial forests also ought to retain a certain number of large living trees that would eventually die and repopulate the dead wood resource in the managed forests. If we decide to harvest trees in a given place, they should not be dead trees because these harbour too much 'life.' To date, the extraction of wood products from forests, except in the small areas that have been 'protected,' has dominated forest management at the expense of their natural, aesthetic and recreational values, amongst others. It is high time to change this overarching forest management objective to one that promotes multiple 'products.'

Within the framework of forest management, the particular tools and methods used, including the timing of their application, can drastically affect the potential trajectory of the managed forest. There are negative side effects on the remaining trees in a clear-felled area, and on the soil where logs are 'yarded,' and these in particular should be avoided or minimised. The success of an improved forest management strategy largely depends on the professionalism and good will of the forest managers and the application of new and less disruptive equipment and procedures.

The importance of the 'odds and ends' are obvious in the following example. Certain artificial situations, such as clearings where timber is temporarily stored, to some extent simulate natural biotopes such as gaps created by bark beetles or windblows that attract unnaturally high numbers of insects, often rare and endangered species. These species mate there and lay their eggs in sites suitable for larval development, in this example, on the logs in the timber stacks. When the logs, after some time, are removed from the forest, the deposited eggs and foraging larvae are destroyed. Thus, this artificial environment has become a sort of trap, draining from the ecosystem perhaps a large portion of the reproductive output of specific entomofauna. The potential for endangerment of saproxylic species is often increased by such situations. The potential for harm could be reduced or avoided if the timing of the timber harvest and its temporary storage considered the critical timing of the life cycle of rare species.

Logs for wildlife:

When one walks through the rather dull and tidy woodlands – say in the managed portions of the New Forest in Hampshire (England) – that result from modern forestry practices, it is difficult to believe that dying and dead wood provides one of the two or three greatest resources for animal species in a natural forest, and that if fallen timber and slightly decayed trees are removed the whole system is gravely impoverished of perhaps more than a fifth of its fauna.

(Charles Elton, 1966).

Logs are also considered to be more important as wildlife habitat as they provide cover, runways, and denning sites for a variety of species, often different species than used by snags; in the absence of fire, some tend to persist for relatively long periods of time (...).

The size of the material is important for many species (...). For example, a limb 10-centimeters (4 in) in diameter is large enough to give protective cover to a tiny shrew, but a log 25 centimeters (10 in) in diameter will afford protection to a deer mouse. In general, the larger the diameter and the greater the length of a log the more useful it is (...).

From the management tips, Pacific Northwest USDA Forest Service:

At least five uncharred class 1 or class 2 logs per hectare (two/acre) should be retained as wildlife habitat. Furthermore, all class 3, 4, and 5 logs, which have little or no commercial value but are acceptable as fuel loading, should be retained. For a maximum function as wildlife habitat, the logs should be at least 30-43 centimeters (12 to 17 in) in diameter at the large end and 6 meters (20 ft) or more in length.

The removal of natural, stable woody material, especially logs, may seriously damage the stream channel at the streamside riparian habitat. Such woody material provides excellent habitat to aquatic and amphibious wildlife and for many small terrestrial animals; it should be left in place when possible.

MASER et al. 1979

In commercial forests, a certain acreage containing the most complete suite of natural forest characteristics should be left without silvicultural intervention, and in addition, 5-10 large dead trees should be retained per hectare across the remainder of the commercial forest, as is recommended in North America.

The amount of dead wood and populations of its associated flora and fauna in such forests could be improved if higher stumps (up to 3 m), very important for many saproxylic species, were left in place as required in Swedish forests.

As it does not entail any economic costs, the policy of leaving certain quantities of dead wood could be easily and immediately applied to commercial forests. For hardwood species, it should not provoke any concern, even among 'traditional' foresters afraid of the 'pests' that hatch in coniferous wood. Even for conifers, if the surrounding forest is less susceptible to mortality or damage by these 'pest' species, permitting larger amounts of dead wood in the forest should not cause unacceptable losses of or damage to living trees. Furthermore, a certain, albeit small, amount of continuing mortality is necessary in functioning forests.

We need to acknowledge that in Poland, as in many other countries, the attitude towards dead wood has improved substantially compared to that of 20 years ago. However, despite this improvement, dead wood policies, from the point of view of nature conservation but also from the perspective of sustainable development of human societies, remain far from ideal.

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Summary of Chapter 7.

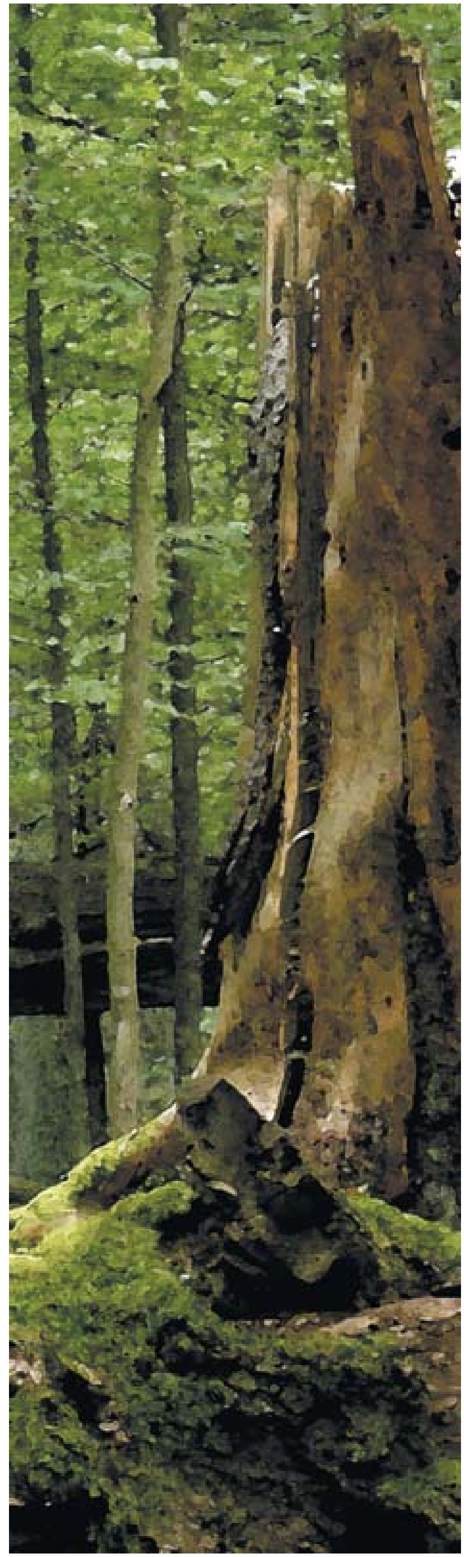
Wood as a raw material is essential for many applications in human societies. These functions are well known and appreciated, and need to be perpetuated in appropriate forests, with certain constraints to improve the position of dead wood and other necessary forest components.

The role and importance of dead wood in forest functions and the maintenance of biodiversity is still underestimated and not appropriately considered in forest policy and management.

In managed forests, the management of the crop should be based on a compromise between the demand for wood and necessary conservation requirements. To a great extent, the demand for wood as a raw material or fuel can be met by plantations of fast growing trees or shrubs, thus permitting the highly valuable older forests to be retained for their ecological and aesthetic values.

Extraction of timber from the rare, generally small and scattered remnants of the natural European forests will likely result in an irreversible loss of the inherited primeval forest biodiversity, which will negatively influence the quality of life for generations to come.

Chapter 8



SUMMARY

Dead wood in forests, i.e. standing dead trees and shrubs, snags, stumps, old trees with dying boughs and cavities, fallen logs and branches etc., provide or contribute to:

- a greatly increased species richness of fungi, plants and animals,
- a higher landscape diversity and tourist appeal,
- a positive influence on the site characteristics (soil, forest litter),
- improved water retention in the ecosystem,
- protection against erosion,
- a source of indispensable forest elements (carbon, nitrogen, calcium, etc.) and energy,
- the facilitation and conditioning of the regeneration of trees,

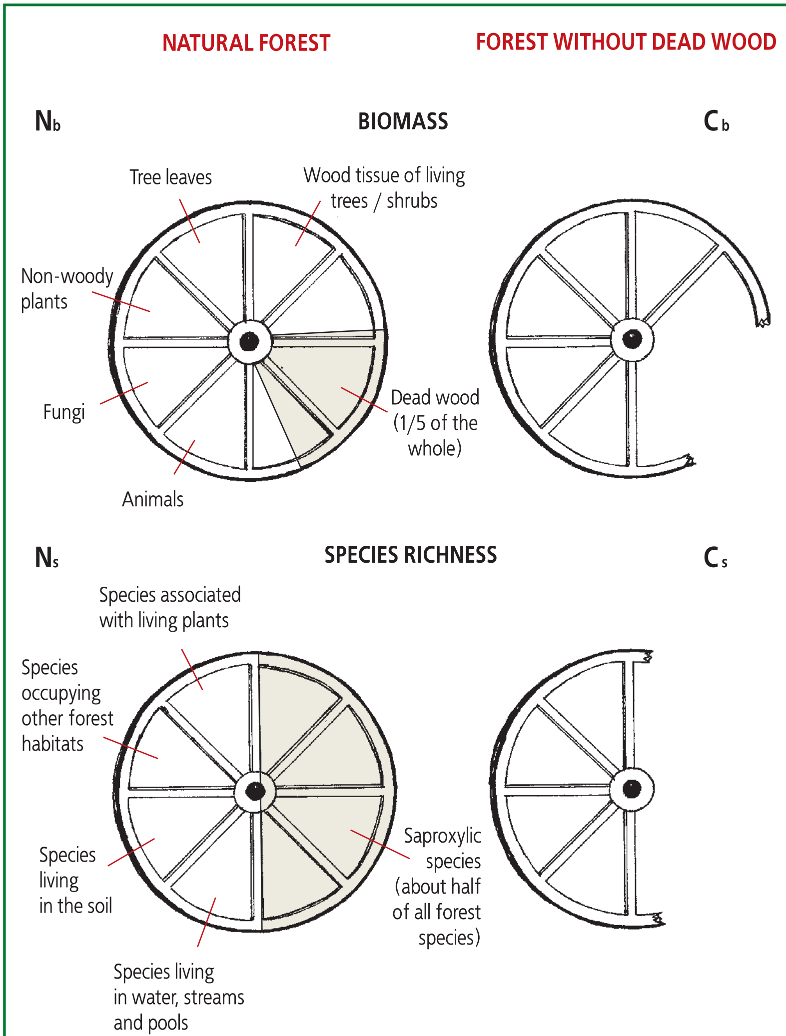


Figure 39. If we illustrate a natural ecosystem with a wheel, its biomass will contribute to about 1/5 of the wheel's surface (Nb), and the species connected with dead wood make up about half of that wheel (Nc); after removing dead wood from the ecosystem, it is not able to function properly (Cb, Cs) – the wheel cannot be used (M. Bobiec)

Considering the functions listed above, dead wood in forests, contrary to current opinions, is much more than an incubator where pests and diseases hatch. It is quite simply an indispensable element of the ecosystem, serving to condition the natural, biological resistance and promote a natural dynamic equilibrium of the forest (fig. 39). Wood should not be extracted from forests that possess primeval characteristics (e.g. large, old trees or copious amounts of dead wood), as such forests are irreplaceable as banks of biological diversity and as models from which we can observe and investigate natural processes and learn from nature so that we can mimic it as forest managers. Wood extraction in protected areas such as national parks and nature reserves should not occur. Regarding managed forests, a portion of each stand should be left unharvested and a certain amount of dead wood should be retained in the forest to perpetuate the suitable conditions for saproxylic organisms.

Conclusions:

1. The quantity of dead wood left in forests should be as large as possible. As a component of the forest, dead wood is as important, or perhaps more so, than living trees or shrubs. Removing and utilising CWD, e.g. as fuel, can cause greater damage to the forest ecosystem than felling a living tree. However, a continual supply of living and eventually dying and dead trees is crucial to maintaining all of the necessary forms of CWD.
2. The CWD resources should reflect the diversity of the living stand, considering species composition and size structure. Promoting a continuous supply of CWD, especially of large-sized material, is crucial to the functioning of the forest and many of the organisms. In particular, dead trees larger than 40 cm in DBH should be left to continue the decay process, for they play a key role in the perpetuation of numerous endangered species as well as other species also associated with dead wood.
3. In forests that resemble natural ecosystems, especially national parks and nature reserves, no dead or dying trees or shrubs should be removed and the quantity of CWD should depend on the course of natural processes. However, the perpetuation of these natural processes may well require larger landscapes than the protected area currently covered and increasing the size of these forests ought to be considered.
4. All remnants of natural or semi-natural forests in Poland should be maintained with no or minimal human intervention. Natural processes do not threaten the durability of forests!

5. Felling dead trees and removing dead wood in forest reserves should not be permitted under a partial protection regime. If intervention is considered necessary, trees should be killed e.g. by girdling or some technique that more closely reflects the natural mortality agents, but left without further manipulation such as barking. However, it is always preferable to leave trees to die 'naturally' rather than to attempt to replace them with trees that have been killed artificially.

6. In wet forests, such as marshy coniferous forests, alder swamps and riparian forests, as well as in high elevation spruce forests, even if not designated under legal protection, all CWD (logs, uprooted trees, etc.) should be left as it provides the conditions necessary for efficient regeneration of trees, and additionally, it reduces erosion in the mountains.

7. Wood harvesting in commercial forests should not take place during the growing season as it interferes with the critical moments in the development of many rare saproxylic species and will maximize impacts to soils and ephemeral plants. Wood that has not been removed within the designated harvesting period should be left in the forest until its complete decomposition. Trees or snags left in the forest should not be felled, barked or sawed into short sections.

8. Regardless of the felling system, after every intensive forest management action, 5-30% of trees should be retained until their natural death and complete decomposition. Trees selected for preservation should represent the species composition and DBH diversity of the managed stand. In the case of a large scale clearcut (simultaneous felling of all trees on up to 4 hectares, usually followed by planting new trees), selected trees should be retained in clusters covering an undisturbed ground surface.

9. When conducting sanitation activities, trees with bracket fungi signify that infected trees are or may eventually become hollow. Such trees are very important habitat components for certain animals and should not be removed.

10. As much organic matter as possible should be retained in the harvested area. When harvesting to improve forest stands (thinning), extraction of wood should take place only if the thinning has some other value to the stand, such as increasing tree growth rates to improve the numbers of large trees and eventually snags or if it is economically justifiable.

11. Slash residues should not be piled or burned in forests where natural fire is not or was not historically a frequent event. It should be retained and randomly scattered on the forest floor.

12. In general, stumps should not be barked. However, sometimes barking is an acceptable practice in coniferous monocultures threatened by massive outbreaks of bark beetles and borers.

13. When removing the trunk of an uprooted tree, the root plate should be prevented from falling back into its crater.

14. The volume of dead wood in all managed stands older than 50 years should not be lower than 5-10% of the living tree volume, and CWD should reflect the stand's species composition and size structure.

15. One should perpetuate the presence of flowering forest plants, especially representing the umbellifers, Rosaceae and Compositae, in close proximity to stands with dead wood (e.g. through the retention of inner-forest meadows, the adoption of a suitable mowing regime such as in some meadows or wood storage locations, the maintenance of the herbaceous character of roadsides, etc.). Such plants provide food to the adults of numerous saproxylic species.

16. It is very important to retain all hollow trees in groves and parks. The hollows of such trees should never be cleared of rot as the decayed material is a suitable environment for many rare stenotopic species of invertebrates. 'Curing' old and weakened trees should be reserved for only those few trees of cultural significance, and it should not interfere with the processes taking place within the rotted wood microhabitats.

17. In reserves and parks, fallen logs should be retained as well as those standing dead trees located a safe distance from roads and parking areas, frequently used trails, designated campgrounds, and other park facilities.

18. An educational campaign, showing the role and significance of dead wood, should be implemented. This campaign should target the society in general, but in particular children and youths as well as the various conservation services and forestry administrations.

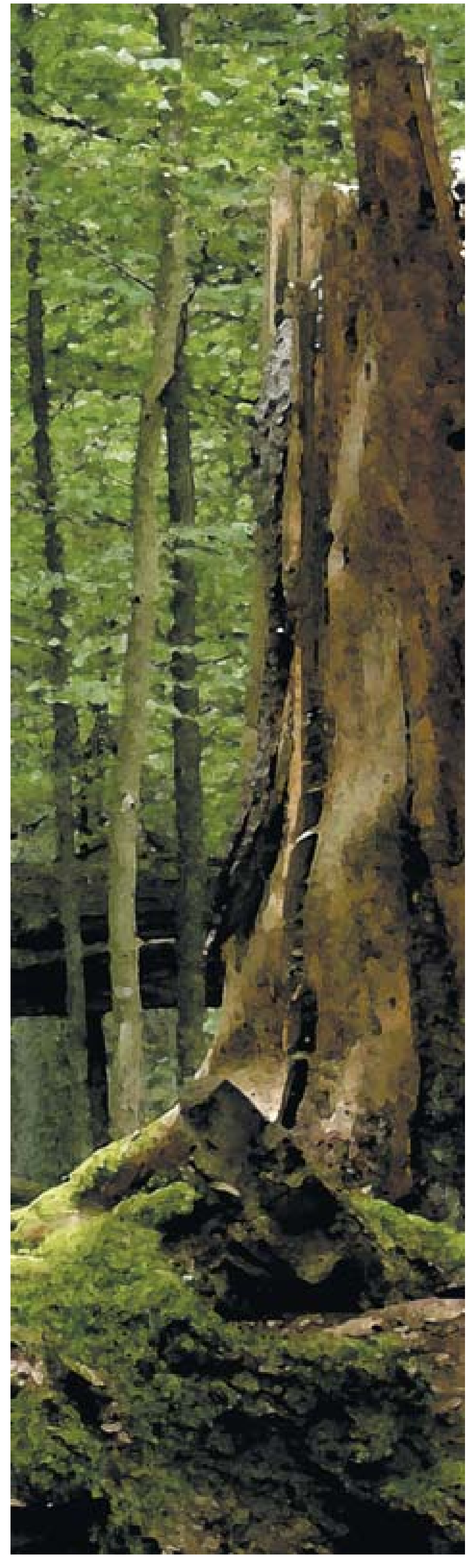
19. Further studies of the many unknown aspects of dead wood and its role in ecosystems are badly needed.

RECOMMENDED AMOUNTS OF DEAD WOOD IN VARIOUS TYPES OF FOREST

Forest type	Reasonable amount and structure of decaying wood
Natural and close-to-natural forests, nature reserves and national parks	Maximum quantity; removal of any amount of the dead wood emerging from natural processes is contradictory to the character and function of these forests
Artificial forests included in nature reserves and national parks	Maximum quantity of wood representing species appropriate to the given site; removal of any amount of dead wood emerging from natural processes is contradictory to the function of these forests. Dead wood originating from alien species should compensate the lack of dead wood from native species so that the total quantity of CWD would not be lower than 10% of the stand's volume. Maximum number of hollow trees
Subalpine spruce and marshy coniferous forests, alder swamps	Maximum quantity of dead wood to meet the needs of species associated with dead wood and to promote tree regeneration in these forests
Forest streambeds	Maximum quantity of dead wood to improve the water retention capacity and shape the stream's biotopes
Complex forests that still retain primeval characteristics	Maintain 15-25% of the total volume of a mature stand on a given site as dead wood; not less than 10 large, complete decaying logs or standing dead trees with a DBH over 40 cm, per hectare of forest. Maximum number of hollow trees
Protected forests that are "valuable fragments of the historical, natural forest" Forests harbouring protected or endangered species connected with dead wood Forests on steep slopes where excessive erosion is of concern Forests in the immediate neighbourhood of mountain streams and the banks of other streams (within about 20 m from the bank) where dead wood is necessary to create pools and alter the stream shape and structure Virgin or other old forests that require protection	Maintain 15-20% of the total volume of the mature stand on a given site as dead wood, not less than 10 large complete decaying logs or standing dead trees with a DBH over 40 cm, per hectare of forest. Maximum number of hollow trees
Other managed forests	Dead wood should comprise 5% of the volume of a mature stand on a given site, but not less than 5 large decaying, complete logs or standing dead trees with a DBH over 40 cm, per hectare of forest. Maximum number of hollow trees

- ☑ Here, "mature stand" is defined as a stand at its felling age as accepted for a given forest type; its volume at maturity can be derived from tree volume tables.
- ☑ The "maximum quantity" of dead wood means that no removal of dead and dying trees should take place.
- ☑ Ecological studies show that there are numerous rare insect species that generally do not occupy smaller trees or debris (<40 cm in diameter), or if they do, the populations are insufficient to be sustained.

APPENDICES



APPENDIX I

by Andrzej Bobiec

METHODS OF QUANTITATIVE AND QUALITATIVE ASSESSMENT OF DEAD WOOD

A simple assessment for the quantification of dead wood in a forest

As the decay of wood is a continuous process, the stage of decomposition can be evaluated either through a detailed laboratory analysis or by referring to certain models of discrete decay classes. Laboratory methods, when applied to questions of forest ecology, can be very laborious and costly, and the results are usually not available in a reasonable time and are generally not appropriate for field assessments. Thus, when general patterns of decay at larger scales than that of a single piece of dead wood are desired, laboratory methods are hardly ever used. Generally, the degree of decomposition is assessed by comparing the observed material with samples or criteria based on an accepted model defining certain classes of decomposition. The model recommended by MASER et al. (1979) for the Pacific Northwest of North America, which distinguishes five discrete classes of decaying wood, is commonly used. However, it is sometimes simplified to only three classes.

Methods of quantitative and structural assessment of dead wood

There are many methods for assessing the quantity of dead wood. The most accurate one requires the direct measurement of all pieces of dead wood (both standing and fallen) followed by the application of the appropriate geometric formulae (a modified formula for the volume of a cone). However, even this method does not guarantee one hundred percent accuracy; it is impossible to imagine finding, let alone measuring, every single branch and fragment of dead wood in even a small parcel of land, and the modified formula does not perfectly reflect the shape of each piece. Because of the great deal of labour needed (even if high-tech laser instruments linked to a portable computer are available), the direct measurement method is used only on small, permanent plots, usually coupled with simultaneous mapping of the wood in the plot.

If an inventory or monitoring update of the CWD resource is desired over a large area, indirect methods should be applied. Comparisons of various methods, their efficiency and accuracy, show that one of the best methods to estimate the volume of dead wood is the line intersect approach of VAN WAGNER (1968). The method was originally applied in modelling forest fire probabilities but can be applied to other questions related to fuels and dead wood. VAN WAGNER's method is based on a simple rule: the number of points where a straight line is intersected by randomly distributed horizontal elements (e.g. woody debris) is dependent on the total length of these elements. If one records each point where an element of dead wood intersects the line and measures the diameters of the debris (at the intersection), one can calculate their volume (total or by defined diameter classes):

$$V = \frac{A\Pi^2 \sum d^2}{8L}$$

V – volume of CWD on a given surface [m^3]; A – area, from which the volume is estimated [m^2]; d – diameter of the debris at the crossing point [m]; L – length of the measurement line (transect) [m].

The accuracy of the method depends largely on the amount of CWD present in the area sampled; the more CWD the greater the accuracy of the estimate. To achieve a 10 percent statistical error, the length of the assessment line per hectare should total:

$$L = 5132e^{-0.04V}$$

L – length of the line in m per hectare; e – base of natural logarithm; V – expected volume of CWD per hectare.

For example, if the CWD volume is expected to be approximately 10 m^3/ha, an assessment line of 3500 m would be required to achieve an estimate with an accuracy of 10 percent error; however, if a volume of 50 m^3/ha (e.g. an old-growth stand in which dead wood was not removed for a few dozen years) is expected, less than 750 m of assessment line would be required, and if a volume of 120 m^3/ha (average volume in Białowieża National Park) is expected, an assessment line of only about 50 m will be necessary (after WARREN and OLSEN, 1964). Because the distribution of CWD is uneven, doubling the length of the assessment line is advisable to meet the 10 percent statistical error desired in the estimate. It is also advisable to carry out the quantitative assessment of dead wood repeatedly (e.g. every ten years or so) on permanent plots, so as to follow the CWD dynamics in the ecosystem. If the sampling is based on quarter hectare plots (50×50 m) we would recommend a grid of twelve 50m-long sections, spaced 10 m apart with six sections each in two perpendicular directions. Sampling plots at a 25-hectare scale (500×500 m) could be performed using a stair-step design (50m-long, alternating perpendicular sections along the plot's diagonals).

The volume of standing dead trees can be estimated on the basis of the "whole tree volume" tables used by foresters (which requires DBH and height measurements), or, for example, by using the geometric formula for the volume of a cone or cylinder (depending on the shape). While the total volume of dead trees is an important characteristic, the number, size and distribution of the trees seems to be even more important. As dead trees are a tempero-spatial function in the landscape, one should remember that reducing them to a mean volume substantially neglects their ecosystem value. The same should be considered while analysing logs. The existing literature offers numerous derivatives and combinations of the basic formulae, but considering the imperfections of measurements (height, small diameter) as well as the irregularities of shape (branches!), one should not exaggerate the accuracy of the models when recommending 'the best' version. Inventories of standing dead trees should be performed on the same plots where CWD is estimated. In the case of large plots (e.g. 25 hectares or larger) we recommend that the measurement of trees be performed in 10 m wide belts along the CWD assessment lines (with 5 m of belt on each side of the assessment line) as described above.

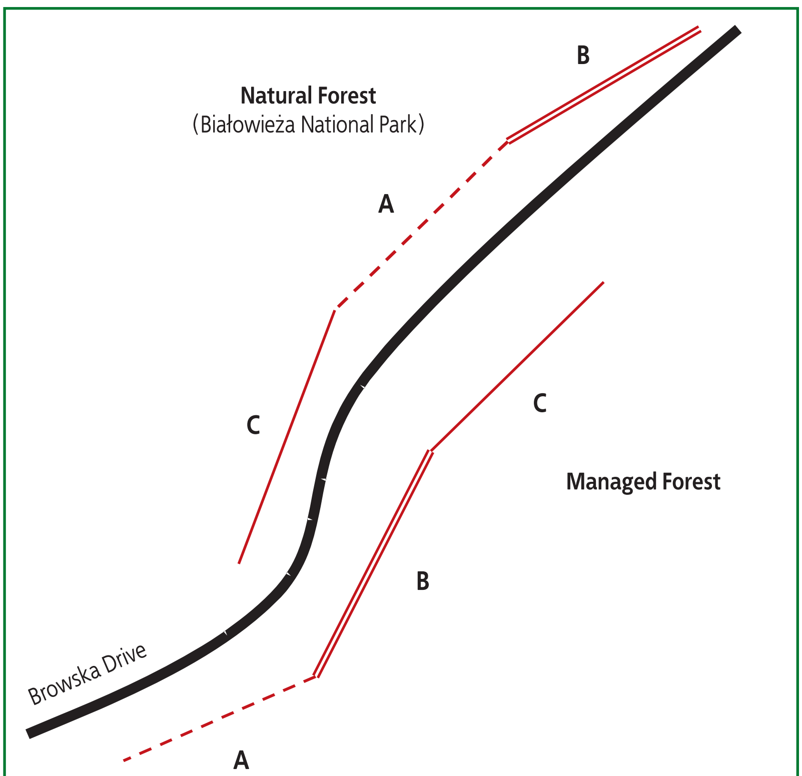
VAN WAGNER's method was successfully used in the CWD inventory on 25-hectare plots (500×500 m) in the Białowieża Primeval Forest. In practice, it consisted of deploying a fabric ribbon along two 1km-long stair polygons (the 'stair steps' are created by 50 m long perpendicular sections as described above). Use of the stair-step line or transect instead of a straight line is necessary to meet the requirements of random CWD distribution in relation to the line as described above (according to previous studies the direction in which trees fall in the BPF is highly correlated with the direction of prevailing winds. The method is very quick, and this efficiency, particularly when an electronic data organiser is available, allows field crew to include additional data such as the tree species (where it is recognisable) or general wood category (soft or hard wood), as well as the degree of decay of the debris that intersects the line. The accuracy of the method is proportional to the length of the deployed ribbon and inversely proportional to the surface area of the dead wood subjected to the inventory. The data can be analysed and presented by diameter classes, species, and/or degree of decay.

An example of the practical implementation of the wood assessment in environmental education

One of the goals of outdoor nature classes is to train the students to become capable of detecting certain features that distinguish a natural forest. The close proximity of the strict nature reserve to managed, manipulated stands, permits a direct comparison of natural and managed forests of the same forest type. Special forms and data collection protocols enable participants to compare a set of selected characteristics from one forest with the same characteristics from the other one. During the presentation of the results, students verify the definition of a natural forest using their own findings.

Ecology Class Description for the Workshop: "Green Leaders for the Future" – May 1, 2000, organised by the Nature Education Centre of Białowieża National Park.

Each of the three groups of students (A, B, C) carried out observations and measurements along their assigned 150 m long sectors of two 450 m assessment



lines along the two sides of Browska Drive: one in the strict nature reserve (natural forest, NF) and the other in the managed forest (MF, fig. 1). Both lines represent the same forest type (mainly mesic deciduous).

Most of the surveyed forest was harvested in the first half of the 20th century. This historic event explains why a typical climax stand dominated by shade tolerant species has been replaced by a stand dominated by pioneer trees such as birch and aspen. As a result of succession being permitted to progress in the NF, these pioneers are gradually replaced by shade tolerant trees, including limes, hornbeams and maples. Simultaneously, the MF is subject to intervention defined as "remodelling", which consists of felling birches and aspens and planting oaks with an admixture of other deciduous species to "adjust the species composition" to the stand model recommended by the management plan.

Large trees (in two size classes: >40 cm and >70 cm DBH), both standing and hollow, were counted in the 10 m-wide belt (5 m on each side of the assessment line), covering an area of 4500 m^2 (450 m × 10 m), in both the NF and MF. The students also collected additional ecological information within the belt transect including ground vegetation, animal tracks, fungi, abiotic characteristics (e.g. soil pH and temperature), as well as detailed observations of dead wood-related microenvironments (e.g. uprooted trees and large decaying logs).

The VAN WAGNER (1968) method was used to quantitatively assess the amount of dead wood. This method consisted of measuring the diameters of each piece of woody debris where it intersected the assessment line. During the indoor portion of the class, the representatives of each of the three groups presented their results, which were then put into a summary table (Table 1) and included in the discussion of the exercise.

Table I
Summary of the data gathered by groups A, B and C

Characteristic	Natural forest	Managed forest
Trees with DBH (number of trees per hectare):		
Greater than 40 cm	73	24
Greater than 70 cm	13	2
Standing dead trees	26	4
Hollow trees	19	4
Downed woody debris in diameter classes (m^3 per hectare):		
10-20 cm	7	2
21-30 cm	46	
31-40 cm	20	
41-60 cm	27	
Total	100	2

Final findings and summary

1. The results of the study showed a greater complexity in the natural forest than in the managed forest – see Tables 1 and 2. This complexity results from unconstrained natural processes. The managed forest is mantained to simultaneously achieve specific goals and to constrain the actions of the natural processes or to minimise their effects when they conflict with the basic management goals.

Characteristic	Managed forest	Natural forest
Objective	tree growth	natural dynamics
Species composition as a result of:	management	natural processes
Timing of ecosystem development:	limited	unlimited
Old trees	few	many
Sick and dead trees	few	many
Dead wood	minimal	abundant
Microenvironments	few	many
Damage from natural factors	present	does not apply
'Pests'-native species hampering the management objectives	present	does not apply

Table II
Summary of other ecological characteristics in the two forests

2. 'Forest protection' (i.e. protection against pests and fungi) is inconsistent with the definition of a functioning forest that embraces producers (including trees), consumers (including fungi, invertebrates and vertebrates), the biotope, as well as the mutual and other relationships between all forest constituents, including spruce bark beetle 'infestations' of spruces, fungal parasitism and deer browsing.
3. The natural forest is a dynamic system in continuous development. The current species composition of the various stands is a combination of the forest's response to historic events and the subsequent dynamics within the forest and with the surrounding environment.
4. Natural forests are definitely necessary:
   - as banks of biological diversity (both species and genetic),
   - as models of the natural inter-relationships in a complex and functioning system (e.g. natural resistance mechanisms),
   - as natural laboratories (of the evolutionary processes, natural selection).

5. Protection of the natural forest does not necessarily mean preservation of the current species composition or forest structure. Protection of natural forests means securing in perpetuity a forested landscape where the natural processes can function unhindered by human activities that would modify the forest's characteristics, functions and interrelationships.

Topical literature:

MASER C., ANDERSON R.G., CROMACK K. Jr, WILLIAMS J.T., MARTIN R.E. 1979. Dead and down woody material. In: Wildlife habitats in managed forests. The Blue Mountains of Oregon and Washington – Thomas, J. W. (tech. ed.). USDA Forest Service, Agriculture Handbook No. 553, Portland – Washington D.C., 78-95 pp.

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APPENDIX II

EDUCATIONAL WORKSHOP: "WHAT ARE DEAD TREES FOR?"

These are outlines of the ecology classes organised in 2001 at the Nature Educational Centre of Białowieża National Park.

by Andrzej Keczyński

I. Trees of the Białowieża Primeval Forest – living and dead

Goal: Introduction to the common tree species occurring in the Białowieża Primeval Forest, factors causing their death and decay, and rates of wood decomposition.

Materials: Herbarium sheets with leaved tree twigs, notebooks, pencils, profiles of tree species, schematic vertical profiles of forest stands, tape measures, guidebooks and tree keys.

Indoor introduction: Preparation of each participant's tree key – copying shapes of leaves (from the herbarium specimens), trees (from the profiles), etc.

A. **Introductory lecture**

- What is a tree, how do trees differ from shrubs, perennials and other herbaceous plants?
- Common tree species of the BPF
- Tree communities – forests – how diverse are they? Why are they diverse?
- Why do trees die? Biotic and abiotic mortality factors
- How quickly does the wood of dead trees decay?

B. **Outdoor studies**

- Organisation of teams, assignment of transects and observational plots, determination of tree species in the belt transects
- Detailed explanation and discussion of the field form

Definitions

Small tree – a tree with a DBH less than 21 cm;

Large tree – a tree with a DBH greater than 21 cm;

Dead fallen tree, fresh – the wood is hard, often with bark attached and remnants of leaves, needles or buds attached to the branches; a tree that was apparently broken or uprooted in the last few years;

Dead fallen tree, in decay – a tree covered with a coat of mosses; the superficial layer of wood is soft whereas the core is still hard; large boughs are still connected to the trunk but the smaller ones are mostly detached; a tree that apparently died more than a few years ago;

Dead fallen tree, decayed – a tree lying on the ground for many years (decades or longer), covered by mosses, vascular plants, dwarf shrubs and young trees; the wood is strongly decomposed, soft, sponge-like and wet, and the shape of the trunk and boughs is barely visible as the woody elements decay and are hidden by other plants, or the arrangements of the invading plants reflect the remains of the trunk and boughs;

Young generation – trees of all species with heights ranging from 0.1 to 4 m and diameters less than 5 cm

Two equal-sized belt transects (5 m wide and at least 25 m long) should be established, one in the NF and one in the MF. They are divided into 5×5 m quadrants.

Tasks

- Identification of the tree species along the transects using leaf and bark characteristics as identification criteria; estimation of species composition (percentage of stand) and diameter distribution (percentage of stand)
- For the dead trees encountered: determining the causes of mortality, quantitative estimation of standing and fallen trees, degree of decomposition
- Observations of the young generation of trees – how numerous are the trees, what are the characteristics of their structure, what proportion has a good chance of survival, growth, and eventually becoming dominant in the stand?

C. **Final indoor exercises or activities**

- Preparing the summaries of living and dead trees, with their general characteristics
- A description of the young generation of trees (circumstances of their development and growth, chances of survival)

- Final conclusions:
  - What are the differences between natural and managed forests from the results of the data collected?
  - What are the roles of dying and dead, standing and fallen trees in established living trees, the young generation, for other plants, fungi and animals?

		Quadrats on the transect										
		I	II	III	IV	V	VI	VII	VIII	IX	X	∑
Tree species												
Living trees (number)	Small											
	Large											
Standing dead trees (number)												
Fallen dead trees (number)	Fresh											
	In decay											
	Decayed											
Young generation	Species											
	Number											

II. Insects and other invertebrates

by Bogdan Jaroszewicz

Goals

1. Exploring the diversity of invertebrate organisms living in dead wood and on living trees
2. Building awareness of the importance of invertebrates to the natural cycle of organic matter in the forest
3. Comparing the biological diversity of invertebrates occupying dead wood and living trees

Necessary materials: Pencils, notebooks, magnifying glass x10, vials with caps or stoppers (one for each participant), penknife, invertebrate guidebooks and keys

Introduction

1. The preparation of students for the exercise should be carried out by the teacher of the biology class:
   - Identification criteria (discriminating characteristics) of invertebrate genera
   - characteristics of major groups of insects related to dead wood,

- characteristics of major types of insect larvae

2. Before leaving for the forest, the students should gain knowledge about the invertebrates of the Białowieża Forest:
   - ecological groups of invertebrates (e.g., foliophages, xylophages, saprophages, predators and parasites)
   - general characteristics of the succession of organisms occupying dead wood
   - the classification of dead wood-related invertebrates and their microhabitats,
   - the observation of invertebrates associated with dead wood in their natural habitat is often very difficult due to their hidden lives, and in the case of insects, the short time the imagoes are visually detectable (though the imagoe stage is the most visible in the developmental cycle)

The outdoor assignment

Participants should be organised into small groups dealing with specific tasks. We recommend that the groups search for invertebrates and other secondary evidence of their presence:

a) on living trees (in the cracks of bark, on buttresses, lichens, mosses, etc.);

b) on dead trees (on the surface, under bark, in decaying wood, in the wood fragments fallen to the forest floor, on the ground);

c) to describe and delineate the microenvironments inhabited by invertebrates on living and dead trees.

Groups A and B may work on the same 5×5 m plot while group C works on a separate plot. Each group should be subdivided into 2-3 person taskforces. Each of them should complete the standard data form using "+" to mark a single observation in a given plot (e.g. three observations of snails on the same plot should be marked with "+++"), with a plot being the same 5×5 m areas described earlier in this appendix. Identification of the organisms should be determined to the systematic level specified on the form.

The participants should collect 1-2 representatives of the invertebrates encountered in their vials. Each team should precisely record the location where each organism was captured so that they can be returned to that exact location. After the search is completed, the class leader pours out the contents of each vial in turn on a sheet of white paper and talks about each organism, characterising the systematic affiliation of each animal, summarising its biology as well as its role in the ecosystem, and providing other information about each species that seems relevant.

CAUTION!

If the class is to take place in a nature reserve or national park, the organiser(s) should:

1. have the location, time and methodology approved by the appropriate authorities;
2. return all the captured organisms and fragments of wood to their original sites.

Summary

After the exercise, the results should be recorded on the summary data form.

An organised discussion of the results should cover the following topics:

a) which groups of organisms occur exclusively on or in dead wood or which groups' abundance is higher in dead wood than in other environments? (In a functioning forest, the number of species occupying dead wood is always considerably higher than those occupying living trees);

b) which groups of organisms occur in relatively equal numbers on both dead wood and other kinds of substrate? (This equality can be deceptive, because the material collected was only superficially examined and identified and the results do not reflect the actual species diversity);

c) which microenvironments are found only in living trees or only in dead wood?

The most Frequently Asked Questions are:

- What causes the differences in the number and diversity of invertebrate fauna occurring on living trees versus dead wood?
- What types of microenvironments are missing in managed forests?
- Why do most of the invertebrates associated with dead wood belong to rare and endangered species?
- What is a 'pest?' When does an organism qualify as a 'pest?'
- What are the ecological roles of invertebrates living in dead wood?

Collective Table

Organism / Environmental	Earth-worms	Snails	Spiders	Myriapods	Insects (development stage and group)	Phytophagous and saproxylic organisms	Predatory and saproxylic organisms	"Refugees"
Dead wood								
Living trees								

by Arkadiusz Szymura

III. Birds and other vertebrates

1. **Indoor introduction**

Discuss woodpeckers as birds specialised in procuring their food from dying and dead wood:

- construction of the beak
- features of the tongue
- application of their very long tongue to extract insects from within the bark or wood of trees (the role of hyoid bones)
- structure of the tail feathers
- construction of legs, toes and claws
- anatomic adaptation to foraging and drumming

Explain the concepts of cavities, hollows and semi-hollows.

Discuss the species that nest in the cavities, hollows and semi-hollows created or formed in dead trees, e.g. left by black woodpeckers or established as a result of tree breakage. Explain the importance of dead tree-related sites for birds (food resource, forging hollows and their use by other species such as tits, swifts, nuthatches and owls, e.g. Tengmalm's owl).

2. **Preparatory class in the Nature Education Centre**

A systematic overview of the bird species discussed above in block 1: woodpeckers (sexual dimorphism), tits, nuthatches, owls and swifts.

Necessary materials: Images of birds for a slide presentation or other visual medium, bird keys, binoculars, tape measures, callipers, pencils and notebooks.

3. **Field class**

During the journey to the strict nature reserve of the BNP – watch and listen for birds. Divide participants into three groups. Each group should survey a rectangular plot (50×25 m) in the mesic deciduous forest:

1 – plot with hornbeams dominating the forest

2 – plot with limes dominating the forest

3 – plot with other tree species, including oak, maple and ash, dominating the forest

Each group should then measure the DBH of trees greater than 7 cm, recording species of tree. The trunks and boughs of all trees should be carefully scrutinised for natural hollows that could be occupied by birds and for cavities excavated by woodpeckers. All observations of birds feeding on standing trees or fallen wood should be recorded together with the degree of wood decay present where the bird was positioned. All of this information can be recorded in the table below.

Plot No						
Tree species	DBH	Category (living, snags, fallen CWD)	Natural hollows	Cavities excavated by woodpeckers	Feeding evidence	Degree of wood decomposition

Summary

- How does the tree species composition of the forest stand influence the potential for suitable nesting conditions for birds that nest in hollows or cavities?
- On which tree species do woodpeckers feed?
- Where do you find the most evidence (e.g. scaling and foraging excavations) of woodpecker feeding sites: on living trees, standing dead trees or fallen logs? What was the degree of decomposition of the most favoured foraging site?

Conclusions

- What is the relevance of dead wood to birds?
- For what systematic group is it most important?

by Karol Zub

IV. Fungi, thallophytes and vascular plants

A. **Indoor introductory class**

1. Basic information on the biology of fungi
   a) What are the key characteristics of the fungal kingdom?
   b) Anatomy
   c) Reproduction
   d) Life strategies (parasitism, symbiosis, saprophytism)
2. The role of fungi in our lives

B. **Indoor class preparation for the field trip**

1. General information about fungi
2. Short slide presentation showing fungal richness and diversity in the BPF
3. Discussion, in greater detail, of several selected species (specimens, slides, posters)
4. Discussion about the value, both positive and negative, of fungi to the forest

C. **Field work**

This course was once held adjacent to Browska Drive, on the border between the strict nature reserve of Białowieża National Park (NF) and a managed forest (MF).

Form of fruiting body	Cap mushroom	Bracket fungus (hoof shaped)	Other permanent fruiting bodies (small, spreading, protruding, flat)	Fleshy fruiting bodies of various shapes (bowl, flat, irregular, puffball)	Puffball	Total
Living standing trees						
Standing dead trees						
Lying logs						
Fallen boughs and branches						
On the ground						
In total						

Activities:

1. Establishment of two 50 m long transects perpendicular to the road; one into the NF, another into the MF
2. Participants should be divided into two teams
3. Participants should be provided with instruction on the fungus inventory method and the use of the forms
4. See below for the form:

The inventory should be performed in a 2m-wide belt transect (1 m from each side of the 50 m long assessment transect), such that the sampled area will total 100 m^2 in both forests.

If there are many participants, the groups can be subdivided into smaller task-forces charged with investigating specific microenvironments, e.g. living trees or fallen logs.

After the inventory, the results should be accumulated into a summary table. The instructor may discuss a few more interesting fungi. Depending on time, participants may try to identify several specimens to species level using keys.

Summary

1. Presentation of the results from both forest transects.
2. Conclusions:
   - the diversity of fungi in natural forests is immense
   - fungal species living on dead wood dominate the fungal assemblage
   - fungal species with no direct importance to human economy (inedible saprophytes) dominate the fungal assemblage
   - fungi are not nuisances in a functioning natural forest but are part of the essential processes underlying the existence of the forest
3. Final remarks
   - comments on the degree of endangerment of fungi and on protected species and the causes of their decline (posters)
   - the role of the BPF in the preservation of fungal diversity

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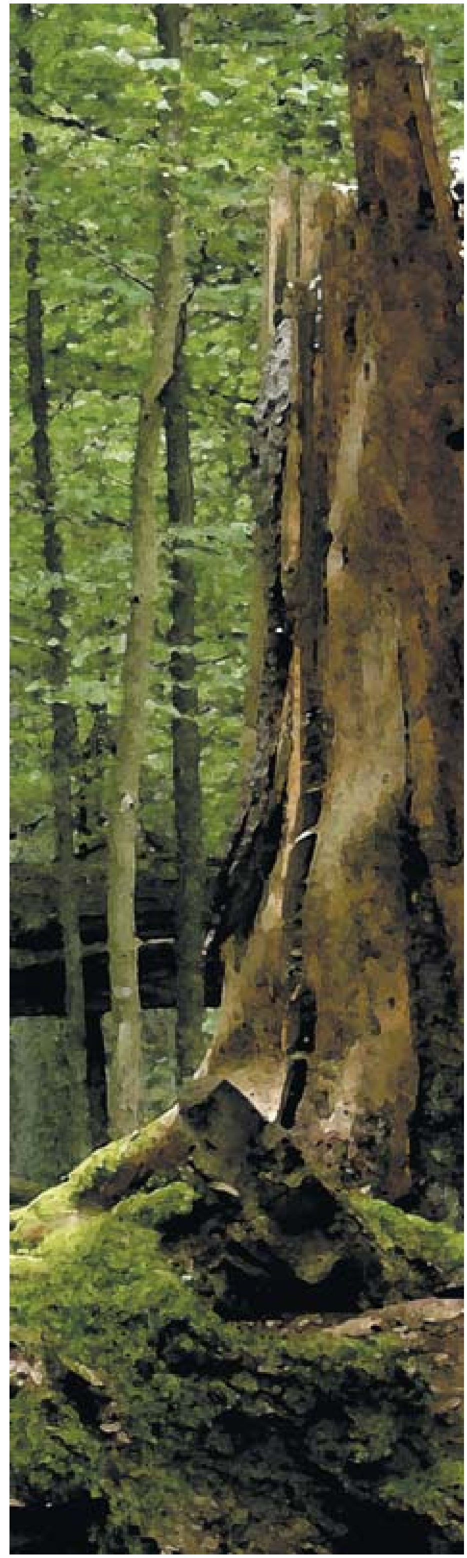

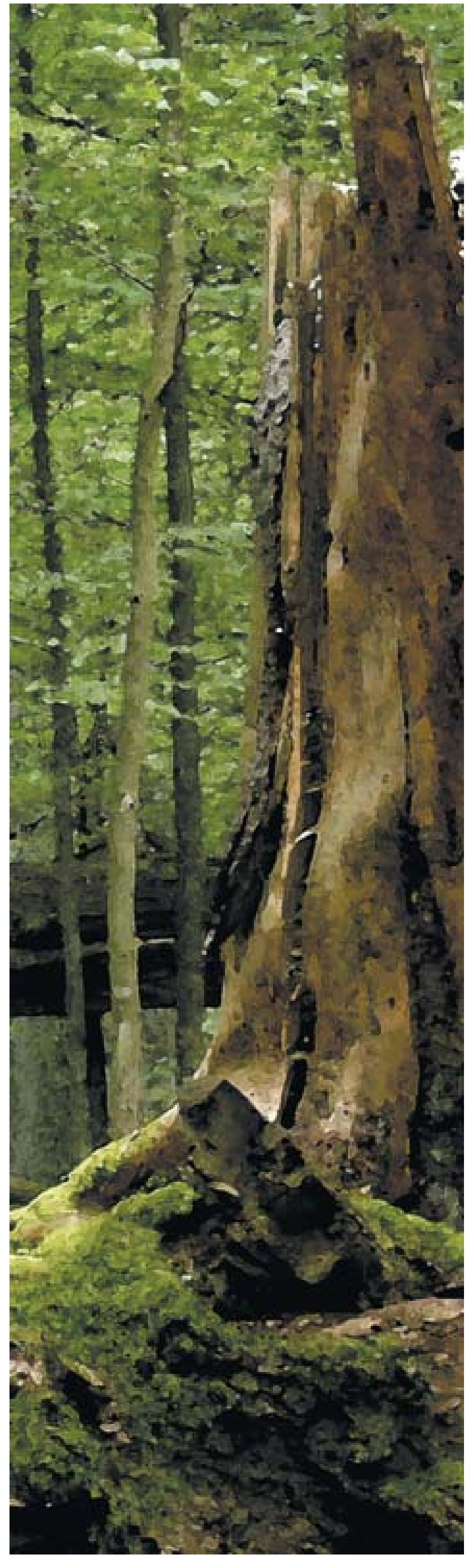

AUTHORS

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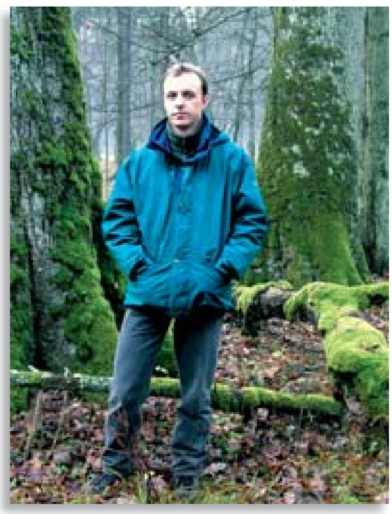
Jerzy M. Gutowski (1954), Ph.D. in forest sciences, is currently Docent at the Natural Forest Department, Forest Research Institute in Białowieża. He has a doctorate and holds a professorship in forest sciences. He is an expert in forest entomology and is particularly knowledgeable about saproxylic species, spruce bark beetle ecology, and systematic monitoring of forest invertebrates. He has published more than 70 scientific papers and around 30 scientific-popular features. In 2002, he received an award from the Minister of Environment as a co-editor of the Catalogue of the Fauna of Białowieża Primeval Forest. Dr. Gutowski is a member of the scientific boards of the Forest Research Institute, Institute of Zoology, Polish Academy of Sciences, and Białowieża National Park. He is a strong advocate for the protection of saproxylic insects and for the preservation of Białowieża forests.

William F. Laudenslayer, Jr. (1948), Ph.D. in Zoology from Arizona State University. He has served as a wildlife biologist for several US federal agencies and taught wildlife biology at Mt. San Jacinto College. As a Research Wildlife Ecologist with the USDA Forest Service, Pacific Southwest Research Station in Fresno, California, he investigates the processes of dead wood dynamics in pine forests of western USA. The research encompasses responses of terrestrial vertebrates and vegetation to different forest structures and disturbance regimes. Dr Laudenslayer has authored or co-authored some 70 substantial publications, lectured at universities, and co-organised "Symposium on the Ecology and Management of Dead Wood in Western Forests" in 2001. He is a recipient of the Raymond F. Dasmann Professional of the Year Award, Western Section of The Wildlife Society, and is a co-founder of the Association for Fire Ecology.

Paweł Pawlaczyk (1966) holds a BSc from the Faculty of Forestry at Poznań Agricultural University. For several years he worked at the Białowieża Geobotanical Station of Warsaw University and at Drawieński National Park. He is currently associated with the Naturalists' Club. An author and co-author of several dozen articles on geobotany, ecology of forest ecosystems, nature protection and management including the manual for Natura 2000 implementation in Poland. Dr Pawlaczyk is a co-author of the plans for protection for several protected areas in Poland. He is a member of the State Council of Nature Protection and Committee of Nature Protection, Polish Academy of Sciences.

Karol Zub (1968), Ph.D. in biology, is currently a wildlife ecologist at the Mammal Research Institute, Polish Academy of Sciences in Białowieża. He is a co-author of numerous scientific and popular scientific publications on the ecology of birds and mammalian predators. He is also interested in forest fungi. The leading subject of his current research is the body sizes of weasels. Dr Zub is a long-term associate of the Nature Education Centre at Białowieża National Park, as well as the author and leader of a variety of educational workshops in forest ecology.



OPINIONS

The magnificent and irreplaceable Białowieża Primeval Forest in Poland is the jewel in the forest carpet of central and western Europe, containing an extraordinary rich flora and fauna dependent on primeval forests. Obviously this biodiversity has inspired the authors of this book to explain why it is so important to retain old trees and dead wood. A conviction that a deep understanding of the many roles that dead wood play in a natural forest will change attitudes and practices is felt throughout the book. I sincerely hope that they will succeed in their mission, so that coming generations of biologists and others also can admire all this diversity of forms, colours, sounds and smells emerging from the many thousands of dead wood dependent species. There is very much to learn from this book, both for researchers and the general public regarding forest ecology, nature conservation and attitude.

Professor Sven G. Nilsson – Lund University, Sweden

Have you ever wondered what happens to a tree after it dies? This book adeptly describes the life after death of trees – an interesting and diverse life it turns out to be! While we humans are used to thinking about dead trees as a hazard or a waste, this book makes a compelling case that dead trees are exactly what many organisms need to complete their life cycle, and that nature rarely wastes anything. Full of interesting facts and figures, the reader will also find alternative viewpoints on forest management and policy which will help shape the future of these very important ecosystems.

Professor Mark E. Harmon – Oregon State University, USA

WWF has been interested in deadwood for years. We have conducted and supported a variety of activities towards the protection of natural processes in forests, including the preservation of dead and dying trees. Deadwood is among key naturalness indicators with its quantity and quality attesting a forest's health and richness. WWF's 2004 report „Deadwood – living forest" highlights the role of deadwood in the protection of biodiversity in the forests of Europe. It stresses the urgent necessity for political, legislative and practical measures aimed at both protected areas as well as managed forests. WWF calls on European governments, forest owners and the forest industry to commit now to conserve biodiversity by increasing the number of veteran trees and restoring 20-30 cubic meters of deadwood per hectare by 2030. We are deeply convinced that the book „The after life of a tree" shall be instrumental in achieving this aim and help decision makers responsible for environmental protection and forest management to make conscious choices for the good of nature and man.

Stefan Jakimiuk, WWF Poland